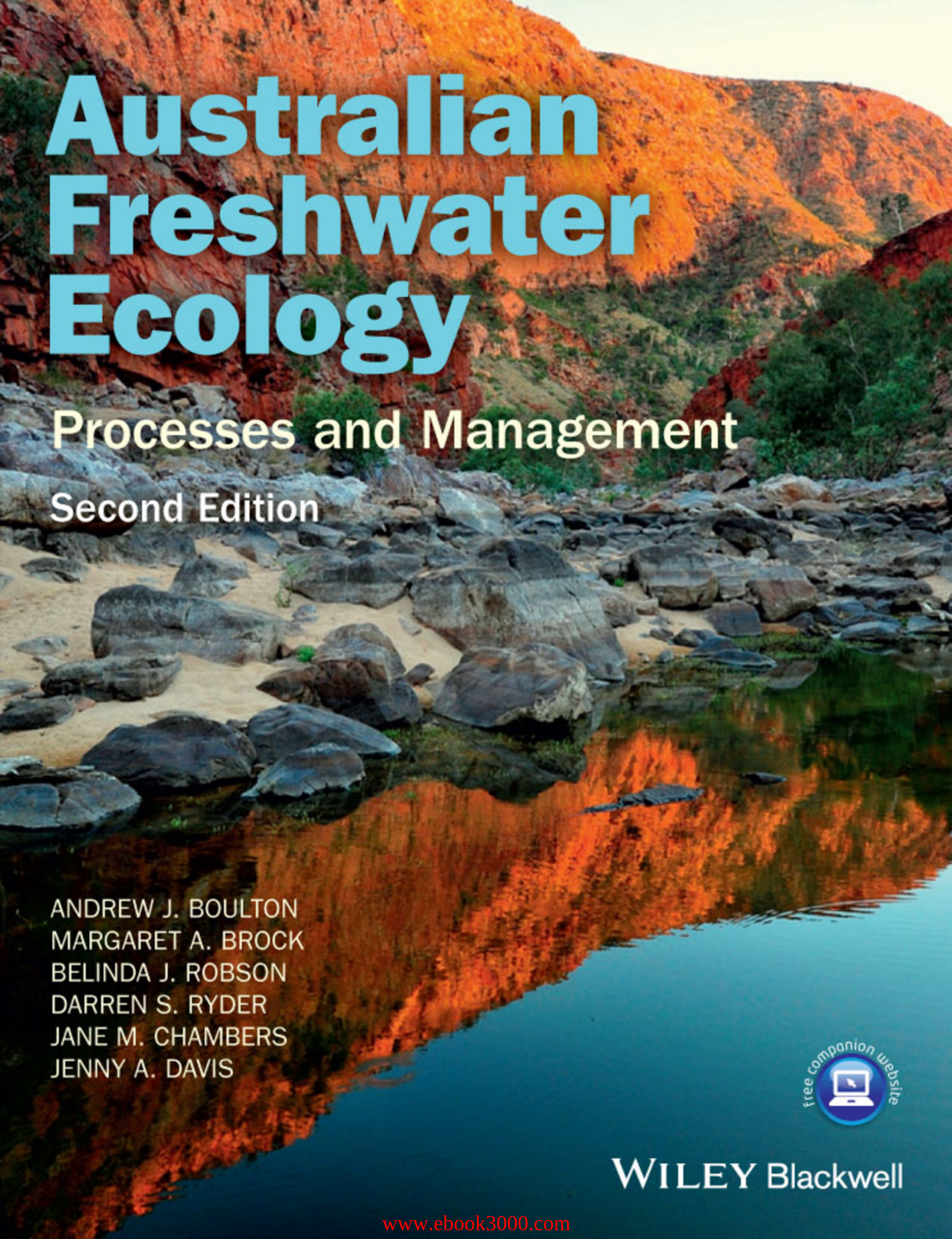

Australian Freshwater Ecology

Processes and Management

Second Edition

ANDREW J. BOULTON
MARGARET A. BROCK
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free companion website

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About this book

This book was written for you if you're interested in the ecology and management of Australia's inland waters, including groundwaters, temporary waters and salt lakes. It is intended to be an introductory text for biologists, water chemists, hydrologists, engineers, consultants, policy makers, social scientists, natural resource managers and the general public – in short, anyone curious about how aquatic ecosystems work and how they are affected by human activities.

Since publication of the first edition (Boulton and Brock 1999), our understanding of the ecology and management of inland waters has advanced immensely. This updated second edition incorporates these advances yet retains the first edition's popular features: succinct and broad coverage, simple diagrams, a focus on Australian examples, and the invited 'boxes'. We are very grateful to the 117 box authors for enriching this edition with their contributions, often tightly edited to fit our harsh word limits.

We thank Peter Jarman, Keith Walker and Rob Rolls for reviewing the entire text, and Paul Wettin for detailed comments on the management chapters and the outline. We also thank Bruce Chessman, Daniela Cortez, Barb Downes, Stefan Eberhard, Barry Hart, Ian Houshold, Jill Lancaster, Rebecca Lester, Sarina Loo, Richard Marchant, Vincent Post, Jane Roberts, Rob Rolls, Fran Sheldon, Kate Smolders, Brian Timms, and Moya Tomlinson for comments on early outlines, large sections of the book or both. Edwin Chester, Margaret Davies, Stefan Eberhard, Arthur Georges, John Gooderham, Scott Hardie, Kerrylyn Johnston, Peter Novak, Joan Powling, Brad Pusey, Tarmo Raadik, Paul Reich, Eddie Tsyrlin and Dan Warfe also contributed multiple photographs. The cover photo was generously provided by Ian Kidd.

We are very grateful to Belinda Cale who drew all the excellent line diagrams. We also thank Ward Cooper, Kelvin Matthews and Audrie Tan at Wiley-Blackwell for editorial guidance and advice. We are grateful to project manager, Aileen Castell, and copy editor, Lynette Woodward, for their assistance. Every effort was made to obtain permission for the use of copyright material, and we thank all those who responded positively. We apologize for any errors or omissions. The Australian Society for Limnology funded much of the book's preparation, and we appreciate their support. Finally, a big thanks to the community of Australian aquatic scientists, students and managers who have generously helped with this project, and to Professors Bill Williams and Peter Cullen who supported publication of the first edition – their legacy continues here.

We need to explain how we provided references to other authors' work. Giving credit where it is due is difficult in a book where brevity is the aim. As in the first edition, large sections of unreferenced text cover general aspects of limnology found in most textbooks whereas for specific examples, we have usually included one or two citations. We do not exhaustively review the literature nor have we cited all the key papers on every subject.

In this second edition, a chapter on groundwater has been added whereas information on temporary waters (a separate chapter in the first edition) is now integrated throughout the book. There is also more detail on topics such as biodiversity conservation, climate change, multiple stressors and ecosystem goods and services. As in the first edition, we omit estuaries and marine systems but include saline waters and temporary waters as they are the most common inland waterbodies across much of Australia. Also, as in the first edition, we focus on ecology and how ecological theory can be applied to management issues.

Our aquatic ecosystems are precious. We need good science to understand and manage them effectively so that their values can be enjoyed by future generations. We hope this book stimulates your interest and helps you make your own contribution to the study and wise use of surface waters and groundwaters, especially here in Australia.

AB, MB, BR, DR, JC and JD, August 2013

About the companion website

This book is accompanied by a companion website:
www.wiley.com/go/boulton/freshwater

The website includes:

- Powerpoints of all figures from the book for downloading
- PDFs of tables from the book

PART I

PROCESSES IN AQUATIC ECOSYSTEMS

Ecologists study the interactions of living organisms with their physical, chemical and biological environments. These interactions are complex, dynamic and occur across multiple **scales** of space and time. To help describe, understand and predict these complex interactions, ecologists use various ways to classify ecological systems. For example, areas can be classified into different **habitats** according to the species or assemblages that live there. In turn, the interacting assemblages of organisms in these different habitats are defined as ecological **communities**. The species in these communities and their habitats, along with crucial ecological processes such as the transfer of energy and nutrients, are interwoven to form **ecosystems**. Although we talk of aquatic and terrestrial ecosystems, in reality these are tightly linked as well. Processes occurring at **interfaces**, such as the land-water edge, are vital to sustaining the ecosystems on either side, and these interfaces or **ecotones** are often 'hot-spots' of chemical and biological activity.

Humans depend entirely on the natural ecosystems around them. The ecological processes that integrate energy, nutrients and water flowing through freshwater, marine and terrestrial ecosystems provide humans with essential **ecosystem goods and services**. Goods include oxygen, fresh water and food. Services include assimilation of nutrients and carbon dioxide, provision of recreational opportunities and aesthetic pleasure (e.g. the beauty of a lake) and protection from extremes of weather. Underpinning the sustained provision of these goods and services are multiple, interacting **ecological processes**. Ecological processes also govern the important characteristics of all habitats, communities and ecosystems. Consequently, they provide a useful framework to organize chapters in this first part of the book.

Physical processes provide and sustain the structure of aquatic habitats and influence how light and solar energy enter aquatic environments, affecting factors such as water density and photosynthesis. In turn, physical processes govern many **chemical** processes such as the cycling of dissolved gases and nutrients in the water column. Together, both types of processes provide the habitats and other requirements of the organisms that mediate **biological** processes such as energy transfer between producers, consumers and decomposers.

Part I of this book begins by reviewing the diversity of inland waters in Australia, emphasizing the importance of **variability in water regime** and the significance of **linkages** across multiple scales, from molecules to the global hydrological cycle (Chapter 1). As the flow of water has a major effect on physical, chemical and biological processes in aquatic ecosystems, we have split our treatment of processes into **standing (lentic)** waters (Chapters 2–4) and **running (lotic)** waters (Chapters 5–7) to illustrate ecological parallels and contrasts. The section concludes with an integrative chapter about the main physical, chemical and biological processes in **groundwaters** as well as aspects of their management (Chapter 8). In Part II, we explore how human activities have affected ecological processes in Australian aquatic ecosystems and how we can best use our understanding of ecological processes to manage, conserve and, where necessary, restore them.

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CHAPTER 1

Australian waters: diverse, variable and valuable

1.1 THE CHALLENGE FOR AQUATIC ECOLOGISTS

Aquatic ecologists study how organisms in inland waters interact with their environment and each other. Such studies often explore how human activities modify aquatic ecological processes and the quality and quantity of fresh water. Not only do the findings of these studies help water managers, they also add to our basic knowledge of ecology and environmental science. This book is about that basic knowledge and how we can use it to better manage and protect our fresh waters.

Fresh water is essential for all life. Therefore, we must protect and manage aquatic ecosystems that supply fresh water. Aquatic ecosystems provide essential **ecosystem services** (Daily 1997) for humans, ranging from flood control and water purification through to cultural values and recreational benefits (Millennium Ecosystem Assessment 2005). These services are often overlooked because many of them are subtle (e.g. the role of groundwater in supporting many terrestrial plant communities, Section 8.7) but, without them, humans and other dependent organisms could not survive. Most ecosystem services are mediated by ecological processes. Aquatic ecologists investigate how these processes work and how we can sustain them in inland surface waters and groundwaters.

Every day, the media report concerns about the quantity and quality of the country's water resources. Growing anxiety about the effects of climate change and increasing human population densities on finite water resources is not restricted to Australia; worldwide, scientists and managers grapple with unprecedented environmental pressures, burgeoning urbanization, agricultural problems and intensifying threats to biodiversity. Technological advances have helped resolve some of these issues but, ironically, have also exacerbated many of the multiple stressors on aquatic ecosystems such as salinization, eutrophication, sedimentation, acidification and other forms of pollution.

To address these problems, aquatic ecologists need an integrated knowledge of a wide variety of different disciplines such as physics, chemistry, microbiology, hydrology and geomorphology as well as ecology, biology and genetics, along with hybrid fields such as ecohydrology and ecohydraulics (Rice *et al.* 2010). This broader discipline, encompassing the physical, chemical and biological sciences of aquatic ecosystems, is called **limnology**. Our book synthesizes threads of these diverse sciences, focusing on interactions among physical, chemical and biological processes in surface and groundwater ecology. We then outline ways in which this scientific information can be used to tackle problems such as erosion, salinization, eutrophication and urbanization in Australian inland waters. These problems challenge aquatic ecologists worldwide, but across most of Australia their solutions are complicated by the continent's great natural variability in water regimes and the shortage of long-term empirical data for nearly all our aquatic ecosystems.

This is an exciting time to be an aquatic ecologist. Much fundamental science remains to be done, important and complex management issues abound and Australian inland waters are, for the most part, beautiful places to work. We have plenty to learn and do.

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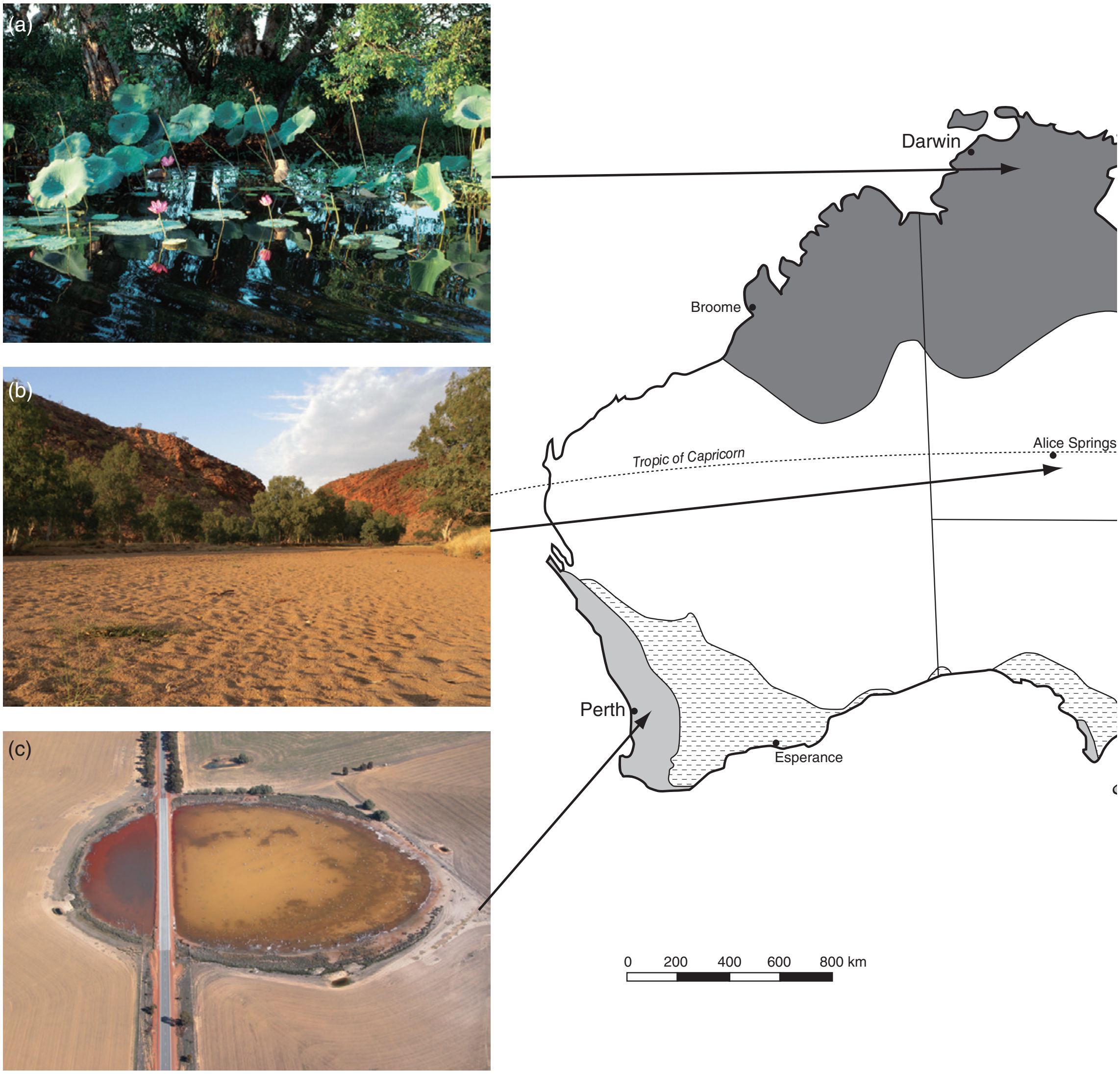

Figure 1.1 Major seasonal rainfall zones of Australia and six examples of inland waters: (a) tropical billabong in Kakadu National Park, NT, (b) temporary river near Alice Springs, NT, (c) salt lake in the WA Wheatbelt.

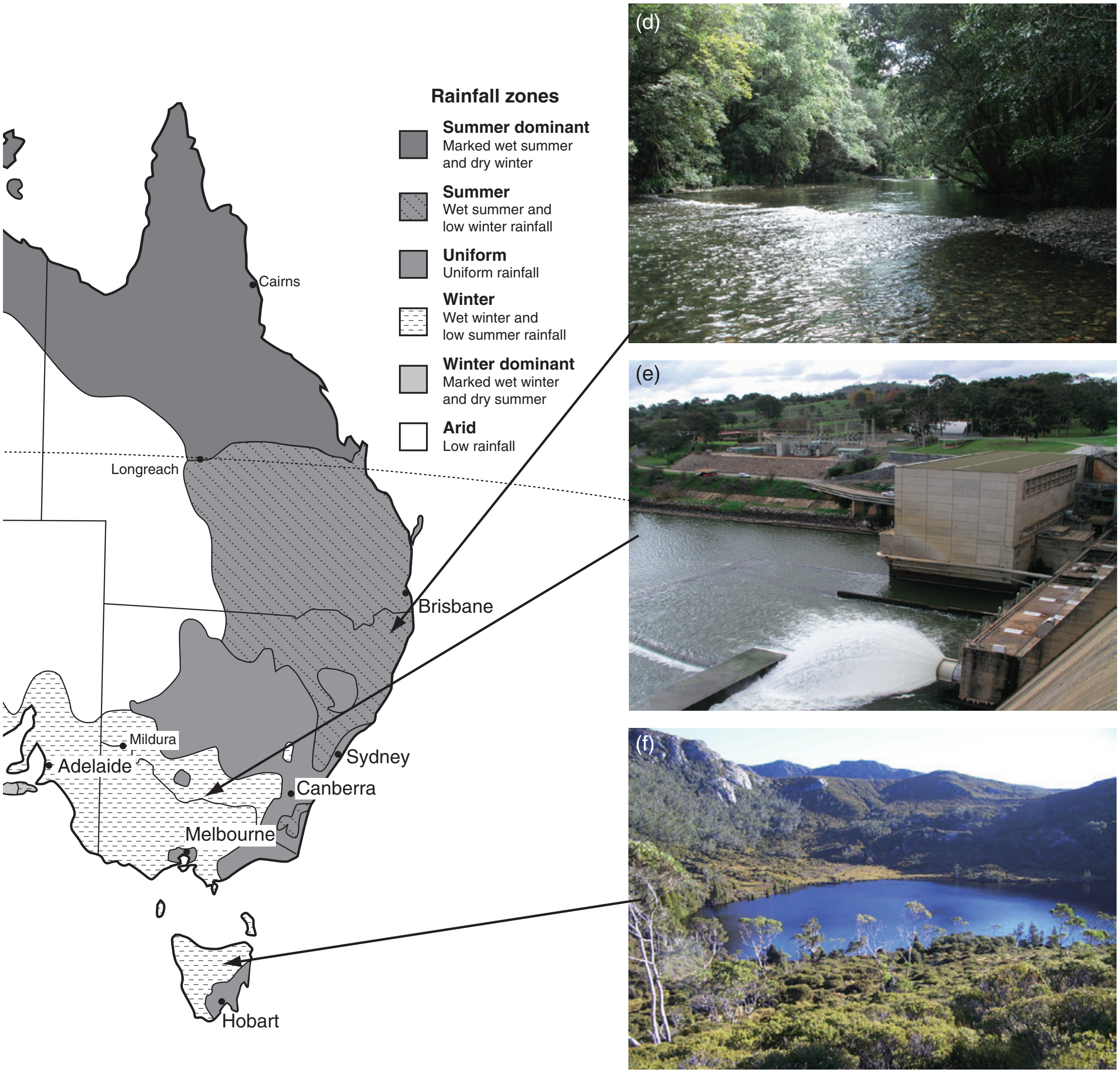

Figure 1.1 (continued) (d) coastal gravel-bed river in northern NSW, (e) Hume Dam near Albury, NSW, (f) Tasmanian mountain tarn). (Source: (a) Jane Chambers; (b), (d) and (e) Darren Ryder; (c) Jenny Davis; (f) Belinda Robson. Map reproduced with permission of the Bureau of Meteorology, Australian Government.)

1.2 DEFINING SOME COMMON TERMS

Before going further, let's define a few terms used repeatedly in this book. In the previous section, we referred to **aquatic** ecologists. Although 'aquatic' means 'associated with water', this book excludes estuarine and marine ecosystems and focuses on the ecology of fresh and saline inland waters, both temporary and permanent as well as groundwaters. Throughout the text, we use 'fresh' to specifically mean non-saline water, and 'aquatic' as a general adjective for all inland waters. All inland waters (encompassing everything from the deepest permanent fresh lake to the most fleeting saline pool) are collectively referred to as 'inland waters', 'waterbodies', 'waters' or 'aquatic ecosystems', and we use the terms interchangeably.

Although there are numerous definitions that seek to capture the diversity of inland waterbody types, we prefer this one that also explicitly recognizes the implications of water regime (Section 1.4) for the biota and ecological processes:

> *Any area of temporarily or permanently waterlogged or inundated land, natural or artificial, with water that is standing or running, ranging from fresh to saline, and where inundation by water influences the biota and ecological processes occurring at any time.*

This functional definition, modified from the widely used one in the Ramsar Convention on Wetlands (Section 12.3), encompasses *physical* features of the water regime, *chemical* features (e.g. salinity, nutrient concentrations) of the aquatic environment and *biological* features (i.e. biota and ecological processes) as well as specifying their interactions and influences.

In the first section of this book, we focus on the linkages and interaction among these three types of features and their ecological implications. In the second section, we show how understanding these linkages and interactions is essential to managing aquatic ecosystems successfully. Throughout the book, we refer to a number of 'themes'. These are intended to help you draw links between the chapters, see how ideas relate to each other, and reiterate important concepts such as the ecological significance of water regime, variability and connectivity. You may want to make a list of them as you read the book and add a few of your own.

1.3 AUSTRALIAN INLAND WATERS: THEIR DIVERSITY AND DISTRIBUTION

Australia boasts a diverse array of types of inland waters, reflecting the size of the continent, its topography, and the fact that it spans multiple climatic zones from northern wet-dry tropics to cool southern temperate areas. In southern temperate areas, winter-dominant rainfall (Figure 1.1) supplies numerous permanent swamps, wetlands and lakes as well as short coastal rivers and streams that drain to the sea. As most Australians live around the south-eastern coastline, many of these running waters have been impounded to provide water for cities and coastal towns. This, of course, creates further types of inland waters in the form of reservoirs, weir-pools and storage tanks.

Inland and further north, much of the continent is arid (Figure 1.1) and usually receives less than 500 mm of rain annually. Across this vast area are numerous shallow lakes that are mostly temporary, saline or both. Most stream and river beds carry water only after unpredictable rain, and may lie dry for years or even decades. A few inland, semi-permanent rivers drain either to Lake Eyre or into the Murray-Darling system, but most of their water evaporates, seeps into the ground or is diverted for irrigation. Occasionally, heavy rains in parts of the catchment result in vast expanses of water across the floodplain that fuel incredible 'booms' in plant and animal life until the inevitable 'bust' when the systems dry out once more.

North of 23°S (Tropic of Capricorn, Figure 1.1), much of the continent has distinct 'wet' and 'dry' seasons, resulting in a predominance of seasonally filled wetlands, lakes and rivers (Box 1.1, Pusey 2011). The key difference between these and the non-permanent surface waters of the rest of the mainland is that the filling and drying of the tropical waters is much more predictable. The fundamental importance of **water regime** – the permanence, predictability and variability of the presence and timing of water – to aquatic ecology is a central theme in this book. In Australia, the wide diversity of inland waters (Figure 1.1) has an equally wide diversity of water regimes. Are there common ecological features among these waters? What are the main differences? What physical, chemical and biological processes operate and when? How do human activities and climate change influence these in the short and long terms? What are the main management issues for these different waters and should we manage them differently?

Box 1.1 Seasonal predictability in Australia's tropical waterbodies

Nowhere is the influence of a highly seasonal water regime more apparent than in Australia's wet-dry tropics (Warfe *et al.* 2011). Each year, the wet season's monsoonal rains dump over a metre of water in just a few months, breaking half a year of baking drought. Groundwater aquifers recharge, dry creeks flood and isolated waterholes swell and connect along the large rivers, which eventually fill before overtopping their banks and spilling out across thousands of square kilometres of coastal floodplains. Within hours of the first waters arriving, creek beds teem with life. Frogs emerge from the earth and their tadpoles soon join the mix while insects arrive from refugial water holes to recolonize the abundant aquatic habitats. Fishes move onto the floodplains where a frenzy of feeding and breeding occurs before they retreat to the main channel as the dry season begins. Energy accrued on the floodplain is either transported downstream to the estuary or upstream to perennial springs or persists in refugial waterholes until the monsoons roll in and this dramatic but predictable seasonal cycle starts all over again.

Michael Douglas, Charles Darwin University

1.4 THE WATER REGIME: 'WHERE, WHEN AND TO WHAT EXTENT WATER IS PRESENT'

The diverse types of inland waters around us are a consequence of hydrology (the sources, distribution and movement of water), geomorphology (shape and changes of landforms), climate and scale. These factors determine the water regime or, in other words, 'where, when and to what extent water is present' (Bunn *et al.* 1997). In standing or lentic waters (Chapters 2–4), water regime varies with depth, which usually influences patterns of circulation within the waterbody. In running or lotic waters (Chapters 5–7), water regime is associated with flow and can be expressed as changes in discharge or water level over time. In temporary waters, surface water is absent for a period of time, and frequency and duration of filling are important. Finally, the water regime of groundwaters (Chapter 8) includes fluctuations in the water table as well as groundwater flux and pressure.

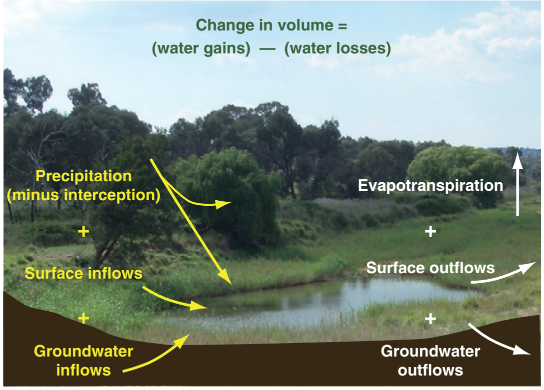

Figure 1.2 In a water budget, the change in volume equals water gains (left-hand side) minus water losses (right-hand side) for a given waterbody over a given time. Some precipitation is intercepted by plants and does not enter the waterbody. Evapotranspiration is the combined loss of water via evaporation and transpiration. (Source: Andrew Boulton.)

1.4.1 Water budgets, scale issues and human influences on water regimes

Changes in the volume of water within a waterbody are usually expressed as a **water budget**, calculated by subtracting gains from losses (Figure 1.2) over a given time. Gains are net precipitation (precipitation less water intercepted by plants), surface inflows and groundwater inflows. Losses are by evaporation, transpiration, and surface and groundwater outflows. Evaporation and transpiration are usually considered together as evapotranspiration because their rates are affected by the same factors of air temperature, humidity and wind speed.

Water budgets are often used to predict the effects of human activities on water regimes (Chapter 9). For example, Krasnostein and Oldham (2004) measured the water budget of Loch McNess, a wetland near Perth, and developed a conceptual model that showed how declines in groundwater would lower the wetland's depth. The predicted fall in its water level is now occurring as a consequence of declining groundwater levels owing to climate change and extraction. Using empirical data on water gains and losses, water managers can apply this model to guide strategies to slow the rate of drying in this groundwater-dependent ecosystem.

Gathering data on water gains and losses is challenging. This is especially true for large waterbodies with diffuse sources of surface inflows or those lying in heterogeneous sediments that have complex groundwater flow paths. Where it is impractical to measure all inputs and outputs, appropriate hydrological models and software are used. However, it is essential to recognize the limitations and uncertainty associated with most modelling approaches, and to temper predictions about changes in water budgets and water regimes accordingly.

Scale, in time and space, influences our perceptions of water regime and must be considered whenever we explore physical, chemical and biological processes (Biggs *et al.* 2005). Most ecological studies tend to be done in only one or a few waterbodies and over a relatively short time frame (say, less than five years). Such studies might only consider the water regime within that time period and only for those waters. However, the water regimes of nearby surface and groundwaters may also be ecologically relevant to the studied waterbodies, as may be their history of water regime prior to the study. Even microtopography can be important; an aquatic plant just a few centimetres higher up the bank than another may experience a very different water regime. Although the term 'water regime' is typically applied at the scale of the waterbody, it can also refer to the water requirements of an organism or its habitat (Roberts and Marston 2011).

Human alterations of water regime (Chapter 9) interact with other major threats to the ecological integrity and biodiversity of inland waters (Chapters 10–12). Successful management of our inland waters entails understanding how our activities affect water regimes and seeking ways to use our water resources without irreparably damaging them (Chapter 13). Throughout this book, we revisit the theme that most physical, chemical and biological processes in surface waters and groundwaters are controlled and constrained by the water regime and its components.

1.4.2 Components of the water regime

The primary components of the water regime in surface waters are **spatial** (related to extent and depth, volume, variability and, in running waters, discharge) and **temporal** (related to timing, frequency, duration and variability of the presence of water) (Bunn *et al.* 1997, Table 1.1). Volume, extent, depth and discharge are inter-related spatial features (Table 1.1) that co-vary in time and space (Figure 1.3) to produce a wide spectrum of hydrological conditions within and among waterbodies. Similarly, the temporal aspects of timing, frequency, duration and variability all interact, governing the life histories of most aquatic plants and animals (Chapters 4 and 7).

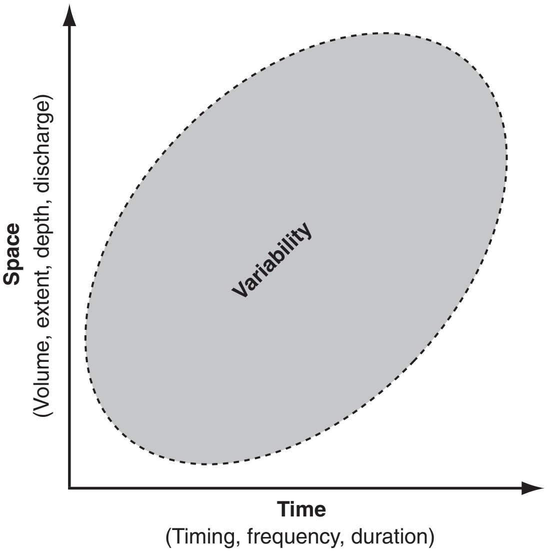

Figure 1.3 The relationship between the spatial and temporal components of water regime. Water regimes of many Australian waterbodies vary widely (grey area) in these components along both axes.

Table 1.1 Components of the water regime of inland surface waters.

Component	Definition
Spatial	
Extent and depth	The area of inundation and the depth of the water.
Volume	Depending on the shape of the waterbody, extent and depth influence the amount of water at any given time.
Discharge	The volume of water flowing through a given cross-sectional area in a specified time period.
Variability	The degree to which the above features change at a range of spatial scales.
Temporal	
Timing	When water is present. Within-year patterns are most important in seasonal waterbodies whereas among-year patterns and variability in timing are relevant to many other temporary waters (Table 1.2).
Frequency	How often filling and drying occur. Ranges from zero (permanent waters) to frequent in very shallow waterbodies that fill and dry many times a year.
Duration	Period of inundation. Days to years, varying within and among waterbodies. Rates of rise and fall may be important (e.g. flood pulses, Walker *et al*. 1995).
Variability	The degree to which the above features change at a range of timescales.

Australia abounds in temporary waters. In this book, we use the term 'temporary' to refer collectively to any waterbody that dries out. Many classifications of temporary waters use the criteria of **permanence** (duration of time that free water exists in the basin or channel) and **predictability** (reliability of filling). On this basis, temporary waters can be arranged from the least predictable and least permanent ephemeral waterbodies to the most predictably permanent ones (Table 1.2, Paijmans *et al.* 1985). Such a classification imposes boundaries upon a continuum of wetting and drying, creating problems in definitions (Williams 2006). Given this, as well as the many different classifications of 'degrees of intermittency' and the tendency for most temporary waters to vary in water regime from year to year, it is best to explicitly show the water regime at a given spatial and temporal scale (e.g. using a hydrograph, see Figure 1.4) to avoid confusion when a precise description is needed.

1.4.3 Water regime variability

Arguably, the **variability** of the water regime of all temporary waters is the major driving factor influencing their physical, chemical and biological features (Larned *et al.* 2010). This variability arises from variation in the components of the water budget (Figure 1.2), especially those associated with water loss through seepage and evapotranspiration. Such variability is crucial when classifying temporary waters. It relates to predictability in that the water regime may be predictably variable (e.g. ephemeral waterbodies), predictably regular (e.g. seasonal waterbodies such as in the wet-dry tropics, Box 1.1) or unpredictably variable. However, the spatial and temporal scales of the variation must also be considered in the context of the target organism or process. For example, an organism with a brief aquatic stage that coincides with the period of filling in a temporary waterbody is less likely to be as affected by the water regime as another whose aquatic

Table 1.2 A classification of inland waters based on predictability and duration of filling.

Waterbody	Predictability and duration of filling
Temporary	
Ephemeral	Only filled after unpredictable rainfall and runoff. Surface water dries within days to weeks of filling and can support only short-lived aquatic life.
Episodic	Annual inflow is less than the minimum annual loss in 90% of years. Usually dry but filled after rare and large, unpredictable rainfall events. Surface water persists for months to years, and often supports longer-lived aquatic life.
Intermittent	Alternately wet and dry but less frequently or regularly than seasonal waters. Surface water persists for months to years, and often supports longer-lived aquatic life.
Seasonal	Alternately wet and dry every year, according to season. Usually fills and dries predictably and annually. Surface water persists for months, long enough for some plants and animals to complete the aquatic stages of their life-cycles.
Permanent or near-permanent (perennial)	Predictably filled, although water levels may vary. Annual inflow exceeds minimum annual loss in 90% of years. During extreme droughts, these waters may dry. Usually supports diverse aquatic life, much of which cannot tolerate desiccation.

life-cycle extends beyond the duration of filling. In this sense, sweeping judgements of the environmental 'harshness' of temporary waters are meaningless; indeed, some species rely on wetting and drying for their persistence (Chapters 4 and 7).

Our perception of variability depends on scale. Therefore, it is crucial to define spatial and temporal scale explicitly. For example, Puckridge *et al.* (1998) assessed the hydrological variability of 52 large rivers worldwide. As their study was a broad-scale one in space, they selected rivers for which they could find at least 15 years of continuous hydrological data. At this inter-annual scale, flow patterns clearly differed between the tropical and dryland rivers. For example, in the tropical Mekong River receiving regular monsoonal rain, the hydrograph (the pattern of discharge over time) appears rather predictable compared to records from a dryland river such as Cooper Creek (Figure 1.4). However, on a finer scale, even the least variable of hydrographs differs from year to year in magnitude, duration and other features. If we compared hydrographs within a year, we would find further variation at monthly and daily scales. At all scales, variations in flow govern ecological processes in every

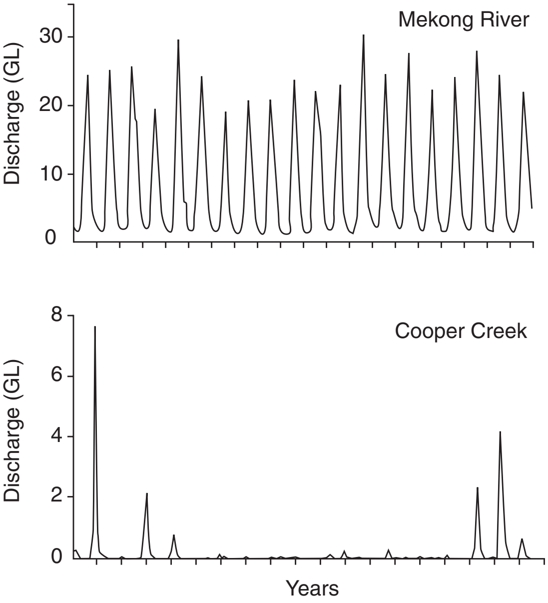

Figure 1.4 Twenty-year hydrographs of a tropical river (Mekong River) and a dryland river (Cooper Creek). GL are gigalitres (10^9 L). Note the different scales on the vertical axes.

river (Biggs *et al.* 2005), and this is why we must explicitly state the scales of our study.

1.5 LINKAGES IN AQUATIC ECOSYSTEMS: FROM MOLECULAR BONDS TO GLOBAL EXCHANGES

Linkages occur across multiple spatial scales, from the finest scale of the chemical linkages in the molecular structure of water that confer many of its unique properties through to the largest scale of the global connections among different components of the hydrological cycle. In between lie the intermediate spatial scales most familiar to ecologists: linkages across habitats, individual waterbodies, catchments and landscapes. Let's look at the finest scale first.

1.5.1 Wonderful water and its molecular linkages

Water is an extraordinary substance with many ecologically significant chemical properties. It owes these special properties to its two types of linkages at the molecular scale: **covalent bonds** and **hydrogen bonds**. Strong covalent bonds link the two hydrogen atoms to the oxygen atom (Figure 1.5), and take a lot of energy to break. These bonds hold the atoms at an angle of 104°27', which causes the water molecule to have a dominance of negative charge at the oxygen atom and a dominance of positive charge at the two hydrogen atoms (Figure 1.5). This 'charged' molecule can now form weak hydrogen bonds with nearby water molecules because the positively charged H atoms of one molecule are attracted to the negatively charged O atoms of another.

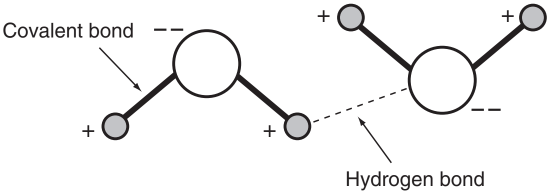

Figure 1.5 The bonds within (covalent) and between (hydrogen bonds) water molecules confer many of water's special chemical and physical properties. The negatively charged O atom is shown by the larger open circle.

The charged (or polar) nature of water molecules means they can 'attack' ionic crystals such as salts and bring them into solution, rendering water a **powerful solvent** of these chemicals. This has major implications for water chemistry such as salinity and dissolved nutrient concentrations in all aquatic ecosystems (Chapters 3, 6 and 8) as well as the management of issues associated with water quality (e.g. salinization and eutrophication, Chapter 11). On the other hand, most atmospheric gases are non-polar compounds and relatively insoluble in water. Their solubility depends on temperature, pressure and their atmospheric concentrations (Section 3.2). One exception is carbon dioxide, a polar molecule that is highly soluble, existing in equilibrium with ions of carbon (i.e. carbonate and bicarbonate) that affect water chemistry, biota and ecological processes in many surface and subsurface waters (Chapters 3–8).

There are other significant physical, chemical and biological implications of these molecular linkages. One is that water can exist in **three phases** at the Earth's surface: a vapour, a liquid and, with the hydrogen bonds forming a block-like lattice, solid ice. This lattice enables ice to float, and means that when deep waterbodies freeze over, aquatic organisms such as fishes can persist in the water below the floating ice. When we heat ice, the molecules are agitated and the hydrogen bonds break or distort, causing the open lattice to fill in. This increases the density of fresh water to a peak at about 4°C. Further heating then reduces the density until, at 100°C, pure fresh water at sea level (a pressure of one 'atmosphere': 1 atm) boils and becomes a vapour. Differences in water density caused by changes in temperature influence physical processes in standing waters (Chapter 2), with major implications for their chemistry (Chapter 3) and biota (Chapter 4).

Heat taken up or given out during changes in phase is termed **latent heat**. For water, the latent heat of fusion (i.e. the energy needed to convert ice to water once melting starts) is quite low. However, the latent heat of evaporation (when liquid water vapourizes) is high because the lattice structure of water must be completely broken down. Water evaporates at temperatures below 100°C as long as the water content of the air in contact with the water surface is below saturation. The latent heat of evaporation cools the remaining water, and can influence fundamental physical

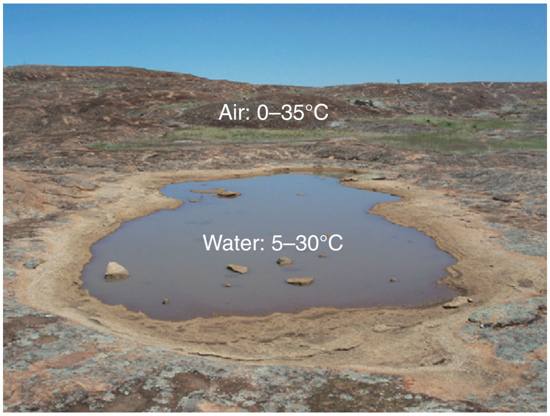

Figure 1.6 The high specific heat capacity of water, as a result of its molecular linkages, means that daily ranges in air temperature typically exceed those of waterbodies in the same area. (Source: Andrew Boulton.)

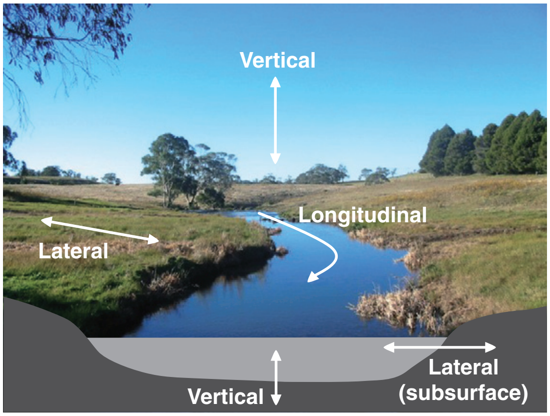

Figure 1.7 Linkages at the catchment scale include lateral linkages between the catchment and the waterbody, longitudinal linkages of upland streams to lowland rivers, and vertical linkages with the air above and groundwater below. (Source: Andrew Boulton.)

processes such as thermal stratification (Section 2.5). The molecular linkages also give water its high **specific heat** capacity. It takes about five times as much heat to raise a given mass of water by 1°C as it does to raise the same mass of dry soil through the same temperature range. One biological consequence of this is to buffer the temperature within a waterbody compared to that of the overlying air (Figure 1.6), shielding aquatic inhabitants from the greater range of temperatures experienced in the surrounding terrestrial area.

Hydrogen bonds among the molecules also mean that water has the second highest **surface tension** (after mercury) of any liquid on the Earth's surface. Surface tension allows capillary forces to wet soil above the water table without filling all the interstitial cracks (Section 8.2). This is essential for plant roots that require not only water but also gases. The high surface tension of water also enables the leaves of certain aquatic plants to float and an assemblage of organisms to hang down from the air-water interface (e.g. mosquito larvae) or to walk on water (e.g. water striders, Section 4.2). Finally, the hydrogen bonds holding the water molecules together contribute to its moderate **viscosity**. It takes a pressure difference (usually a gradient down a slope) to start water moving and to keep it flowing, overcoming friction (Gordon *et al.* 2004). Viscosity affects how animals, especially small ones, move through water or filter-feed using beating limbs and fine combs of bristles or hairs (Chapters 4 and 7).

1.5.2 Linkages at the catchment scale

Between the scales of molecular linkages and the global hydrological cycle (Section 1.5.3) lie the spatial scales of aquatic linkages within and among catchments. One of these linkages is the familiar longitudinal one (Figure 1.7) that extends down streams and rivers. A second is the lateral one between a waterbody and its catchment, often evident during flooding (Figure 1.7). Early recognition of these two linkages spawned the generalization that inland waters act to 'integrate' catchment processes because, ultimately, changes in land cover and land use in the catchment of a waterbody affect its water chemistry, sediment load and biota via these linkages (Chapters 2–7, 9–12).

Vertical linkages are less obvious (Figure 1.7) but still very important. The vertical linkage with the air above controls gaseous exchanges across the air-water interface and therefore water chemistry (Chapters 3 and 6). This linkage also has management

Table 1.3 Estimates of the major compartments, volumes and mean residence times of global water. The mean residence times of temporary lakes and rivers would be even shorter. These estimates vary; we have drawn ours from Brown (1983) and Shiklomanov (1993).

Compartment	Volume ($\times 1000\,\text{km}^3$)	Percentage	Mean residence time
Oceans	1 370 000	94.202	3000–3200 years
Groundwater	60 000	4.126	5000–10 000 years
(Actively exchanging groundwater)	(4 000)	(0.275)	(100–300 years)
Glaciers and ice caps	24 000	1.650	100–8600 years
Lakes and inland seas	230	0.0158	<1–100 years
Soil water	82	0.0056	1–12 months
Atmospheric vapour	14	0.00096	8–15 days
Rivers	1.2	0.00008	2–6 months

implications. For example, atmospheric pollution can increase the acidity of rain with devastating ecological consequences (Section 11.5). A second vertical (and lateral) linkage occurs between surface waters and the groundwater below (Figure 1.7). Many rivers in temperate regions flow because of water gained from the groundwater whereas much water in arid-zone rivers seeps down into the ground or is lost by evaporation. These vertical linkages influence the water regime of many inland waters as well as that of associated shallow groundwaters (Chapter 8).

The three spatial dimensions (i.e. longitudinal, lateral and vertical) of aquatic linkages are the context for most processes occurring in inland waters, and directly or indirectly influence water chemistry and the life in and around them. The linkages may run in both directions, depending on local climatic conditions and the water regime. For example, a flooding river may supply material to the catchment at some times, whereas at other times surface runoff carries material into the river. Evaporation and precipitation and the below-ground hydrological exchange between surface waters and shallow groundwaters operate in both directions (hence the double-headed arrows in Figure 1.7).

1.5.3 Linkages at the global scale: the hydrological cycle

At the global scale of the hydrological cycle, linkages are represented by the pathways potentially travelled by a water molecule among the major compartments of water on and above the planet (Figure 1.8). Water travels vertically and horizontally, and exists in three different phases (gaseous, liquid and solid; Section 1.5.1). A key point here is that the volume and residence time of water within the compartments are as important as the linkages among them. Although estimates vary among authorities and across climatic zones (the ranges in Table 1.3), volumes and residence times of the various compartments of water differ by more than seven orders of magnitude. This causes substantial lag times in some of the aquatic linkages at the global scale, and largely explains the delays common in detecting groundwater pollution (Chapter 8).

The hydrological cycle is the continuous circulation of water between the Earth and its atmosphere, and is powered by gravity and solar energy. Direct solar effects are readily evident. For example, the sun provides the energy for the linkage of evaporation to atmospheric reserves of water. Solar energy also influences the circulation of weather cells, generates wind, and induces the variability in climate. Thus, the relative contributions of the linkages in the hydrological cycle change over time and among regions. Together with human influences, these variations in the hydrological cycle dictate the distribution and water regimes of inland waters across the world (Bengtsson 2010). Predicted climate scenarios imply dramatic changes to local and global volumes of the water circulating through the hydrological cycle, with parts of the world expected to receive greater and more

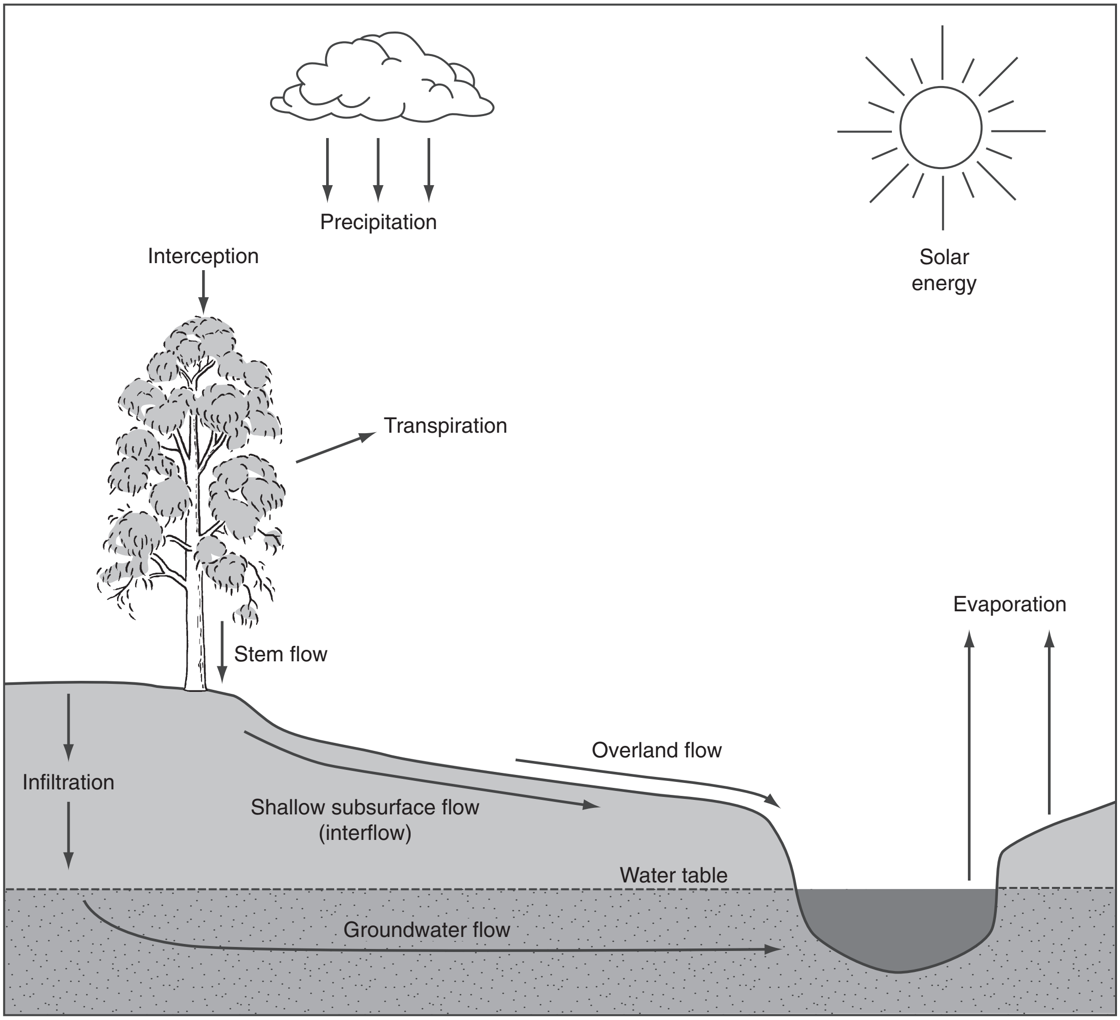

Figure 1.8 Simplified diagram of the hydrological cycle. Some water movements (e.g. capillary movement in soils) have not been included.

variable precipitation while other regions become drier and warmer (Section 12.9). For example, the increase in water vapour in a warmer climate is predicted to lead to more intense precipitation and cyclone activity (Bengtsson *et al.* 2009).

When we consider water gains and losses across the compartments of the hydrological cycle, we are looking at another water budget (Section 1.4.1) but this time at a much grander scale. Globally, some 119 000 km^3 of precipitation annually falls on land (less than one-third of the global surface) and 72 000 km^3 returns by evapotranspiration from land to the atmosphere (Figure 1.9). The difference (47 000 km^3) eventually runs off as surface or groundwater. Evaporation from the oceans exceeds the precipitation that falls on them (Figure 1.9). This spatial 'imbalance' in the water

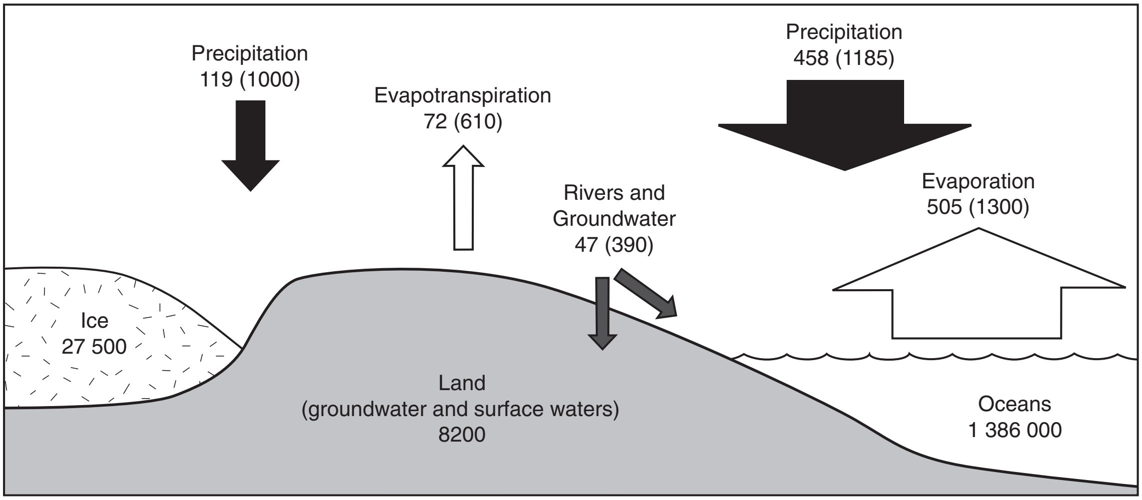

Figure 1.9 Average annual global hydrological cycle and stores of water by volume in thousands of km^3 and, in brackets, as millimetres. A similar but revised estimate based on more recent models is presented in Trenberth *et al.* (2007). (Source: Smith 1998. Reproduced with permission of Oxford University Press Australia and New Zealand.)

budget ensures the existence of lakes and rivers on the land. Patterns of water exchange between land and sea also vary regionally. For example, two-thirds of the net transport of water to the continents comes from the Atlantic, with the rest mainly from the Indian Ocean. Conversely, most of the water in the Pacific Ocean recirculates internally and there is little net transport towards land (Bengtsson 2010).

At the continental scale, the average annual Australian hydrological cycle comprises precipitation of 455 mm, evapotranspiration of 399 mm (88%), river runoff of 52 mm (11%) and groundwater recharge of 4 mm (1%) (Smith 1998). Of course, these values have little practical significance because of the massive annual and spatial variability in rainfall and climate across the continent. Much of this book deals with inland waters on a finer scale, and we shall see that the hydrological linkages at the landscape or catchment scales are usually more relevant. Nonetheless, the continental water budget of precipitation, runoff, storage, evapotranspiration and groundwater exchange dictates the water regime and regional distribution of surface waters in Australia, interacting with topography, catchment characteristics and land use. Therefore, human alterations of this budget, especially through river regulation, water extraction and anthropogenic climate change, have major implications for aquatic ecosystems and pose substantial challenges for management.

1.5.4 Continental linkages and surface waters in Australia

Australia is often described as the ‘driest inhabited continent’ (Antarctica is drier but not considered inhabited). Low average annual rainfall (Figure 1.10a) and its high proportional loss through evaporation (Figure 1.10b) and transpiration result in a mean annual runoff of only 1% of the world’s total (Lake *et al.* 1986). Furthermore, average annual river flows are nearly three times more variable than the world average, and those in Australian arid-zone streams are especially variable (McMahon *et al.* 1992). Two-thirds of the continent receives less than 500 mm of rain annually, and across three-quarters of the land area, evapotranspiration limits runoff to less than 5% of the rainfall.

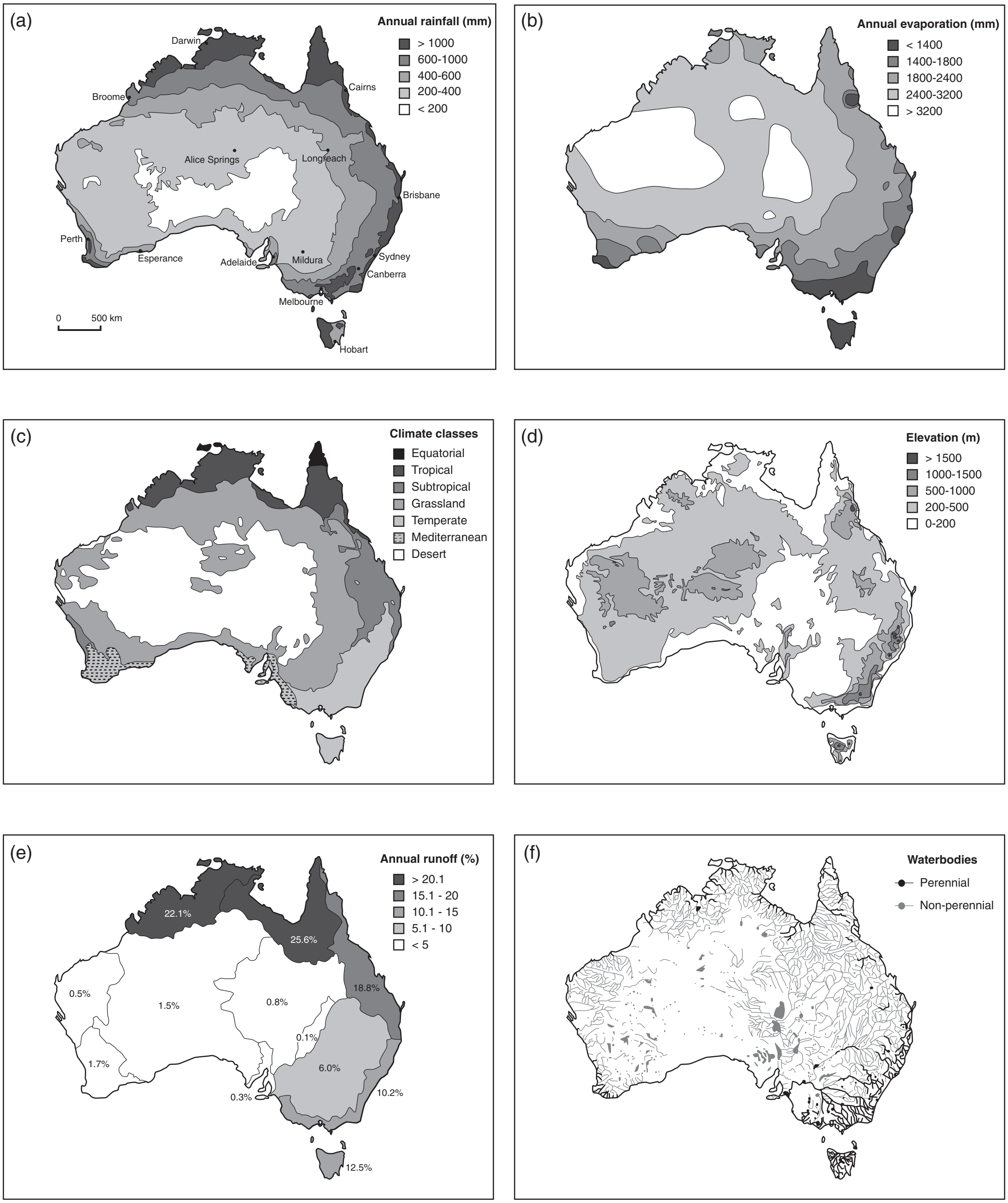

Figure 1.10 Average annual rainfall (a) and evaporation (b), broad climate (c), topography (d), runoff as percent of annual total (e) and surface water permanence (f). (Source: (a), (b) and (c) reproduced with permission from the Bureau of Meteorology, Australian Government, (d) redrawn with permission from GeoScience Australia © Commonwealth of Australia (Geoscience Australia) 2013. This product is released under the Creative Commons Attribution 3.0 Australia Licence, (e) redrawn with permission from the National Water Commission, © Commonwealth of Australia 2006, and (f) reproduced with permission from Australian Government Department of Sustainability, Environment, Water, Population and Community using data from the Australian Hydrological Geospatial Fabric (Geofabric) v1.0; Bureau of Meteorology from the State of the Environment Committee 2011.)

Part of this aridity reflects the continent's geographic location in the mid-latitude, high-pressure belt of the Southern Hemisphere. This means that its climate is controlled mainly by anticyclones moving eastwards. The borders of these pressure cells yield regular monsoonal rains to the north during the wet season (December–February). Occasionally, cyclones sweep further south-east, dumping heavy rain in the arid interior and causing spectacular flooding. In southern Australia, rainfall is usually highest during winter and spring, and the climate is more temperate (Figure 1.10c) but still seasonal.

Another cause of the continent's aridity is its low topographical relief (Figure 1.10d) and lack of large permanent snowfields. Only 2% of the land lies above 1000 m. The Great Dividing Range and its narrow coastal strip receive the majority of rain carried from the east. Thus, most runoff occurs to the north of the continent (tropical climate) and the eastern coast (tropical and warm temperate), with smaller contributions from the south-western and south-eastern corners of the mainland (Figure 1.10e). As you might expect, this is reflected in the distribution of permanent surface waters (Figure 1.10f).

Australia's surface drainages, comprising 245 river basins (listed in www.bom.gov.au/hydro/wr/basins/index.shtml), have been grouped into 13 drainage divisions (Figure 1.11), although older classifications recognized only twelve divisions. The landscape water yields (i.e. surface runoff plus groundwater discharge) from these divisions have been modelled as a function of rainfall and evapotranspiration (Commonwealth of Australia 2011), and vary widely (Table 1.4). Tasmania contributes almost half of Australia's total landscape water yield whereas the seven large drainage regions that comprise the south-western two-thirds of the continent (Figure 1.11) contribute only 13.3%. Conversely, Tasmania's mean annual percentage runoff is less than that from the tropical drainage divisions to the north of the continent (Figure 1.10e).

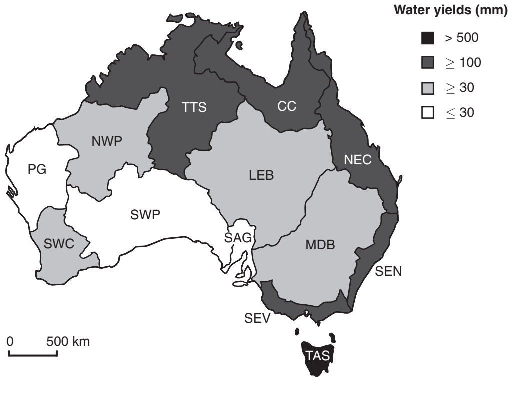

Figure 1.11 The 13 drainage divisions of Australia (acronyms in Table 1.4), shaded by water yield (mm of surface runoff plus groundwater discharge). (Source: Reproduced with permission from the Bureau of Meteorology, Australian Government.)

River systems draining to the sea are described as **exorheic** (literally, 'outer + flowing'). Nearly half of mainland Australia (49%) either has no coordinated drainage (**arheic**) or the rivers drain to inland lakes (**endorheic**, 'inner + flowing'). This contrasts with the pattern of river drainage prevalent in other continents and used as examples in Northern Hemisphere textbooks, and poses its own unique set of ecological and management issues (Chapters 9–13).

One common misconception is that fresh water flowing to the sea is 'wasted', and often there are calls in the media to divert or dam this water for human uses. However, the water that runs to the sea in these exorheic rivers supplies estuarine and near-shore coastal ecosystems with crucial water, nutrients and energy while the waterways themselves act as migration routes for many species of fishes and other aquatic life. When the volume of river runoff to the sea is reduced, the productivity of local estuarine and coastal fisheries often declines sharply (e.g. Logan River, south-east Queensland, Loneragan and Bunn 1999). Preserving the seasonal pattern of river runoff may be just as important (review in Gillson 2011). The water is certainly not 'wasted', and these river-sea linkages provide ecosystem goods and services for coastal communities and most of Australia's capital cities.

One striking example of the ecological impacts of reduced river flows on near-shore coastal waters is the Coorong and Lower Lakes at the mouth of the Murray-Darling system, listed under the Ramsar Convention as a Wetland of International Importance. Hydrological modelling of flows into this estuary-lagoon complex has been used to develop rules for determining the volume and delivery regime of river water to maintain salinities, water levels and freshwater volumes at or below specified thresholds (Box 1.2).

Table 1.4 Areas and average (1911–2010) rainfall, evapotranspiration and landscape water yields of the 13 drainage divisions illustrated in Figure 1.11. (Source: Data collated from the regional reports of the Australian Water Resources Assessment 2010.)

Topographic drainage divisions	Acronym	Area (x 1000 km^2)	Area (%)	Rainfall (mm)	Evapo-transpiration (mm)	Landscape water yield (mm)	Landscape water yield (%)
Pilbara-Gascoyne	PG	478	6.3	259	226	26	1.7
North-Western Plateau	NWP	716	9.4	316	276	36	2.4
Tanami-Timor Sea Coast	TTS	1162	15.3	656	551	108	7.1
Carpentaria Coast	CC	647	8.5	744	622	135	8.8
North-East Coast	NEC	451	5.9	827	698	138	9.0
Lake Eyre Basin	LEB	1200	15.8	242	190	35	2.3
Murray-Darling Basin	MDB	1061	14.0	458	422	35	2.3
South-East Coast (NSW)	SEN	129	1.7	995	829	152	10.0
South-East Coast (Victoria)	SEV	135	1.8	734	608	100	6.5
Tasmania	TAS	68	0.9	1398	629	691	45.3
South Australian Gulf	SAG	118	1.6	306	272	23	1.5
South-Western Plateau	SWP	1093	14.4	232	218	11	0.7
South-West Coast	SWC	326	4.3	439	399	37	2.4

Box 1.2 Requirements of estuaries and coastal lagoons (The Coorong) for fresh water

Exorheic river flows are important to many coastal and marine ecosystems. For example, estuaries such as the Coorong, at the bottom of the Murray-Darling Basin, rely upon freshwater inflows to create a zone of mixing between fresh and marine waters. The diverse habitats from estuarine to hypersaline (salinity $>$ seawater) support a multitude of birds, fish and other aquatic life, making it a wetland of international significance. Using linked hydrological, hydrodynamic and ecological models (Lester *et al.* 2011), we identified freshwater flows and associated characteristics (e.g. water level, salinity) as the primary drivers of biotic assemblages in the Coorong. These models enable us to predict physicochemical and biotic characteristics under climate change, sea level rise and environmental flows. We predict climate change will reduce freshwater inflows to the Coorong, resulting in lower water levels, higher salinities and lower diversity of birds, fishes, benthic invertebrates and aquatic vegetation. Environmental water allocations, such as those legislated under the Murray-Darling Basin Plan, may ameliorate the worst of these impacts, assuming appropriate timing and volumes of water delivery (Lester *et al.* 2013).

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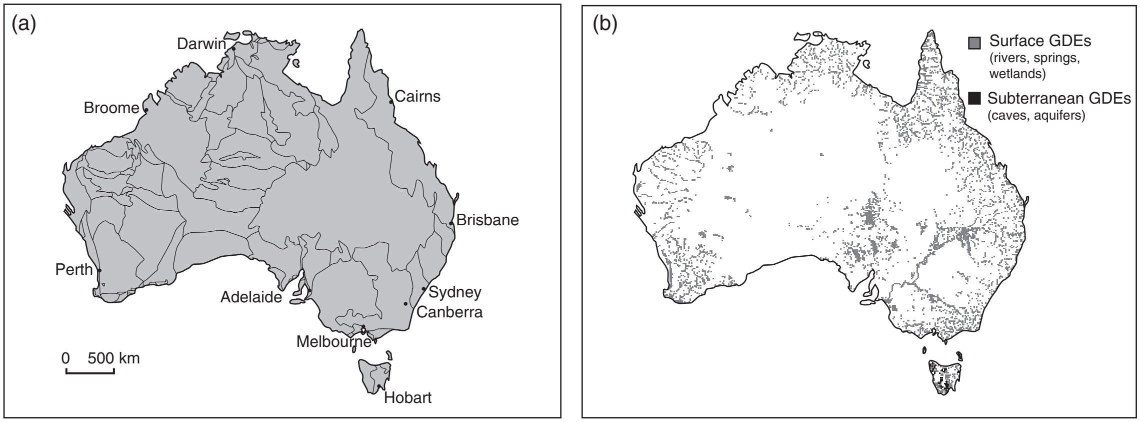

Figure 1.12 Groundwater provinces (a) and some of the main groundwater-dependent ecosystems (GDEs) (b) in Australia. The largest basin is the Great Artesian Basin. (Source: (a) reproduced with permission from the Australian Government Department of Sustainability, Environment, Water, Population and Communities - National Land and Water Resources Audit 2001, Australian Water Resources Assessment 2000, National Land and Water Resources Audit, Canberra, ACT, (b) reproduced with permission of the Bureau of Meteorology, Australian Government.)

1.5.5 Continental linkages and groundwaters in Australia

Groundwaters are hidden from view of the casual observer and are often challenging to access and sample. Therefore, the study of their ecology has lagged far behind that of surface waters, and aquatic ecology textbooks devote little attention to them. However, there have been recent advances in our knowledge about the ecology of Australia's groundwaters as well as greater recognition of the dependence of many of our surface ecosystems upon groundwater (Section 8.5.5). Groundwater can be defined as 'water that is present in soils and geologic formations for sufficient time to undergo physical or chemical changes resulting from interactions with the aquifer environment' (Tomlinson and Boulton 2008). This water occupies the saturated interstitial spaces below the Earth's surface – spaces that can range from minute voids less than a tenth of a millimetre through to vast caves hundreds of metres wide that contain underground lakes and streams.

Australia is well endowed with groundwater, and major sedimentary aquifers of variable water quality lie under some 60% of the continent. Surface drainage divisions are of limited use for describing the distribution of groundwater reserves because surface and groundwater catchments may not coincide. Thus, groundwater resources are separately assessed in 61 'groundwater provinces' (Figure 1.12a). Nonetheless, many surface waters feed or are fed by groundwaters at some time (Chapter 8). One theme of this book is the need to recognize that surface waters and groundwaters should be studied and managed as a single resource (Winter *et al.* 1998). This is all the more important when we realize that many terrestrial, aquatic and even coastal marine ecosystems rely on groundwater. These **groundwater-dependent ecosystems** (GDEs) are widespread (Figure 1.12b), and frequently diverse and beautiful, such as the ones on North Stradbroke Island, Queensland (Box 1.3).

Historically, the availability of groundwater facilitated the inland spread of European settlement (and the construction of all those iconic windmills). Even today, groundwater is the most important water resource in much of inland Australia because it is more reliable and less prone to evaporation than the sparse surface waters. Perhaps the best known example is the Great Artesian Basin (Figure 1.12a), which is among the world's largest aquifers at 1.7 million km^2 and up to 3000 m thick. It has been heavily exploited and, in some places, natural springs that used to be

Box 1.3 Groundwater-dependent ecosystems of North Stradbroke Island

Queensland's North Stradbroke Island is one of the world's largest sand islands. It comprises wind-blown sand in Pleistocene- and Holocene-aged dunes up to 219 m high, overlying bedrock well below sea level. Rainfall readily permeates the dunes to recharge a 930-GL regional aquifer forming a mound up to 40 m above sea level within the sand, plus numerous local perched aquifers formed by layers of low permeability within the sand mass. Surface expressions of groundwater support many freshwater wetlands. These occur as mosaics of permanent and ephemeral streams, perched and window lagoons and lakes, and fringing wet heath communities. Most are oligotrophic, with acidic and very fresh water, sometimes stained brown with humic substances. They support a depauperate, but specialized biota with several endemic species (Marshall *et al.* 2011). Intimate association with groundwater insulates these wetlands from short-term rainfall variability, making them relatively stable aquatic environments and likely climate refuges. Blue Lake is a fine example; recent evidence suggests hydrological stability over thousands of years (Barr *et al.* 2013). However, this dependency means that regional groundwater use must consider potential impacts on the surface wetlands and streams.

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permanent have now dried up. Effective management and conservation of groundwaters, such as those of the Great Artesian Basin, must include the complex hydrological linkages among aquifers and with surface waters.

1.6 THE STRUCTURE OF THIS BOOK

In this book, we have divided our treatment of surface waters into standing and running because flow modifies so many physical, chemical and biological processes. We emphasize a **process-oriented approach** because this best illustrates the mechanisms by which physical, chemical and biological attributes govern the ecology of aquatic ecosystems. Although the processes discussed in Chapters 2–7 are common to all surface waters, they may produce different outcomes. For example, a given volume of rainfall may fill a dry inland lake whereas the same amount could cause flooding in a permanent river. The physical, chemical and biological consequences of this event will differ among lentic and lotic permanent and temporary waters at a range of scales. Furthermore, each process may yield different results depending on the type and shape of the waterbody, its water regime, the history of the process at a range of scales, and human activities in the waterbody and its catchment. The chapter on processes and management in groundwaters (Chapter 8) also addresses the groundwater-dependence of many surface ecosystems, emphasizing the vertical linkages and connectivity.

We then turn our attention to management issues, with the underlying theme that understanding physical, chemical and biological processes is essential to effective management of surface and groundwaters so that we can manage ecological causes of the problems instead of simply treating the symptoms. Alterations of water regime (Chapter 9), physical features of the waterbody and its catchment (Chapter 10) and water quality (Chapter 11) are the three fundamental modifications wrought by human activities. Superimposed on these 'big three' are allied issues that affect biodiversity, including the effects of invasive species and climate change (Chapter 12). Attempts to restore aquatic ecosystems and protect their biodiversity rely on a sound understanding of ecological processes and how these are likely to be affected by factors such as climate change and invasive species. Aquatic ecologists contribute to wise water resource management through their basic research, field monitoring and collaboration with policy makers, social scientists, economists, consultants, managers and the public. However, this collaboration comes with its own challenges and opportunities, and discussion of these provides a fitting conclusion (Chapter 13) for a book on freshwater ecology and management.

CHAPTER 2

Physical processes in standing waters

2.1 DEPTH AND PHYSICAL PROCESSES

The depth of a standing waterbody is a primary driver of its biophysical processes, especially in determining the underwater light environment. In shallow clear waters, light reaches the bottom and allows algae and rooted aquatic plants to grow there. Light and heat penetration also govern patterns of stratification and mixing of water, influencing many features of the chemistry (Chapter 3) and biota (Chapter 4) of lentic environments (Figure 2.1).

In this chapter, we explore how depth affects light penetration, vertical temperature profiles, and stratification in standing waters. We then discuss the different types of stratification and circulation patterns, focusing on how they are influenced by physical features such as waterbody shape and depth. Finally, we review the modes of formation of deep and shallow lentic environments because this also affects many physical processes, especially the probability and persistence of stratification.

2.2 LET THERE BE LIGHT ...

The primary source of energy in virtually all aquatic ecosystems is the sun. This energy may be stored in the chemical bonds derived from photosynthesis (Section 3.2.1), such as in leaf litter in the catchment or within the waterbody. Energy as heat also influences many aquatic physical, chemical and biological processes. To understand these processes in standing waters, we need to know how much solar radiation reaches the surface of a waterbody, how far it penetrates, and how it affects organisms in the water column.

Light speeds from the sun at 299 790 km s^{-1}, travelling as a pulsating field of electromagnetic force composed of a series of waves. Energy is contained in quanta that are proportional to the frequency or number of waves produced per second. Individual rays have their own frequencies and wavelengths across a broad spectrum but only a small fraction reaches the Earth. The human eye can see wavelengths between 380 and 780 nanometres (nm, 10^{-9} m) and we call this 'light'. This also approximates the range of wavelengths used in photosynthesis by virtually all autotrophs and is termed **photosynthetically active radiation** (PAR).

The wavelength of a quantum of electromagnetic radiation energy (a photon) is proportional to its frequency. Red light at 750 nm contains 38.13 kcal of energy per mole whereas violet light at 380 nm contains 75.13 kcal per mole. Light energy is used to transfer electrons from donor to acceptor molecules (Chapter 3) during the complex process of photosynthesis. Chlorophyll absorbs red and violet waves, and reflects intermediate greens and yellows (which is why plants appear green to us).

2.2.1 Light reaching the water surface

Some light reaching the water surface is reflected, depending on the sun's angle of incidence (varying with time of day, latitude and season) and the effects

Australian Freshwater Ecology: Processes and Management, Second Edition. Andrew J. Boulton, Margaret A. Brock, Belinda J. Robson, Darren S. Ryder, Jane M. Chambers, and Jenny A. Davis.

Companion Website: www.wiley.com/go/boulton/freshwater

Figure 2.1 Physical processes in large shallow lentic waters such as this coastal lagoon in northern NSW are strongly influenced by currents generated by the wind. (Source: Darren Ryder.)

of wind on the surface. Cloud cover, dust, smoke, shade and other factors can all reduce the amount of light reaching the water surface (Figure 2.2).

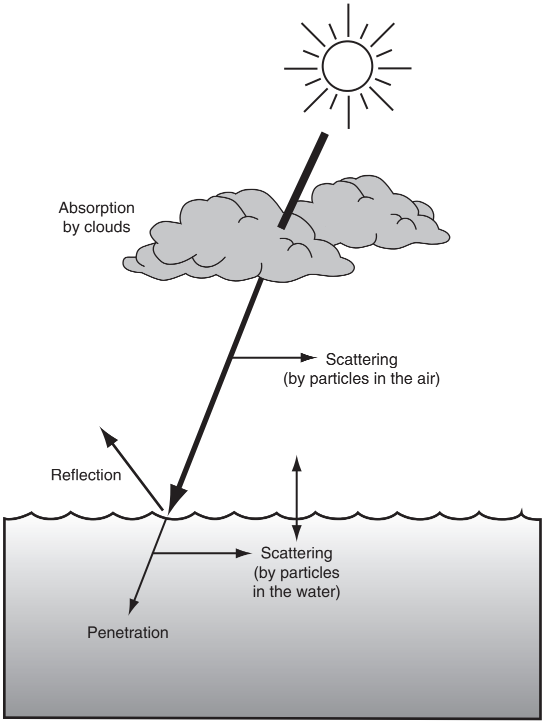

Figure 2.2 Factors affecting light at the water surface. The declining widths of the arrows as they descend remind us about the decline in light as it becomes absorbed, scattered or reflected.

2.2.2 Light below the water surface

Although water is transparent, light passing through it is eventually extinguished with depth. A beam of monochromatic light (one colour) entering chemically pure water is absorbed exponentially; absorption varies with the logarithm of the depth of the water (sometimes called Bouguer's or Lambert's Law). However, under natural conditions, polychromatic light strikes the water surface from many angles, is refracted, and passes through water in which concentrations of ions and particles, density, or both may vary with depth. A second law (Beer's Law) states that the absorbing capacity of a solution is directly proportional to the number of absorbing entities. By combining these two laws (into the Beer–Lambert Law), we can estimate the absorption of light by different components in the water column, expressed as the **vertical absorption coefficient**. This includes absorption in pure water (k_w), absorption by suspended particulate matter (k_p), and absorption by dissolved substances (k_c). The sum of these gives the total coefficient of absorption (Figure 2.3) and, for a given depth, represents the light available to aquatic organisms.

However, there is also considerable scattering of light within water, and this increases the probability of absorption by water or suspended particles. For example, when light has penetrated the water of a natural waterbody to a depth of 1.0 m, the average distance travelled by the rays may be nearer 1.2 m because of the oblique paths followed by much of the light as it bounces off suspended particles (Kirk 2011). As light passes through water, it is constantly being absorbed and scattered. Almost all absorbed light is converted to heat.

Light that is not reflected or absorbed is transmitted. **Transmittance** varies with wavelength (Figure 2.4). Objects seen at depth appear blue because blue light penetrates water well. However, natural water often contains substances that differentially absorb light.

For example, dissolved materials from plant decomposition (Box 2.1) can capture 70–80% of the photons. In some highly coloured waters, orange light penetrates deepest. In general, as the absorption coefficient increases, longer wavelengths of light are transmitted further (Kirk 2011). Consequently, deep clear lakes appear blue whereas lentic waters containing tannins and other humic acids appear brown, regardless of depth.

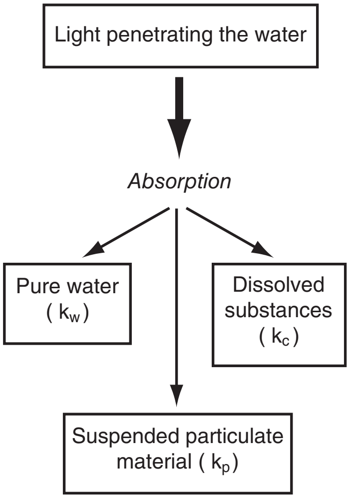

Figure 2.3 The vertical absorption coefficient is the sum of absorption by pure water (k_w), suspended particulate material (k_p) and dissolved substances (k_c).

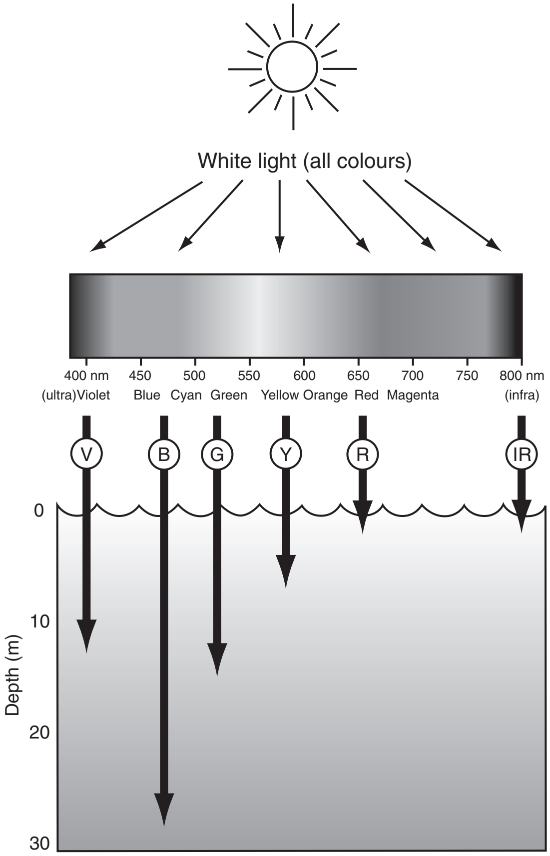

Figure 2.4 Vertical paths of selected wavelengths of light through clear water, showing differential penetration.

Box 2.1 The influence of dissolved organic carbon on light penetration and biological processes

Dissolved organic carbon (DOC) plays a pivotal role in regulating biological processes in freshwater environments. Not only does DOC influence light penetration and therefore primary production in freshwater environments, it can also stimulate heterotrophic activity because it is a major source of energy to microorganisms. Freshwater environments with high DOC concentrations can therefore display a decrease in primary production because of reduced light penetration and, at the same time, an increase in heterotrophic production owing to the availability of labile (i.e. biologically available) organic matter for microorganisms to respire. In south-east Australian floodplain systems, dissolved carbon leached from algae was the dominant basal resource utilized by consumers, suggesting that in-stream primary producers underpin trophic pathways in these systems (Hadwen *et al.* 2010). Increased DOC concentrations have direct effects on rates of primary production through the attenuation of light in the water column and by reducing the depth of the euphotic zone, and indirect effects on aquatic food webs by reducing the labile DOC produced by algae that would be available to microbial consumers.

Wade Hadwen, Griffith University

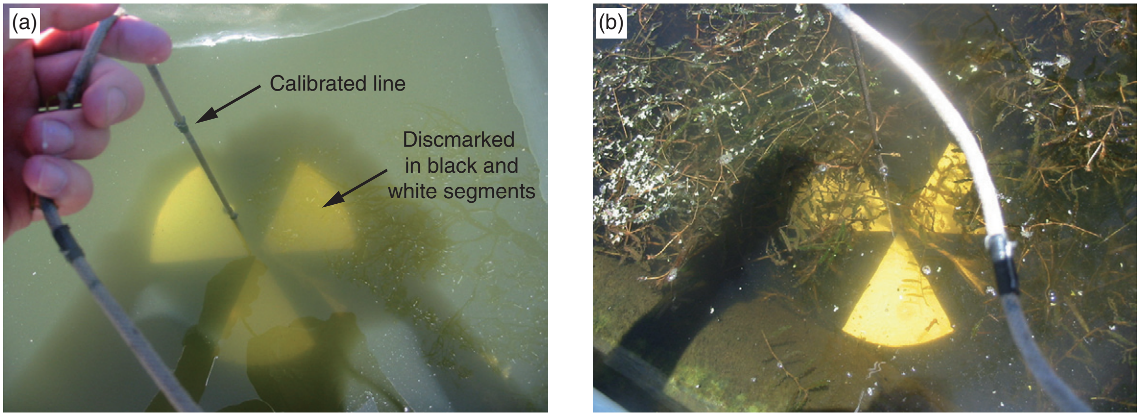

Figure 2.5 A Secchi disc lowered in turbid water containing a phytoplankton bloom (a) is less visible than one lowered to the same depth in clear water dominated by submerged plants (b). These photos were taken in full sunlight for best contrast; Secchi depths should be measured in the shade. (Source: Peter Novak.)

2.2.3 Seeing through water: Secchi discs and quantum sensors

A measure of vertical visibility is helpful because it indicates how much light may penetrate the water, potentially controlling the depth of photosynthesis in a waterbody. One simple way is to slowly lower a weighted black-and-white Secchi disc (named after its Italian inventor) with the flat face horizontal into the water on a calibrated line (Figure 2.5a,b) until just before it cannot be seen. The exact depth at which it becomes invisible is the **Secchi depth** (Z_{SD}) or Secchi disc transparency, and is half the distance light travels to the disc and back to the operator's eye. It is best measured between 10:00 a.m. and 2:00 p.m. off the shady side of a boat. It is affected by the eyesight of the user, the contrast between the disc and surrounding water, the reflectance of the disc, and to some degree, the size of the disc (a diameter of 20 cm is common). Despite these sources of variance, Secchi disc transparency is a quick, easy and cheap general measure of light penetration. Clear, unpolluted waters may have Z_{SD} $>$30 m whereas the turbid Darling River (NSW) seldom has a Secchi disc transparency more than 10 cm.

Although Secchi disc transparency can give a rough idea of light penetration in water, quantum sensors are a better way of measuring photosynthetically active radiation (PAR) at a given depth because the specialized photocells record the number of photons with wavelengths of 400–700 nm falling on a specific area for a given time. This measure, termed photon flux density, allows us to estimate the potential amount of photosynthesis under varying conditions of depth or turbidity, for example.

2.3 THE EUPHOTIC ZONE

The rate of photosynthesis is governed by the amount of PAR received by the plant (Section 2.2). The minimum amount of subsurface light that permits photosynthesis has been set arbitrarily at 1% of incident light at the water surface, although some shade-adapted algae can get by with less. Thus, the region from the surface to where 99% of the light has been reflected, absorbed or scattered is termed the **euphotic** zone, and is where the vast majority of aquatic photosynthesis occurs (although currents can carry suspended plants such as some algae into and out of the euphotic zone).

The depth of this zone is best determined using a photometer or quantum sensor, expressing the result as a fraction of 100% incident light at the surface. Alternatively (and more simply), the depth of the euphotic zone can be roughly estimated as equal to two to three times the Secchi depth. However, in turbid waters, the true euphotic zone may exceed three times the Secchi depth. This is because although the disc quickly disappears, diffuse light scattered by the particles can penetrate deeper into the water.

Of course, simply measuring light intensity does not provide a reliable estimate of the amount of photosynthesis that can occur. This will depend upon the presence of photosynthetic organisms, the suite of pigments they contain, and the available wavelengths of light at any particular depth. Furthermore, we should not assume that light intensity will always be low in water underneath a dense surface canopy of leaves (such as below mats of floating or submerged aquatic plants). Field measurements show that intensity can actually increase under the canopy because light is reflected and scattered from the bottom (e.g. Loo *et al.* 2009).

2.4 LIGHT AND LIFE

The predominant pigment used in photosynthesis is **chlorophyll *a***. This absorbs light at two peaks: 670–680 nm and 435 nm. Wavelengths of the first peak are abundant in shallow water; wavelengths of the second go deeper (Figure 2.4), supporting photosynthesis at a range of depths. Accessory pigments absorb other wavelengths to supplement photosynthesis, and hence, most aquatic plants use nearly the whole spectrum from 400–700 nm (i.e. PAR).

Like plants, aquatic animals also respond to light levels in standing waters. Many species of zooplankton (Chapter 4) show marked daily migrations, moving upwards in diminishing light and downwards as light strengthens (Kobayashi *et al.* 2009a). However, this is by no means universal, and there are examples of 'reverse migration' when many individuals occur near the surface during the day and descend to the bottom at night (Bayly 1986). Even photosynthetic organisms at the air–water interface must still contend with daily and seasonal variations in light intensity in addition to fluctuations in temperature, wind and rainfall (Butler *et al.* 2007).

Interestingly, some tiny algae (e.g. the green alga *Dunaliella*) and microcrustaceans living in shallow waters have red pigments (derived from various carotenoids) or dark melanin (e.g. *Daphniopsis*, a salt-lake microcrustacean) inferred to be an adaptation to excessive ultraviolet light ('sun block'). However, there is a trade-off between being protected from photo-oxidation versus being more visible to predators. Some of these animals are 'better red than dead', especially when vertebrate predators are excluded by, for example, high salinity (Hairston 1981). In other waterbodies, large and intensely coloured species may be so heavily preyed upon that this selective pressure overcomes the benefits of the protective chemical sun block.

2.5 TEMPERATURE AND STRATIFICATION

In addition to light, the sun also provides **heat** energy to waterbodies. As solar radiation passes down through water, it disappears exponentially and the heating wavelengths are absorbed rapidly. However, the vertical temperature curve does not match the light curve described earlier. Instead, for many standing waters, wind mixes the upper layers of water, distributing the absorbed heat downwards. Early in the process, the wind-generated currents are sufficient to overcome the density differential caused by surface heating, and the lake remains fully mixed while it warms. Eventually, there comes a point where the currents cannot overcome the differential, producing a 'layered' change in temperature with depth (Figure 2.6). This layering effect is termed direct **stratification**. Cool and dense water in the **hypolimnion** (*hypo* = below or beneath) lies below the warmer, less dense **epilimnion** (*epi* = above or upon). Between these two layers is the

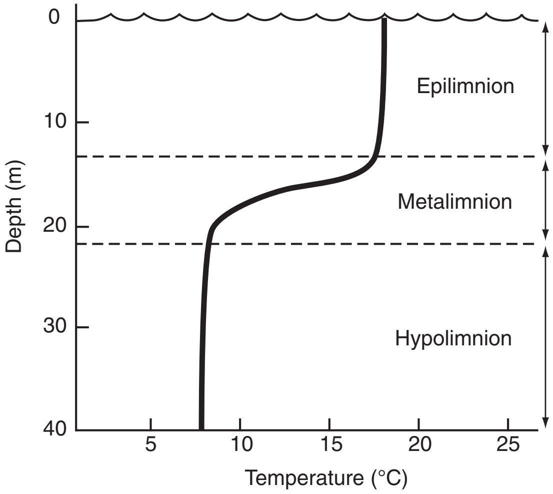

Figure 2.6 Vertical temperature profile with depth under conditions of direct stratification in a standing water. The metalimnion contains the thermocline, the plane where the greatest change in temperature occurs.

metalimnion (Figure 2.6), a zone containing the **thermocline**, which refers to the horizontal plane where the greatest rate of change in temperature occurs. Be aware that many authors use terms 'thermocline' and 'metalimnion' interchangeably.

Thus, in stratified waters, we have a well-lit, wind-stirred upper stratum where primary production prevails overlying a darker lower region. Much of the organic matter produced by photosynthesis in the epilimnion sinks to the hypolimnion to be mineralized by bacteria and other microbes (Section 3.9.3). Consequently, we can view a stratified waterbody as two almost distinct subsystems where quite different ecological processes prevail. Now you can see why the presence and causes of stratification are fundamental physical processes to consider when we explore the chemical and biological processes of standing waters in the next two chapters.

2.5.1 Causes of stratification

Temperature is the major factor affecting the density of fresh water and hence, thermal stratification. Usually, warm water overlies cold. However, under ice, a natural inverse stratification can occur because water is most dense near 4°C (Figure 2.7, Section 1.5.1). In temperate regions of Australia, density differences in the water column over ambient temperature ranges (5–25°C) are relatively small. Conversely, in tropical and arid areas high ambient air temperatures and water temperatures that exceed 30°C can lead to pronounced differences in water density. Stratified waterbodies in these regions have a shallower epilimnion and are more thermally stable (i.e. need more energy to mix the layers) than their temperate counterparts. For example, in the Mary River, NT, diurnal cycles of heat gain and loss drive thermal stratification, with infrequent and short-lived deep mixing events providing oxygen-rich water to the hypolimnion of the river's floodplain wetlands (Townsend 2006).

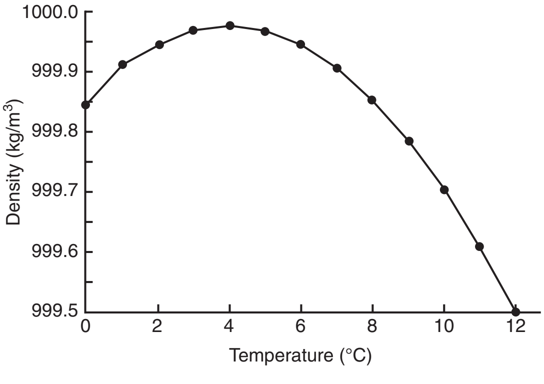

Figure 2.7 Change in the density of pure fresh water with temperature.

Other factors can affect the density of water including **pressure** (associated with changes in altitude), **salinity** and **suspended particles**. For example, warm water may persist below colder strata where greater density of the bottom layer is maintained by a high salt concentration. On Rottnest Island off the WA coast, shallow lakes of salt water concentrated by evaporation are inversely stratified because fresh water from runoff and rain lies on top of the dense salty water for part of the year. Solar radiation penetrates the fresh upper layer, heating the saline bottom stratum until it is warmer than the upper layer. However, despite being warmer, the density of the lower layer caused by salinity prevents the warm water from rising and the lake is said to be inversely stratified (Bunn and Edward 1984). When the fresh water evaporates during summer, the lake returns to being an unstratified salt lake.

Shallow waters containing suspended particles (i.e. **turbid**) or dissolved organic material often stratify as well. In a turbid or darkly stained waterbody on a hot day, water temperature can change sharply within a few centimetres' depth because suspended particles or dark dissolved materials near the surface absorb heat rays so effectively. As many natural Australian lentic waters are shallow and turbid, stratification owing to turbidity may be more widespread than the thermal stratification described for clear water in most textbooks. In this country, standing waters such as salt lakes, shallow (<1 m) floodplain wetlands, and temporary waters seldom stratify for long periods but may do so almost daily as a result of heating during the day and cooling overnight. For example, in south-western WA, Ryder and Horwitz (1995) showed that shallow wetlands with dark peat-stained water stratified daily before wind-driven mixing occurred in the afternoon.

The number of waterbodies in Australia that stratify has increased as a result of human activities. Construction of reservoirs and impoundments across rivers has produced a large number of deep, permanent waters (Kingsford 2000) that thermally stratify. Farm dams, common in rural landscapes, are often turbid and most of them also stratify during hot weather. Several management issues influenced by the effects of stratification occur in these artificial waters (Chapter 9) so it is handy to know the different patterns of circulation that can form in artificial and natural waterbodies.

2.6 USING CIRCULATION PATTERNS TO CLASSIFY STANDING WATERS

When standing waters mix (circulate), there are major effects on the biota and water quality. Therefore, it seems logical to classify these systems based on their modes of mixing, even though these patterns may vary year to year in some waterbodies. The first distinction is between **amictic** ones that never mix (e.g. Lake Fryxell in Antarctica, Smith *et al.* 1993), **holomictic** ones that mix completely, and **meromictic** ones that mix incompletely (Table 2.1).

Holomictic waterbodies are classified further (Table 2.1) according to how often they circulate in a year. Many lakes stratify just once (monomictic) or twice (dimictic) a year. In temperate regions of southern Australia, **warm monomictic** lakes frequently occur. In these lakes, strong winds and cool weather in winter ensure complete mixing whereas in summer, surface layers heat up and form a warm epilimnion overlying cooler, denser water (Figure 2.8). **Cold monomictic** lakes that freeze over and stratify in winter but never heat up enough to stratify in summer, and **dimictic** lakes that stratify twice a year (Table 2.1) are rare in Australia. However, **polymictic** waters that mix almost daily are very common, reflecting the predominance of shallow (<1 m), wind-exposed waters across the continent. We agree with Walker and Likens (1975) about the removal of the ambiguous category 'oligomictic'.

In sheltered waterbodies and many reservoirs, night-time cooling can be the dominant driver of the depth of the metalimnion (MacIntyre and Melack 2010). During the day, although wind may provide plenty of mixing energy, solar radiation more than compensates by stabilizing the water column. This results in the depth of the surface mixing layer being up to a couple

Table 2.1 Broad categories of mixing based on circulation frequency, derived from Hutchinson (1957), Walker and Likens (1975) and Lewis (1983). See Lewis (1983) for further sub-categories of polymictic lakes.

Category	Explanation	Distribution in Australia
Amictic (*a* = without)	Never mix	A few occur under permanent ice cover in Antarctica
Holomictic (*holos* = whole)	Mix completely (i.e. throughout the whole waterbody) at least once in the seasonal cycle	
Cold monomictic (*mono* = one)	Mix once a year. Freeze over in winter but mix in summer when they warm but never stratify	High-altitude waterbodies; rare in Australia
Warm monomictic	Mix once a year. Lack ice cover in winter when they are mixed and stratify only in summer	Many deep lakes in southern Australia (mild winters/warm summers)
Dimictic (*di* = two)	Mix twice a year, during spring and autumn. Stratify in winter under ice cover and in summer	High-altitude waterbodies; rare in Australia
Polymictic (*poly* = many)	Mix frequently, sometimes continuously. Stratify in response to diel temperature changes	Most shallow (<1 m) and wind-exposed basins; very common in Australia
Meromictic (*mero* = part)	Mix incompletely and infrequently	Some deep glacial lakes in Tasmania, deep reservoirs or salt lakes; uncommon in Australia

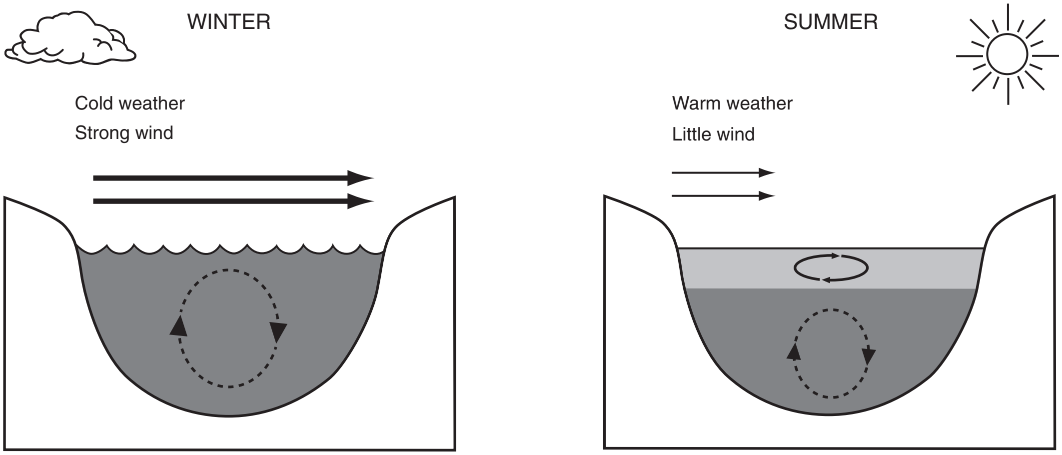

Figure 2.8 Thermal stratification in a warm monomictic standing water, typical of temperate regions of southern Australia.

of metres shallower than at sunrise, when it is almost always at its deepest.

Meromictic waterbodies do not mix completely. Unlike holomixis, the whole waterbody does not circulate very often (decades to centuries) or for long periods (hours to days) because of a dense layer of bottom water where only very slow internal currents occur. This dense and typically anoxic layer is called the **monimolimnion** (Figure 2.9). The upper, more dilute layer is termed the **mixolimnion**, and mixes by wind. Conditions in this upper layer favour organisms that require light and oxygen (Box 2.2). Between these layers, the plane where salinity increases with depth is called the **chemocline** (Figure 2.9). Thus, stratification is still the result of density differences but the cause of the difference in the density of water is not temperature but dissolved material. To make things even more interesting, thermal stratification can occur in the mixolimnion overlying the chemical stratification, rather like a multilayered cake.

Meromixis can arise from a number of factors, and meromictic waterbodies are classified by these causes. These include biogenic (*bio* = life) meromixis where organic substances settle and accumulate in the monimolimnion; ectogenic (*ecto* = outer) meromixis where processes outside the waterbody deliver dilute water to form lenses above pre-existing saline layers or introduce saline water that falls to the bottom of a fresh waterbody; and crenogenic (*creno* = fountain or spring)

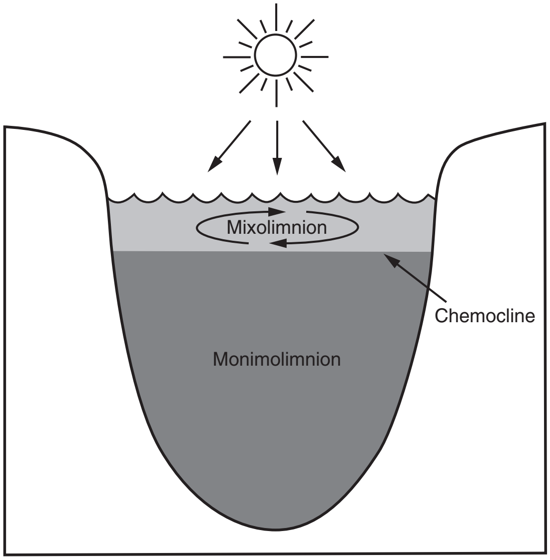

Figure 2.9 Meromictic waterbodies mix only partially in the course of a seasonal cycle. Mixing occurs in the upper mixolimnion but seldom, if ever, in the lower monimolimnion. In between lies the chemocline, where the water chemistry and density change abruptly.

Box 2.2 Meromictic lakes in Tasmania

Among Australia's scarce meromictic lakes, Tasmania's excel. Pinched off from their umbilical river for 2000 years, they graphically and evocatively flaunt the hallmarks of meromixis in their World Heritage wilderness. The knife-edge watershed between the rosy twilight of their dystrophic, oxygenated mixolimnia and their dark, anoxic, sulfuretted monimolimnia is a colourful microbial marketplace, thronged by monerans, protists and metazoans in a strictly segregated vertical hierarchy, a penny stack of thin wafers, a pecking order of form and function straddling the ultimate arbiter of that metabolic divide, the redoxcline. Above is a rich variety of interacting communities – algae, bacteria, rotifers, microcrustaceans and chaoborids. Below the divide, photosynthetic bacteria eke out a life in the crepuscular zone of these blackwater lakes. One red photon per day perhaps! Alone among eukaryotes, a few ciliates have mastered that anoxic Precambrian analogue, their hydrogenosomes and their symbiotic methanogens part of the enabling mechanism, their syntrophic metabolic cascade.

Peter Tyler, Deakin University

Box 2.3 Using destratifiers to affect circulation patterns in reservoirs

Artificial destratification involves introducing mechanical energy to a stratified waterbody to reduce the strength of the density stratification. Usually, temperature is the dominant cause so destratification aims to reduce the vertical temperature difference in the water column to about 0.5–1.0°C. In many Australian reservoirs, artificial destratification increases dissolved oxygen in and below the metalimnion without greatly increasing the depth of the epilimnion. Thus, nutrient release from deep sediments is reduced by increasing hypolimnetic oxygen concentrations (decreasing the annual sustainable algal biomass) whereas the physical habitat of the epilimnion (especially light availability and turbulence) remains favourable to nuisance algae.

Artificial destratification is usually done by either introducing bubble plumes at the bottom of the water column using compressed air or by using surface mixers (large impellers) to pump surface water downwards through the thermocline. Conceptually, both techniques produce large-scale circulation and enhance downwards transport of heat and oxygen from surface waters. The influence of surface mixers may not always extend as deep as that of bubble plumes introduced at the bottom of a reservoir, and the choice of technology depends on the specific issues being addressed.

Brad Sherman, CSIRO

meromixis arising from subsurface flows of saline, dense water into a waterbody.

2.7 ECOLOGICAL IMPLICATIONS OF THE DIFFERENT TYPES OF STRATIFICATION AND MIXING

Stratification is ecologically relevant because it potentially limits the productive volume of a waterbody. It does this by preventing plants and animals from the euphotic zone occupying particular strata. For example, in a stratified waterbody (Figure 2.6), primary production by phytoplankton (planktonic algae) may occur in only a limited stratum (the epilimnion) rather than in the entire euphotic zone, owing to density differences that prevent vertical migration by the phytoplankton. Where stratification is caused by differences in temperature, the euphotic zone is usually within the epilimnion. However, in very clear, deep lakes, sufficient light for photosynthesis can penetrate below the thermocline into the hypolimnion.

Deeper, denser water below the thermocline can become hypoxic and lethal to most aerobic organisms (Box 2.2). This means that large volumes of deep stratified waters may be devoid of consumers and the majority of the biodiversity is limited to the thinner upper layers where oxygen is available. One solution is **artificial destratification** (Box 2.3) which aims to break down or limit stratification by reducing the strength of the vertical differences in the density of water, especially in reservoirs.

When stratified waters mix or circulate, there are also ecological implications. For example, nutrients may be mobilized from the sediments or hypolimnion and promote primary productivity near the water surface. Dissolved oxygen concentrations near the bottom typically rise and this allows aerobic consumers access to previously unavailable parts of the waterbody.

The major cause of mixing in most natural waters is wind. Wind adds kinetic energy to the waterbody through the shear it imparts to the water surface. This shear drags the water downwind, causing lateral patterns of surface circulation as well as vertical mixing (Figure 2.10) that, in shallow waters, can resuspend bottom sediments and nutrients. These lateral and vertical circulation patterns can also move plants and animals that are either floating at the surface or suspended in the water column. Wind blowing across water often produces elongate spinning spirals of water that rotate about axes broadly parallel to the wind. Some suspended organisms (plankton) are able to use these Langmuir spirals (named after their discoverer) to migrate in the water column, rather like soaring birds use thermals. These spirals are also why plankton nets should always be towed at right angles to the wind.

When winds blow along an exposed waterbody, water may pile up downwind (Figure 2.11). In shallow waters with gently sloping edges, this accumulated water often inundates large areas of downwind shoreline while exposing the shoreline upwind. When the wind ceases, the water, relieved of pressure, flows back in the opposite direction. This oscillation is termed a **seiche** (pronounced 'saysh'). Not only does this influence the ecology of the downwind and upwind shorelines, but internal waves can form when the thermocline oscillates because of seiche movements. Although the surface seiche may be small, it can have a huge effect on the dense layer of water below the thermocline. A rocking thermocline starts out of phase with the surface seiche as it is forced down by the wave crest over it. This creates internal turbulence that can mix and transport heat, nutrients, gases and plankton throughout the water column.

Direct inflows such as groundwater, overland or tributary inputs may also cause mixing that has implications for the water chemistry and biota of standing waters. For example, in reservoirs on large rivers, river inflows following rainfall can provide the turbulence necessary to break stratification. In shallow wetlands, even the physical impact of rainfall on the water surface can be enough to induce density currents and cause some mixing.

Much mixing occurs at microscales that are significant for sediment nutrient release, gas transport and dispersal of small organisms. Many of these microscale movements of water are caused by differences in water density owing to temperature, and can be observed in a glass of coloured water containing a block of clear-water ice. In the hypolimnion of a deep waterbody, water movements may be caused by local chemical changes or induced by bacterial or animal activity. In the epilimnion, tiny surface waves and ripples distribute heat, nutrients and gases within the layer, while along the shore, micro-processes of erosion and deposition affect the biota occupying the water's edge. The shape of the shoreline may both influence and be caused by water movements at a range of scales. In

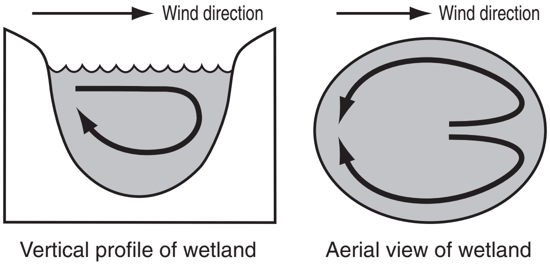

Figure 2.10 Persistent wind blowing across a standing water circulates water vertically and laterally, affecting the distribution and movement of nutrients, suspended materials and some organisms.

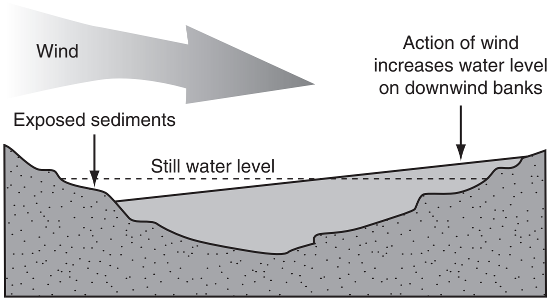

Figure 2.11 Strong wind can cause a seiche, piling water on the downwind bank.

turn, this affects where stands of aquatic plants grow or debris strands form, and these influence the distribution of waterbirds, invertebrates and other organisms.

By now, you can start to see the implications of stratification and mixing to many aspects of the chemistry and ecology of standing waters, and this will be explored further in the next two chapters. We conclude this chapter by exploring the interactions between depth, physical processes and how deep and shallow standing waters have formed in Australia. This will help illustrate how the mosaic of different lentic environments of different depths and formed in different ways underpins a diverse array of chemical and biological processes across the landscape.

2.8 DEEP VERSUS SHALLOW STANDING WATERS: DEPTH MATTERS

As we have seen, the depth of a standing waterbody is ecologically relevant in at least two ways. The first is in respect to light penetration and the extent of the euphotic zone relative to the depth of the waterbody. In clear shallow waters, light usually penetrates to the bed and so the euphotic zone is the entire waterbody. In contrast, light does not penetrate to the bottom of deep waterbodies, restricting photosynthesis down there.

The second is in respect to the probability and persistence of stratification. Clear shallow waters are less likely to thermally stratify than deeper ones. Further, deeper waters that do stratify are likely to stratify for longer (e.g. months, or for meromictic waters, even longer) whereas shallow waters may stratify for only brief periods (e.g. days). Although latitude, altitude and climate will influence the type and stability of stratification, the morphology (shape) of the basin and water depth are probably the main determinants. Where light reaches the bed, some heat is also transmitted, so surface and bottom layers are less likely to differ enough in temperature to cause thermal stratification. Shallow and exposed systems are also more easily mixed by wind, breaking down any stratification that might form. In standing waters, the importance of depth is best appreciated by considering the system from the top down because the top is where heat is added or lost and is where most wind stirring occurs. All else being equal, we would expect the same stratification upwards from the metalimnion. Therefore, depth becomes most relevant when it determines the volume of the hypolimnion and the euphotic zone.

Depth is a major driver of ecosystem processes such as primary production and energy dynamics (Chapter 4), and is why ecologists distinguish shallow standing waters from deep ones. The actual distinction between 'shallow' and 'deep' is completely arbitrary; we follow convention (Scheffer 1998, Padisák and Reynolds 2003) in adopting the value of 3 m to separate the two. This range has been derived from many field studies of light and heat transmission and the probability or persistence of stratification. As the depth of standing waters is largely influenced by how they formed (Box 2.4), we review the

Box 2.4 The role of basin formation in standing water processes

How a lake forms determines its depth, shape and size, and influences most ecological processes (Timms 2009). Mean lake depth is inversely related to its productivity. Deep lakes, formed by earth movements, glaciation, explosive volcanism or big landslips, permit thermal stratification, generally of the warm monomictic or dimictic type (Table 2.1). In contrast, shallow lakes created by volcanic damming or by river or wind action are typically polymictic. These different stratification processes have different limnological and ecological effects. Shape is also important. In round (e.g. crater) and rectangular (e.g. glacial valley) lakes, littoral influence is minimal compared to pelagic processes. The opposite applies in dendritic drowned-valley lakes. Vertical lake profiles resembling that of a beaker (e.g. crater lakes) mean little shallow water, so deep water processes dominate. Conversely, conical and trumpet-shaped lake profiles (e.g. solution lakes) mean that littoral processes are likely to dominate. Finally, size is important. In large glacial and tectonic lakes, there is more wind-induced mixing than in the protected waters of small crater and cirque lakes. Wind and wave action also promote physical shore processes in big lakes.

Brian Timms, University of Newcastle

processes that create deep and shallow waterbodies in Australia.

2.8.1 How deep standing waters form

Most natural deep waterbodies arise from entirely geological events. Tectonic ones form during spectacular movements of the deeper parts of the Earth's crust. This is often via faulting, either between masses of a single fault or in a downfaulted trough or graben (Figure 2.12a). Australia has a few **graben lakes** (e.g. Lake Edgar, Tasmania; Lake Torrens, SA; Lake George, NSW). Overseas, the best known graben lake is Lake Baikal in eastern Siberia, the deepest lake in the world at 1620 m and containing some 1200 animal species of which over 80% occur only in this lake.

Volcanic activity creates waterbodies in several ways. When material is ejected upward to create a void, or after released magma cools and distorts, depressions form and may fill with water. **Caldera lakes** occupy collapsed volcanic craters (Figure 2.12b) left after the magma has flowed out. Other waters form in **maars** derived from subterranean explosions that create low rims but leave little cinder or laval material. Maar lakes in the Red Rock area near Alvie, Victoria, are spectacular examples of multiple explosion craters from volcanic activity some 6000–12 000 years ago. **Coulee lakes** are made by laval impoundment, usually by molten material flowing across a river. An Australian example of a caldera lake formed through a volcanic vent is Lake Mumblin, western Victoria, and this is Australia's roundest lake (Timms 1992). Lake Purrumbete near Camperdown in Victoria and Blue Lake near Mt Gambier in SA (Figure 2.12b) exemplify maar lakes, and are major tourist attractions.

Landslide lakes occur when landslides dam rivers or leave hollows in mountain sides that fill with water. Lake Tali Karng (Figure 2.12c) in the Victorian highlands is a landslide lake of 16.2 ha with a maximum depth of 51 m. Glacial activity has also played a role in the formation of a number of deep Australian lakes. **Cirque lakes** form in the upper portion of ice-scoured glaciated valleys (Figure 2.12d) where freezing and thawing hollow out rounded structures called cirques. These include Blue Lake near Mt Kosciuszko and many Tasmanian lakes (e.g. Dove Lake, Cradle Mountain). **Kettle** or **pit lakes** derive from melted blocks of ice left behind by a glacier, and also abound in Tasmania. **Moraine lakes** form where streams have been impounded by the glacial moraine deposited as the ice scours channels between the mountains. At the lower end of a glacier, a 'dam' of rubble accumulates as the ice bulldozes and abrades the rock material below and alongside. When the glacier melts, an elongate lake can be held behind the dam. Lake St Clair in Tasmania is Australia's deepest natural lake (>170 m) and formed in a valley scoured by a glacier.

Finally, some of our deepest waterbodies have been built by humans to serve as water storages or reservoirs (e.g. Gordon Dam, Figure 2.12e). Physical processes within these artificial waters usually resemble those in nearby natural ones of similar depth and shape. Most of them stratify for much of the year and hypolimnetic water may be of low quality and require careful management (Chapter 11).

2.8.2 How shallow standing waters form

The arid climate and flat topography across much of the continent (Section 1.5.4) mean that most of our standing waters are shallow (<3 m). In contrast to the tectonic or glacial origin of many deep waterbodies, most shallow waters form from the interaction of wind and geomorphology with water (rainfall, surface runoff, river flow or groundwater). Other types of shallow lentic environments are created by organisms, including humans.

In arid and coastal regions, wind may redistribute broken rock or sand to create **dune lakes** (Figure 2.13a) that either form behind the dunes (dune contact lakes) or where the groundwater table is high enough to create a 'window' lake between the dunes. **Perched lakes** also are common in these areas and occur where organic input from vegetation helps create an impervious bed of organically bonded sand-rock (Figure 2.13a). Lake Boomanjin on Fraser Island, Queensland, is reputedly the largest perched lake in the world. Iron and aluminium leaching through the soil profile beneath the lake bind with organic materials (colloids) to produce a 'coffee rock' layer that helps seal the bed.

Across much of the arid interior, wind can erode almost horizontal strata, often piling the material in crescent-shaped mounds (lunettes) downwind, and creating **claypans** or **playas** (Figure 2.13b). These shallow waters fill during rain and are typically ephemeral (Table 1.2). They may become more saline as the water evaporates and many inland salt lakes have formed this way (Timms 1992).

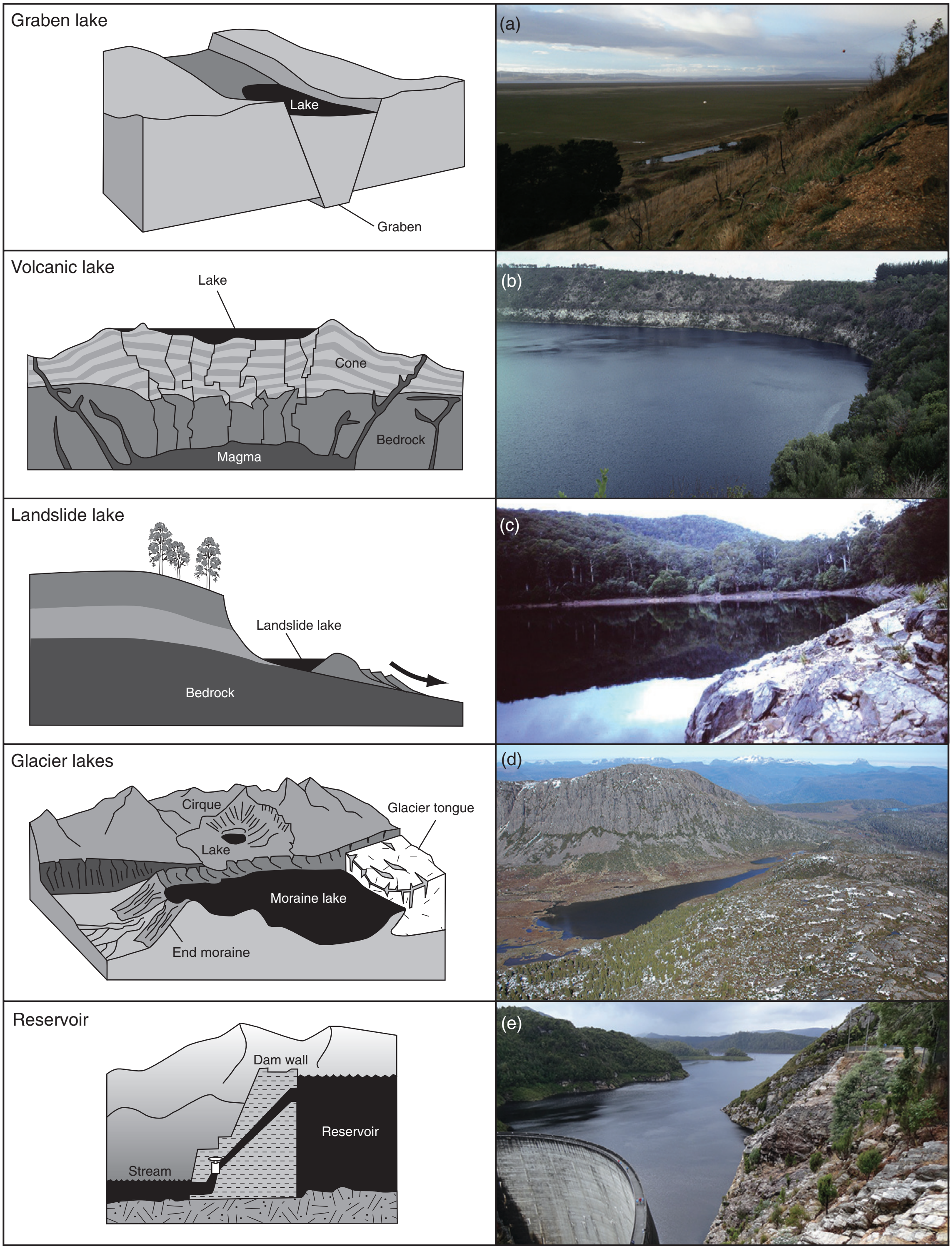

Figure 2.12 Modes of formation and examples (named in brackets) of several types of deep waterbodies in Australia: (a) graben lake (Lake George, NSW); (b) volcanic lake (Blue Lake, Mt Gambier, SA); (c) landslide lake (Lake Tali Karng, Victoria); (d) glacier lakes (Walls of Jerusalem National Park, Tasmania); (e) reservoir (Gordon Dam, Tasmania). (Source: (a) Ian McCallum, (b) Belinda Robson, (c) Diagram of landslide lake modified and reproduced with permission from J. David Rogers; Image: Ian Campbell, (d) Jenny Davis, (e) Margaret Brock.)

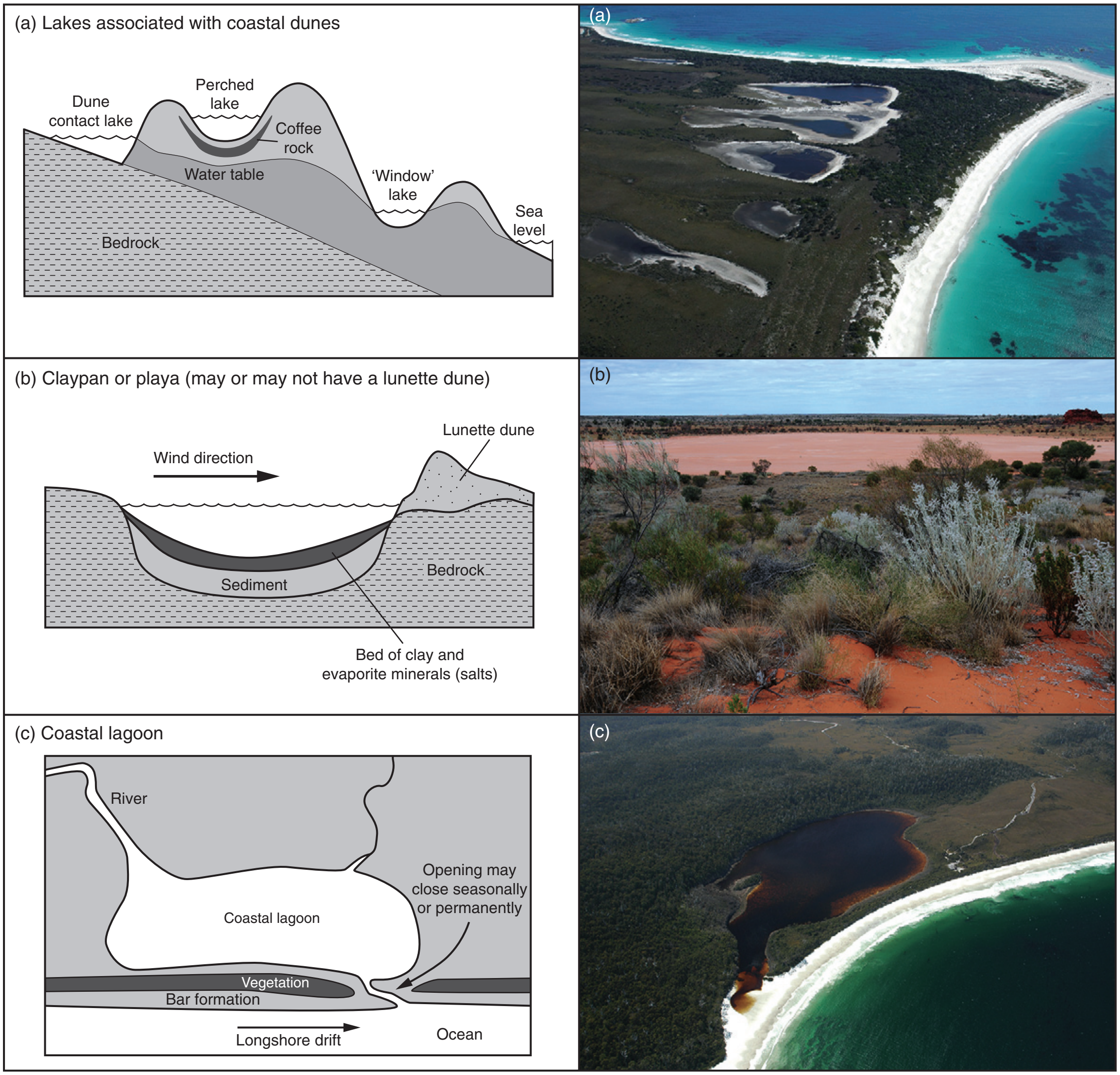

Figure 2.13 Modes of formation of several types of shallow waterbodies in Australia: (a) lakes associated with coastal dunes; (b) claypans and playas; (c) coastal lagoon. The formation of billabongs (ox-bow lakes) is described in Section 5.7.5. (Source: Diagrams (a) and (b) modified and reproduced with permission from Tracey Saxby, Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/imagelibrary/). Images: Jenny Davis.)

Irregularities along the coastline may create an opportunity for a bar to form across the concavity, sealing off a new waterbody. Long shore drift of sand forms bars across many estuary mouths (especially on the south coast) and can create **coastal lagoons** (Figure 2.13c) until increased discharge down tributary rivers caused by winter rains washes the bars away. Over time, with declining or negligible river flows and the continued accumulation of sand through coast-building processes, sandbars may become permanent. The Tuggerah Lakes in NSW are good examples of cut-off coastal embayments.

Shallow depressions can arise where deposits of soluble rock are dissolved by percolating water. Most commonly, this is the solution of limestone (calcium carbonate) by slightly acidic water containing carbon dioxide (Chapter 3) and typically produces circular basins. However, not all **solution basins** are formed by water percolating downwards; some examples such as Ewens and Piccaninnie Ponds near Mt Gambier probably formed through the action of upwelling water (Timms 1992). Even granite can be dissolved by acidic water, especially along joints, to form shallow pools known as **gnammas** (Box 4.9, Bayly *et al.* 2011).

Many shallow standing waters (as well as some deeper than three metres) form through river activity (Chapter 5). When flow ceases, pools along the river course or at the base of dry waterfalls often persist. In lowland regions, shallow waterbodies may form when levee banks are deposited across the mouths of small tributaries. Sometimes, a major flood down a side-tributary can deposit enough sediment to impound the main channel and form a waterbody. Most familiar to many Australians is the **billabong** or ox-bow lake, usually created when an eroding meander on the floodplain is cut off from the main channel by deposition of alluvial material (Section 5.7.5).

Finally, many organisms create shallow waterbodies, ranging from tiny ones in pitcher plants or the perched burrow waters of 'terrestrial' crayfishes (*Engaeus* spp.) through to wallows created by introduced buffalo in northern Australia. Humans also create shallow waterbodies, including ornamental ponds, 'constructed wetlands', swimming pools and sewage treatment ponds in suburbia, and farm dams and ring-tanks in agricultural areas. This activity produces a complex mosaic of lentic environments throughout the landscape, many of them with water regimes that differ from nearby natural waters. For example, there are now over half a million **farm dams** (Figure 2.14) in Australia, making this one of our most abundant types of waterbody. These dams may provide reservoirs of biodiversity in agricultural landscapes, creating 'stepping stones' between undisturbed and modified habitats (Box 2.5, Brainwood and Burgin 2009) and partly countering the fragmentation caused by many agricultural practices.

Figure 2.14 Farm dams are scattered throughout the Australian landscape, often providing valuable reservoirs of aquatic biodiversity in agricultural regions. (Source: Meredith Brainwood.)

2.9 SYNTHESIS

The key driver of depth, interacting with the extent of light and heat penetration into the water column, governs the probability and persistence of stratification in standing waters. Depth is related to water regime (Section 1.4), and in this chapter, we have seen how water regime, depth and waterbody morphology interact to control ecologically significant physical processes in standing waters, both temporary and permanent. We have also seen how the depth, shape and size of a standing waterbody are governed largely by how it formed. For example, most natural deep waterbodies (>3 m) in Australia formed by tectonic activity whereas shallow waters (<3 m) have been formed in many different ways, ranging from wind or river activity through to the actions of organisms, including us.

Box 2.5 Farm dams: stepping stones in agricultural landscapes

In many parts of Australia, numerous farm dams are all that remain of the original waterways. Ranging from gully dams across creeklines, springs and swamps in hilly country to excavated tanks that brought permanent water to the vast semi-arid and arid plains, farm dams now provide a suite of habitats that encapsulate 'snapshots' of the original aquatic invertebrate fauna. Each dam may accommodate a different 'snapshot', and this combines with the reliable source of water to provide habitat resources for a range of flora and fauna species. In many areas, this has become broadly representative of the original fauna, except in the more arid regions where the provision of permanent water has often drastically altered the composition of native wildlife. The greatest diversity across all faunal groups occurs when at least some of the surrounding vegetation is retained. Unfortunately, best management practice of dams encourages the removal of trees to prevent structural weakening, and current water management policies promote an overall reduction in harvesting of runoff for storage in farm dams, neither of which favours their habitat potential or any resultant ecosystem services.

Meredith Brainwood, Applied Ecology Limited

In the next chapter, we explore how chemical processes in standing waters are affected by basin depth, shape and size. We especially focus on the central role of stratification and circulation in governing the distribution of nutrients, sediments and gases across multiple temporal and spatial scales in standing waters. This will then set the 'stage' for us to review the biological processes (Chapter 4) that influence and are influenced by physical and chemical processes in standing waters.

CHAPTER 3

Chemical processes in standing waters

3.1 'THERE'S A CERTAIN CHEMISTRY ...'

In Chapter 2, we saw how depth was a major driver of the type of stratification in a standing waterbody, and how the penetration of light and heat influenced not only biological processes such as primary production, but physical processes of water circulation as well. How do physical aspects such as depth, light and stratification influence chemical processes in lentic environments? What are these chemical processes and how might they be ecologically relevant to organisms living in standing waters?

This chapter reviews the major dissolved gases, ions and nutrients in Australian standing waters, and the effects of the physical processes of stratification and mixing. It explores likely interactions among physical, chemical and biological processes (Figure 3.1), and particularly focuses on how these affect reduction–oxidation (or 'redox') reactions that regulate fundamental ecosystem processes including nutrient cycling, photosynthesis and respiration. Finally, recalling our theme about the central role of water regime and its variability (Chapter 1), we discuss the effects of water regime on water chemistry, especially in temporary lentic waters (Figure 3.2).

3.2 DISSOLVED GASES

Dissolved gases are a logical starting point to examine the chemistry of standing waters, relating to our theme of vertical linkages between a waterbody, groundwater below and the air above (Chapter 1). Gases enter the water column from the atmosphere, runoff, the activity of organisms and groundwater sources (Figure 3.3). Carbon dioxide (CO_2) largely results from respiration and decomposition whereas oxygen (O_2) arises from photosynthesis; both gases also diffuse into water from the atmosphere. Methane (CH_4) is produced by anaerobic respiration, typically deep in the bed sediments. Hydrogen sulfide (H_2S), produced by bacterial and chemical transformations, is extremely soluble in water. Ammonia (NH_3) is also highly soluble, primarily occurring as ammonium (NH_4^+) at $pH < 8$, and arises from bacterial breakdown of organic matter and excretion by aquatic animals.

When any gas is in contact with water, some of it will dissolve into the water. Henry's Law states that, at a given temperature, the amount of gas absorbed by a given volume of liquid is proportional to the pressure in atmospheres exerted by the gas, and proportional to the partial pressure of the gas above the liquid (in other words, $c = \mathrm{K}\mathrm{p}$ where c is the concentration of gas (usually expressed in $\mathrm{mg\,L^{-1}}$), K is a solubility factor specific to each gas and p is the partial pressure exerted by the gas).

Henry's Law applies only for solutions where the solvent does not react chemically with the gas being dissolved. One gas that does react with the solvent (i.e. water) is carbon dioxide. This molecule is polar (Section 1.5.1) and hence much more soluble in water. In general, the solubility of gases decreases as water becomes warmer, pressure declines (such as with

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Australian Freshwater Ecology: Processes and Management, Second Edition. Andrew J. Boulton, Margaret A. Brock, Belinda J. Robson, Darren S. Ryder, Jane M. Chambers, and Jenny A. Davis.

Companion Website: www.wiley.com/go/boulton/freshwater

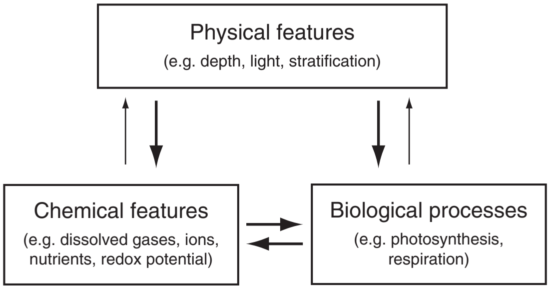

Figure 3.1 Interactions between the physical and chemical features and biological processes in standing waters. Thick arrows indicate strong effects. (Source: Boulton and Brock 1999.)

Figure 3.2 Water chemistry is strongly influenced by water regime and physical features such as depth. In shallow Lake Gwelup on the Swan Coastal Plain, WA, water chemistry changes during seasonal drying. (Source: Darren Ryder.)

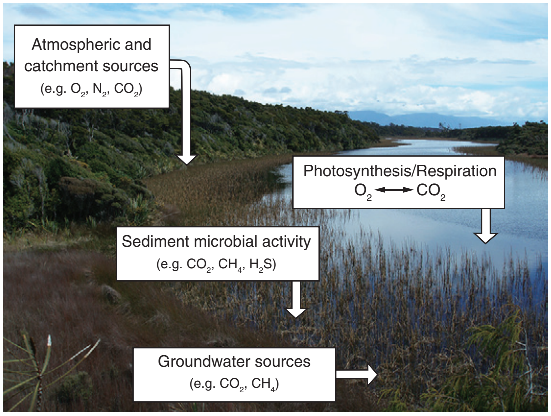

Figure 3.3 Sources of dominant gases in standing waters. (Source: Andrew Boulton.)

increasing altitude), and salinity rises. Let's now look more closely at several gases that play vital biochemical and biological roles in virtually all aquatic ecosystems.

3.2.1 Oxygen

The dominant pathway for dissolved oxygen to enter standing waters is **photosynthesis**. Simply put, in the presence of chlorophyll, light energy is used to transform carbon dioxide and water into 'sugars' and dissolved oxygen:

Photosynthesis:

$$6CO_2 + 6H_2O + \text{Energy (light)} \rightarrow C_6H_{12}O_6 + 6O_2$$

The light energy is converted into chemical energy stored within the sugar molecules. In the presence of oxygen, aerobic **respiration** releases this energy (for most metabolic processes, Chapter 4), also liberating water and carbon dioxide:

Respiration:

$$C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O + \text{Energy}$$

During photosynthesis, the water molecule is split and electrons are transferred from the water to CO_2, using solar energy to reduce CO_2 into sugar. During respiration, energy is released from sugars when electrons associated with hydrogen are transferred to oxygen (the electron acceptor), forming H_2O as a by-product. Like many biologically mediated chemical transformations, these two processes are a **paired redox reaction**: reduction (gain of an electron) in one direction; oxidation (loss of an electron) in the other. Redox pairs like these crop up repeatedly in ecologically significant chemical processes in aquatic ecosystems, and we'll see more of them later in this chapter.

The carbon dioxide and water produced through respiration renew supplies for photosynthetic organisms, and this recycling is crucial for the productivity of aquatic ecosystems. The need for light in photosynthesis means that it occurs only during the day, whereas respiration (including by photosynthetic organisms) occurs continually. The imbalance between these two processes means that dissolved oxygen concentrations often fluctuate over 24 hours, peaking during daylight hours and falling at night when oxygen is still being used during respiration.

Dissolved oxygen (DO) is commonly measured using a meter. There are two broad types: one uses a Clark electro-chemical or membrane-covered electrode whereas the other uses an optical or luminescent sensor. The main difference is that membrane sensors consume oxygen from the water to measure DO whereas optical sensors detect changes in the luminescence of oxygen-sensitive chemicals in the probe. In calm conditions, or where sensors are deployed for extended periods, the consumption of DO by a membrane sensor may provide misleading data, and one solution is to use an oscillating stirrer next to the membrane.

Concentrations of DO are usually given in $\mathrm{mg\,L^{-1}}$ despite the fact it is a gas. Often, values are reported as percentage saturation relative to the atmospheric concentration at a given altitude (pressure), temperature and salinity. When dissolved gases exceed 100% saturation, they are said to be '**super-saturated**'. Photosynthesis in a standing waterbody can generate supersaturation of oxygen, often seen as bubbles of oxygen on the bottom (Figure 3.4), rising through the water column or on the leaves of aquatic plants. Oxygen supersaturation can cause 'gas bubble disease' in fishes exposed to total dissolved gas pressures exceeding 115% for a few hours. Bubbles begin to form in the tissues (similar to the 'bends' in deep-sea divers) and eventually accumulate in the gill capillaries, killing the fish. Although diffusion of oxygen and other gases from the atmosphere into the water is extremely slow, it is a continuous process. All gases diffuse along gradients of high to low concentrations, and consequently, diffusion can also remove gases from the water.

Figure 3.4 Bubbles of oxygen produced by photosynthesis are visible on a benthic algal mat in a shallow waterbody on a windless, sunny day. (Source: Jenny Davis.)

Most decreases in DO result from respiration by plants, animals and aerobic bacteria. Organisms that use oxygen as an electron acceptor in respiration are termed **aerobes**. However, when oxygen is absent, **anaerobes** (microorganisms, primarily bacteria) can respire using alternative electron acceptors such as nitrate, iron or sulfate ions. These terms are also sometimes used to describe environmental conditions in waterbodies or sediments: **aerobic** refers to environments where oxygen for respiration is present and **anaerobic** where oxygen is absent (Section 3.7).

Chemical oxidation or mineralization (i.e. conversion to inorganic form) of organic matter, usually mediated by microorganisms, consumes large amounts of DO. The consumption of DO by all biota is termed **Biological Oxygen Demand (BOD).** Greatest BOD occurs where aerobic microbial densities are high, usually at the interface between organic sediments and the overlying water. Intensive microbial respiration coupled with periods of hot, windless weather can result in low DO. At night, when all organisms are respiring, DO concentrations are at their lowest in the water column. Late in the day, DO is high because of photosynthesis. Sometimes these daily fluctuations in DO can be extreme. For example, nutrient enrichment can cause blooms of algae that supersaturate the surface water with DO (Chapter 11). However, on windless nights, DO concentrations may plummet because all organisms, including the blooming algae, are still respiring. One approach to tackle these extremes in DO in managed standing waters is to aerate the waterbodies artificially but sometimes these methods fail because sediments, stirred up by the aeration, rapidly remove the DO instead. When DO becomes very low, aerobic organisms such as some fishes may still be able to exploit the hypoxic habitat by 'bounce diving' (Box 3.1).

Other decreases in DO are caused by dissolved materials. For example, in saline water with a salt

Box 3.1 Dissolved oxygen and available habitat

In coastal lagoons and estuaries, the lack of oxygen can be deadly (Becker *et al.* 2009). Thus, we deduce that aerobic animals will not go where oxygen is low. But is this always true? Such environments are usually stratified, with low dissolved oxygen in the deeper waters. General wisdom suggests these deeper waters exclude oxygen-dependent species (e.g. fishes). Consequently, habitat availability may depend on an organism's capacity to tolerate low dissolved oxygen. In the Glenelg Estuary, western Victoria, depth varies between 10 and 15 m, and the water column is frequently stratified at ~2 m. If depth along the first 50 km of the estuary averages 12.5 m, this implies that, at times, only 16% of the water column is usable by oxygen-dependent species. Can mobile aerobic organisms somehow exploit the huge remaining percentage of hypoxic habitat? Using baited video and acoustic tracking data, our unpublished studies indicate that black bream *Acanthopagrus butcheri* 'bounce dive' into hypoxic regions to feed. We are not sure how widespread this behaviour is and work continues. However, perhaps there is more habitat available to some mobile aerobes than we first thought.

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concentration of 260 mg L^{-1} (7 times seawater), DO at 20°C is less than 2 mg L^{-1} whereas in fresh water at 20°C, DO is approximately 9 mg L^{-1}. Concentrations of DO below 2 mg L^{-1} are critically limiting for many animals (particularly fishes), and this exemplifies how chemical features may govern the distribution of biota (Chapter 4).

Most dissolved oxygen in lentic environments originates from photosynthesis and atmospheric inputs. Below the euphotic zone in a stratified waterbody (Chapter 2), the hypolimnion is isolated from these sources of DO. Instead, respiration and decomposition processes predominate and oxygen is consumed. Conversely, when the waterbody mixes, both temperature and DO are distributed uniformly throughout the water column. Plotting DO against depth for these well-mixed waters produces a nearly straight line, termed an **orthograde oxygen curve** (Figure 3.5a). This curve typifies waterbodies with low nutrient inputs and low rates of organic matter production. When thermal stratification occurs, algae in the epilimnion (upper layer) produce DO, replenishing that consumed. Meanwhile, in the hypolimnion (lower layer), DO is consumed but not produced. This yields a nonlinear vertical profile of DO, a **clinograde oxygen curve** (Figure 3.5b). Clinograde oxygen curves are common where nutrient inputs and organic matter production are high, highlighting the role of biological processes such as photosynthesis and respiration in regulating DO. The key point is that the physical process of stratification influences the vertical distribution of dissolved gases (in this case, oxygen) that, in turn, reflects and affects the distribution of organisms in standing waters (Box 3.2).

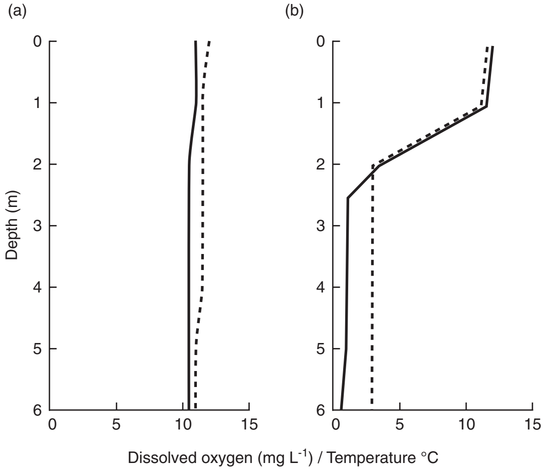

Figure 3.5 Vertical profiles of oxygen (solid lines) and temperature (dotted lines) may either be (a) orthograde (straight) or (b) clinograde, depending on the presence of stratification. (Source: Boulton and Brock 1999.)

Box 3.2 Thermal stratification and plankton distribution in water supply reservoirs

Thermal stratification is common in many lakes, reservoirs and rivers. In deep waters with high transparency, phytoplankton distributions may be skewed away from the surface, creating layers of phytoplankton at intermediate depths across thermal layers and at relatively low light levels. Phytoplankton in these productive layers include non-motile diatoms and buoyancy-regulating cyanobacteria. Water clarity primarily drives the formation and depth of these layers, but vertical nutrient distributions may also be important because the stratified layers intercept the upward and downward fluxes of nutrients. Hamilton *et al.* (2010) identified maximum phytoplankton concentrations at depths closely correlated with euphotic depth in several deep volcanic lakes, suggesting that the depth of light penetration, rather than nutrient availability, largely dictated the depth of phytoplankton production during periods of thermal stratification. Reduced water clarity during eutrophication shifted vertical phytoplankton distribution from a deep layer up to the surface mixed layer when the depth of the euphotic zone was consistently shallower than the depth of the upper mixed layer. Therefore, trophic status also plays a role in determining vertical distributions of phytoplankton in these deep lentic environments.

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3.2.2 Carbon dioxide

Carbon dioxide is another ecologically significant dissolved gas in aquatic systems. Earlier, we saw that it is essential for photosynthesis. Dissolved carbon dioxide also regulates the pH of many natural waters and is responsible for the dissolution of major ions such as Na^+, Ca^{2+}, Mg^{2+}, Cl^- and SO_4^{2-}, without which aquatic life would not be able to exist. Although there is relatively little CO_2 in the atmosphere (<0.05 %), high concentrations occur in natural waters because the polar CO_2 molecule is highly soluble (over 10 times more than oxygen). Rainwater accumulates dissolved CO_2 as it falls, and may pick up even more as it trickles over calcareous sediments or organic soil. Plant and animal respiration and aerobic bacterial decay processes contribute further amounts.

When CO_2 is dissolved in water, a small amount (<1 %) is hydrated to form **carbonic acid** (H_2CO_3). Some of this acid then dissociates into **bicarbonate** (HCO_3^-) ions and hydrogen ions (H^+), lowering the pH (i.e. making the water more acidic). By the time the pH of a standing water body has dropped to 4.3, almost no bicarbonate ion is left (Figure 3.6). When pH increases, carbonic acid begins to dissociate, and by pH 8.3, there are only bicarbonate ions and virtually no H_2CO_3 or gaseous CO_2 left (Figure 3.6). Increasing pH further causes the bicarbonate ion to dissociate, producing H^+ and **carbonate** (CO_3^{2-}) ions. Thus, carbonic acid has the potential to dissociate twice, depending on the pH of the waterbody.

Most natural waters contain carbonic acid and one of its salts, acting as a **buffer solution**. A buffer solution is a one that resists changes in pH when acids or bases are added, and is usually either a weak acid or weak base together with a dominant salt. A strong base added to water will react with carbonic acid to form a bicarbonate salt (e.g. $CaCO_3$) and eventually the carbonate, using up the base in the process (Figure 3.6). Conversely, adding acid to water converts carbonate to bicarbonate and finally to undissociated carbonic acid.

The buffering capacity of water is measured as **alkalinity**, an unfortunate term that has little to do with high pH but instead reflects how many hydrogen ions are neutralized by a given volume (Wetzel and Likens 2000). Some waters are well buffered and resist changes in pH (e.g. some billabongs in the Murray-Darling Basin, Klein *et al.* 2010). Others are poorly buffered, and include waterbodies on sandstone or granite surfaces. Tannin-stained waters are moderately acidic and contain little carbonate and few dissolved salts. This results in a low buffering capacity and pH fluctuates daily from changes in CO_2 in response to diel variations in photosynthesis. Dissolved CO_2 can also fluctuate seasonally, driven by seasonal changes in primary productivity, evaporation and groundwater

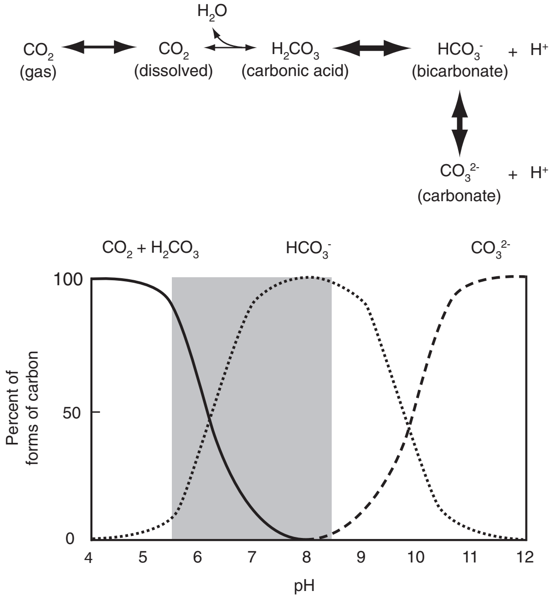

Figure 3.6 Dissociation of the forms of CO_2 and their theoretical relative proportions with respect to pH. The larger the arrow, the faster the reaction. The shaded area encompasses the pH range of most inland fresh waters in Australia, indicating that bicarbonate ions generally predominate over other forms of carbon. (Source: Boulton and Brock 1999.)

inflow, as seen in some standing waters in tropical Australia (Mackay *et al.* 2011).

3.2.3 Hydrogen

In water, hydrogen occurs primarily as the ionic form H^+; only minute amounts exist as the gas H_2. Water is a weak electrolyte so a small proportion of the H_2O molecules dissociates to form OH^- and H^+ ions. The concentration of ionic H^+ is termed pH and is expressed on a log scale ($pH = -\log[H^+]$). As pH is expressed on a logarithmic scale, a common error is to compute an arithmetic mean of two or more pH values. The average of a pH of 4 and of 6 does not equal pH 5! Instead, one must either compute a geometric mean or take anti-logs, calculate the mean, and then take the logarithm of that mean value to transform it back to the log-scale for pH. Knowing this, what is the true average of pH values 4 and 6?

Neutral water (that is, neither acidic nor alkaline) has a pH of 7. Lower values indicate acidity whereas high pH implies the water is basic (i.e. alkaline). Although pH can be measured approximately using specially treated paper strips that change colour in solutions of different acidity (akin to 'a litmus test'), it is usually measured using a pH meter. These often have fragile glass probes that must be kept wet when not in use, and it is wise to frequently calibrate the meter with at least two solutions of known pH (usually standard buffer solutions of about pH 4 and 10).

The major source of hydrogen ions in natural water is carbonic acid (Figure 3.6). Rainwater in equilibrium with atmospheric CO_2 has a pH of 5.6. However, in parts of northern Europe, the US and Canada, industrial emissions of sulfurous and nitrous oxides can dissolve in rainwater to form sulfuric and nitric acid, respectively. This produces 'acid rain' with a pH sometimes well below 3. Predictably, acid rain has devastating environmental consequences, partly addressed by controls on emissions (Chapter 11).

In Australia, acid rain is rare. Far more common is the problem of exposure of **acid sulfate soils**. Drainage, mining or land-clearing on these sorts of soils often causes severe declines in pH (Chapter 11). Acid sulfate soils in Australia occur naturally, and are generally low-lying floodplain or coastal soils that contain high concentrations of sulfide minerals (mainly pyrite, FeS_2) below a shallow water table. Undisturbed, the sulfides in these soils are relatively harmless, but problems arise when changes to the water regime expose the waterlogged soils to oxygen (Hall *et al.* 2006). During drying and exposure to air, sulfidic sediments oxidize and produce sulfuric acid, which may exceed the buffering capacity of the waterbody when it is rewetted, resulting in a pH often less than 4. Metallic cations such as Al^{3+}, Fe^{2+} and Fe^{3+}, as well as other elements such as As, become mobilized by the acid. Impacts from persistent changes to water chemistry on aquatic organisms can range from sub-lethal to devastating (Box 3.3), and may persist for decades. For example, in tropical northern Australia, fish and crustacean populations in wetlands exposed to an acid mine drainage spill in the 1970s remain affected nearly 40 years later (Russell *et al.* 2011).

Many lentic waters in Australia are naturally acidic, reflecting a combination of the flat landscape (Chapter 1), nutrient-poor soils and abundant native plants capable of leaching soluble acids. These acidic waters include swamps, heathlands and peatlands supporting

Box 3.3 Effects of anthropogenic acidification on aquatic ecosystems

Mining and other disturbances by humans of sulfidic rocks and soils can decrease waterbody pH and increase concentrations of solutes (e.g. zinc) and metalloids (e.g. arsenic). Low pH may also mobilize biologically important calcium and magnesium. This anthropogenic acidification of waterbodies often impairs aquatic ecosystem function and biodiversity. Aquatic macroinvertebrates are particularly sensitive to anthropogenic acidification, as well as to the reduction in habitat quality that occurs when precipitates smother the substrate (Figure 3.7). Even biota tolerant of naturally acidic conditions can be adversely affected through disturbances to the broader food web. For example, McCullough and Horwitz (2010) found that phosphorus, an essential nutrient for primary producers, may precipitate with aluminium and iron-oxyhydroxide, decreasing rates of primary production. Bioaccumulation and bioconcentration (defined in Section 11.6.2) of many chemical elements may cause toxicity at higher trophic levels, fundamentally changing food web structure. High concentrations of toxic solutes and metalloids may even pose a risk to human health either directly (e.g. body contact while swimming, Hinwood *et al.* 2012) or indirectly, when consuming fishes and crayfishes (McCullough and Lund 2006).

Clint McCullough and Melanie Blanchette,
Edith Cowan University

Figure 3.7 Acid and metalliferous drainage from coal mines in south-western WA. (Source: Clint McCullough.)

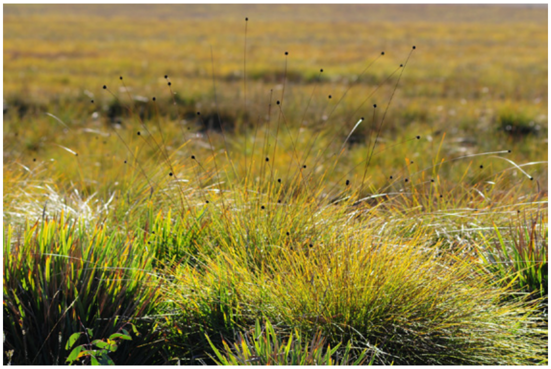

Figure 3.8 Button grass *Gymnoschoenus sphaerocephalus* grows on damp, nutrient-poor, acidic peats such as here in western Tasmania. (Source: Jenny Davis.)

specialized plants (Figure 3.8) and animals tolerant of low pH. Most swamps receive high inputs of benthic organic matter that leach fulvic and humic acids into the poorly buffered water column, turning the water brown and lowering the pH (Whinam *et al.* 2003). In parts of central and western Victoria, there are volcanic lakes that are acidic because of the oxidation of abundant sulfide compounds derived from local weathering. In coastal areas, standing waters usually derive H_2S from microbial decomposition of the benthic organic matter while naturally occurring pyritic soils may also contribute to the production of sulfuric acid.

3.2.4 Methane

Methane (CH_4) is a gas commonly produced by microbial metabolism. **Methanogenesis** (i.e. methane production)

Box 3.4 Methanogenesis and methanotrophy

In freshwater ecosystems, the terminal process of carbon metabolism is undertaken by a group of bacteria called methanogens. These are members of the Archaea – prokaryotes that are obligate anaerobes rapidly killed by exposure to oxygen. They derive their energy by creating methane (i.e. methanogenesis). In the sediments of some floodplain wetlands in north-eastern Victoria, methanogenesis accounted for 30–60% of the total carbon flow. The methane produced by methanogenic bacteria is not always lost from a wetland as gas. Interestingly, a small group of bacteria called chemolithotrophic bacteria can use reduced inorganic compounds such as methane as their source of energy. One important type of chemolithotrophic bacteria in wetlands is the methanotrophs. They obtain their energy by oxidizing the methane produced by methanogens in the sediments. Methanotrophs use oxygen to oxidize methane. Consequently they are obligate aerobes and are limited to the epilimnion or oxic regions of the sediments. They rely on upwards diffusion of methane produced in anaerobic sediments by the methanogens. In doing so, they limit the transfer of this greenhouse-active gas to the atmosphere from natural (e.g. billabongs) and artificial (e.g. rice paddies) wetlands.

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occurs in anoxic environments because methane production is the final step of decomposition in the decomposition of carbon (Box 3.4). Methanogens are microbes that are obligate anaerobes and cannot exist in an oxygenated environment. In most cases, they use CO_2 and H_2 to produce methane, a highly flammable, odourless and colourless gas that may be generated in such quantities that it bubbles up from the sediments. Natural standing waters generate 20–39% of global methane emissions, and contribute substantially to atmospheric greenhouse gases (Parry *et al.* 2007). Atmospheric methane concentrations are very low (around $2\,mg\,L^{-1}$) but are rising at about 1% per year from human activities. This is a concern because methane is a potent greenhouse gas that contributes to climate change (Chapter 12).

Methane enters the atmosphere via three pathways: bubbling, molecular diffusion along the concentration gradient (from high in the sediments to low in the atmosphere) and movement through aquatic plants. Emergent aquatic plants such as *Typha* and *Phragmites* play several roles in the emission of methane to the atmosphere. Firstly, they produce the detrital organic matter necessary for the production of methane. Secondly, they facilitate the release of methane through internal gas flow systems. Emergent plants commonly grow in oxygen-limited conditions and have hollow or porous stems that transport oxygen to the underground parts of the plants such as the roots (Chapter 4). Where oxygen escapes through pores from the plant into the root zone, methane can enter the stem air spaces and subsequently be transported to the atmosphere. The flux through emergent plants can account for up to 70% of the total methane flux into the atmosphere from standing water bodies. Concentrations of CH_4 in standing waters often exceed those of oxygen. For example, in some Australian billabongs, methane in sediments often exceeds $20\,mg\,L^{-1}$ whereas water column DO reaches only $15\,mg\,L^{-1}$. As CH_4 is produced in the sediments, where oxygen is limited, its depth profile mirrors that of DO (Ford *et al.* 2002).

Not all methane produced in the sediments reaches the atmosphere. Methane is highly soluble in water and becomes the prime energy source for **methanotrophic** bacteria, obligate aerobic microorganisms limited to the oxygenated regions of the water column and sediment such as the water-sediment interface and around plant roots or animal burrows. Methanotrophic bacteria use methane from the sediments as an energy source for respiration, 'burning' CH_4 with oxygen to obtain enough energy to fix CO_2. They abound where methane is in high concentrations and their metabolism can cause major changes to DO concentrations in the water column of some lakes (Page and Dalal 2011).

Methanotrophs oxidize much of the methane produced deeper in the sediments, and limit the transfer of this greenhouse gas to the atmosphere. Boon (2000) calculated that methanogenesis accounted for up to 60% of the total carbon flow in several wetlands in north-eastern Victoria (Box 3.4), providing a vital resource at the base of the food web. This methane supports a substantial biomass of methanotrophic bacteria in habitats accessible to microbial and invertebrate grazers that then become food for higher trophic levels. Rates of methane production are highly variable in space and time, and can range over three orders of magnitude, regulated by waterbody permanence and type, temperature and latitude (review in Laanbroek 2010).

3.3 SOURCES OF IONS

The chemistry of the water is strongly influenced by the ions in it. An ion is simply an atom or a group of atoms that has an electric charge. Positive ions, referred to as '**cations**', are formed by the loss of electrons; negative ions, termed '**anions**', have gained electrons. Concentrations of ions and metals in lentic environments vary, owing to differences in climate, geography, catchment topography and land use, biotic activity, time and the interactions among these variables. Although absolute concentrations of an ion may be minute, they can still be vital to many ecosystem processes. Therefore, as aquatic ecologists, we must understand the sources, transformations and roles of ions in water.

Ions enter inland waters from the atmosphere, catchment and groundwater (Figure 3.9). Dust storms can import huge amounts of material into arid-zone waters, sometimes from far away. Catchment runoff carries ions into most temperate and tropical waters but in some parts of Australia, saline groundwater of marine origin can be a significant source of ions too. For example, saline marine intrusion into the Burdekin River floodplain in northern Queensland arose from excess shallow groundwater extraction, changing the ionic composition of floodplain waterbodies towards that of saline marine water (Narayan *et al.* 2007). Where surface and groundwaters exchange, geochemical gradients occur that transform the ionic composition of water of both water sources (Hancock *et al.* 2005, Chapter 8).

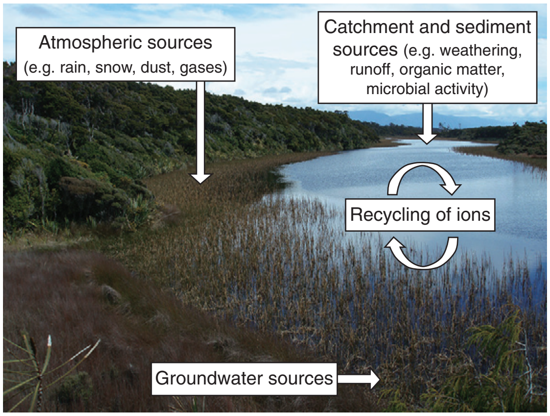

Figure 3.9 Potential sources of ions in natural waters. (Source: Andrew Boulton.)

3.4 IONIC COMPOSITION OF AUSTRALIAN STANDING WATERS

It has long been known that the mysterious recipe for 'world average fresh water' does not apply to Australian inland waters (Bayly and Williams 1973). In general, most waters in Australia, especially those with high conductivities, are dominated by sodium and chloride (Table 3.1) whereas calcium and carbonate dominate 'world average fresh water'. Sea spray provides sodium, magnesium, chloride and sulfate to coastal lentic waters whereas many central Australian salt lakes probably derived their salts from relict marine deposits or atmospheric inputs over millennia (Timms 2005). Those salt lakes whose chemistry deviates from the norm of sodium-chloride domination probably gained their ions from weathering of certain rock strata or from evaporative concentration and selective precipitation of particular salts. When talking about salinity, remember that salinity is defined as the concentration of all dissolved salts (i.e. the sum of all ionic concentrations) and not just sodium chloride. There are many ways to express concentrations of ions (Box 3.5) and although these can be confusing at first, you will see each way has its benefits.

3.5 CONDUCTIVITY, SALINITY AND TOTAL DISSOLVED SOLIDS

Before discussing some of the common anions and cations in inland waters, it is useful to describe how to

Table 3.1 Chemical composition of some Australian standing waters compared with unpolluted 'world average fresh water' and 'world average sea water'. Salinity is in grams per litre (converted from parts per thousand where necessary) and ionic concentrations are in milliequivalent percentages of total cations or total anions (meq %) (Box 3.5). The dominant cation and anion in each waterbody are in bold type. Sources are: 1 = Bayly and Williams 1973; 2 = Williams and Buckney 1976; 3 = Williams 1983; 4 = Williams 1975; 5 = Bowling *et al.* 1993; 6 = Williams *et al.* 1970; 7 = Buckney and Tyler 1973; 8 = Timms 1998; 9 = Bekele 2006; 10 = Woods 1995).

Location and waterbody	Salinity (g L^{-1})	Na$^+$	K$^+$	Mg^{2+}	Ca^{2+}	Cl$^-$	SO$_4^{2-}$	HCO$_3^-$	Source
'World average fresh water'	<3	16	3	18	**63**	10	16	**73**	1
'World average sea water'	35	**77**	2	18	3	**90**	9	<1	1
Oaklands, SA	359	**72**	2	25	<1	**95**	5	<1	2
Weering, Vic.	213	**85**	1	11	<1	**96**	4	<1	3
Eyre, SA	115	**96**	<1	1	2	**97**	3	<1	4
Grace, WA	60	**86**	1	11	2	**94**	5	<1	3
Wyara, Qld	56	**97**	<1	<1	<1	**96**	3	<1	8
Corangamite, Vic.	39	**86**	1	13	<1	**95**	1	4	4
Werowrap, Vic.	39	**95**	4	1	0	**66**	0	34	3
Gungil Billabong, NT	15	**65**	15	12	8	**67**	7	26	10
Magela floodplain, NT	10	**65**	13	11	11	**80**	<1	19	10
Cooloongup, WA	10	**71**	2	27	<1	**87**	5	7	2
Leake, SA	2	**74**	2	20	4	**75**	8	17	3
Gibbs, Tas.	1	**78**	2	16	4	**91**	9	<1	5
Gnangara, WA	0.9	**76**	2	20	2	**90**	6	4	2
Malta Lake, NSW	0.8	**70**	4	19	7	20	12	**67**	6
Swan Coastal Plain, WA	0.44	**97**	<1	<1	<1	**96**	3	1	9
Blue Lake, SA	0.4	**43**	2	31	24	**49**	2	**49**	1
Barrine, Qld	0.05	30	5	**46**	19	35	0	**65**	3
Woods, NT	0.05	10	11	**75**	4	7	19	**74**	3
Boemingen, Fraser I., Qld	0.04	**78**	2	17	3	**86**	15	0	1
Pedder, Tas.	0.04	**54**	3	23	20	**79**	15	6	7
Gordon Lagoon, Tas.	0.02	**67**	2	15	15	**93**	7	0	5
Great Lake, Tas.	0.025	18	<1	**62**	20	40	**50**	10	4
Rowallan, Tas.	0.026	25	4	25	**46**	34	4	**62**	7
Cootapatamba, NSW	0.003	**70**	8	10	12	**37**	30	33	6

Box 3.5 Some chemical terminology

Grams per litre (g L^{-1}), parts per thousand (ppt or ‰), milligrams per litre (mg L^{-1}) and parts per million (ppm) by weight are equivalent ways to express concentrations of ions in water, assuming one litre of water weighs 1 kg. However, when mineral concentrations exceed about 7 ppt, as in many saline lakes, we must adjust for the change in density of the solution (i.e. ppt = g L^{-1} ÷ specific gravity). Millimoles per litre (mmol L^{-1}) is the weight in mg divided by the molecular weight (MW). Hence, 12 mg of CO_2 per litre is 12 ÷ 44 (where 44 is the MW of carbon dioxide) or 0.272 mmol L^{-1}. This is considered by chemists to be the best terminology to use. More traditional is the expression 'equivalent' used to define the weight of the ion taking account of its charge. Thus, milliequivalents per L is mg L^{-1} of ion divided by its 'equivalent weight' (i.e. MW ÷ valency). The equivalent weight of Ca^{2+} is 40.08 ÷ 2 = 20.04. In 1 g of Ca ions, we have 1 ÷ 20.04 = 0.0499, or, if we multiply by 1000 to get milliequivalents, 49.9 meq. Using equivalents allows us to add up positive and negative charges to check they match (e.g. Table 3.1). This cannot be done if the simple mass units (such as mg L^{-1}) are used.

measure their concentrations, and to distinguish **conductivity** (or specific conductance) from **salinity** and the concentration of **total dissolved solids**. Ionic concentrations can be measured down to below one part per trillion using inductively coupled plasma mass spectrometry (ICP-MS), a highly sensitive but expensive and laboratory-based method. Concentrations of individual cations are measured using ICP-MS whereas anions are generally measured colorimetrically or turbidimetrically, using a spectrophotometer. Most ecologists are more interested in just an estimate of salinity rather than the exact proportions of all the ions and so they usually use a field conductivity meter. This method measures the flow of electrons in water between two platinum electrodes set a fixed distance apart, expressing the conductance in units per cm at a given temperature (e.g. $\mu S\,cm^{-1}$ or $mS\,cm^{-1}$ at 25°C). The higher the salt concentration, the more easily electrons pass through the water. The capital S stands for Siemen and is the SI unit of conductance. You will also see reference to electrical conductivity or EC units ($1\,mS\,cm^{-1} = 1$ EC).

Salinity can also be expressed as $mg\,L^{-1}$ and, as a general rule, a water sample with a sodium-chloride salinity of $1\,mg\,L^{-1}$ is equal to $0.64\,mS\,cm^{-1}$. However, take care when using this conversion as it cannot be applied to all aquatic systems, especially those with high concentrations of dissolved organic matter such as humic and fulvic acids. Consequently, the terms 'salinity' and 'conductivity' should not be used interchangeably because organic acids contribute to the conductance of water but not the salinity.

Total dissolved solids (TDS) is exactly that. Measuring it is simple but tedious. A filtered water sample (about 100 mL) is dried in an oven at 105°C until a constant weight is achieved. This TDS estimate includes salts and organic residues. By combusting the filter paper and residue at 550°C, one is left only with the inorganic ash, representing the total salt content of the water because it is assumed that the organic matter is burnt off as CO_2 (Wetzel and Likens 2000). TDS is often similar to salinity. For example, seawater has a TDS close to 35 parts per thousand. However, in some inland waters, much of the TDS may be the organic fraction that is burnt off during combustion of the sample, resulting in a poor relationship between salinity and TDS. A little confusingly, TDS is sometimes used to mean 'total dissolved salts' in which case it is equivalent to salinity. Our advice is to spell out your use of salinity, conductivity and TDS and beware of its loose use in some literature.

3.6 IONIC COMPOSITION AND TROPHIC STATE

Most standing waters in Australia are dominated by very different combinations of anions and cations from those of the world average fresh waters (Table 3.1). The dominance of chloride, carbonate and sulfate anions and sodium, calcium and magnesium cations provide a water chemistry that influences ecosystem processes and the ecology of aquatic life in standing waters (Chapter 4). Further, the prevalence of temporary waterbodies means that concentrations of anions and cations can change dramatically over space and time. Knowing the distribution, variation and environmental chemistry of some of the common ions helps us understand their influence on aquatic biota.

Many of these ions are nutrients whose concentrations control the amount of aquatic plant growth if other factors such as light are not limiting photosynthesis. Waterbodies can be classified by their **trophic state** according to their plant productivity. Low concentrations of nutrients frequently typify **oligotrophic** systems, which generally have limited plant growth, whereas excessive nutrients promoting abundant plant production are **eutrophic**. You might also come across the term **mesotrophic**, which applies to intermediate levels of nutrient and production. Many Australian inland waters have high concentrations of dissolved carbon that stain the water tea-coloured, restricting light penetration. These waters, often called **dystrophic** or humic systems, may have high concentrations of nutrients but plant growth is limited by the low light.

3.6.1 Some common anions

Chloride is usually the most common anion in Australian inland waters (Table 3.1), and is the dissociated form of molecular chlorine (Cl_2), a gas. Usually, chloride combines with sodium to form NaCl (common table salt) but sometimes it combines with magnesium to form $MgCl_2$ (magnesium chloride). So-called 'cyclic chloride' comes from evaporites. These are minerals that form by coming out of solution when seawater or the waters of large lakes evaporate and are readily dissolved into solution on rewetting. Cyclic chloride primarily travels in rain, attached to dust or as sea spray. 'Juvenile chloride' is found in water newly released from minerals or dissolved in igneous rock and adds to the load of chloride (and potential salt) in a waterbody.

Chloride ions that have accumulated in aquatic plants form complex molecular compounds during decomposition, leading to their storage in organic sediments. Keppler and Biester (2003) documented global peat deposits with up to 0.2% by dry mass of chloride ions, and estimated approximately 280–1000 million tonnes of organically bound chlorine are currently stored in peatlands throughout the world.

Carbonate, the most abundant anion in 'world average freshwater' (Table 3.1), occurs most often as bicarbonate and with calcium as $CaCO_3$ (e.g. calcite). A major source of carbonates in freshwater systems is the weathering of limestone, a sedimentary rock composed of calcite and aragonite. Calcite is found generally in littoral (shallow near-shore) sediments where mollusc shells accumulate. Other common forms of carbonate are magnesite ($MgCO_3$) and dolomite ($CaMg(CO_3)_2$). Soda or alkali waterbodies have large amounts of Na_2CO_3 and less soluble $NaHCO_3$, and contain a specialized biota that includes some cyanobacteria, certain zooplankton and a few insects. However, these systems are uncommon in Australia.

One of the most intriguing forms of calcium carbonate in aquatic systems occurs in stromatolites (Greek for 'stony cushion'). These are structures up to a metre tall made from deposition of $CaCO_3$ by cyanobacteria (Figure 3.10). Cyanobacterial cells can secrete a sticky film of mucus that traps sediment, with calcium carbonate precipitated from the water cementing the grains to the structure. In several coastal lakes in Western Australia, there are stromatolites that are constructed by the precipitation of calcium carbonate alone. The water in these lakes can range from saline to fresh, with the source of carbonates being mainly groundwater seepage.

Figure 3.10 Stromatolites in a standing water rich in carbonates in south-western Australia. These rings are approximately 60 cm in diameter. (Source: Jenny Davis.)

Sulfate is the second most common anion in 'world average freshwater' and in seawater. Elemental sulfur oxidizes to various forms as SO_2, SO_3^- and SO_4^{2-}. Sulfate (SO_4^{2-}) can originate from sea spray and coastal rain (seawater can contain over $2.7\,g\,L^{-1}$ of sulfate), and from the weathering of relict marine sediments in inland waters where calcium sulfate ($CaSO_4$) was deposited when these areas were covered by vast inland seas. Under oxygenated conditions, sulfate combines with hydrogen to form sulfuric acid (H_2SO_4) which, as we saw earlier, lowers the pH and can cause serious problems. Human activity now contributes over twice as much SO_2 than natural emissions, especially via coal burning, copper and nickel smelting, and pulping wood to make paper, contributing to the anthropogenic acidification of many aquatic systems (Chapter 11).

One form of sulfur commonly encountered is hydrogen sulfide or 'rotten egg gas'. Bacteria in the anoxic sediments of standing waters reduce sulfates to produce hydrogen sulfide (H_2S), which immediately combines with metals to form highly insoluble metal sulfides such as pyrite (the basis of acid sulfate soils, Section 11.5.2) and ferrous sulfide. Anaerobic bottom sediments are usually black because of the presence of ferrous sulfide-reducing bacteria. Hydrogen sulfide abounds in groundwater and in the hypolimnion of eutrophic waters. Even tiny concentrations are toxic to aerobic organisms because H_2S inactivates cytochrome oxidase, a metabolic enzyme vital to cellular respiration and oxygen transport.

3.6.2 Some common cations

The **sodium** (Na^+) cation dominates almost all Australian inland waters (Table 3.1). This alkali metal is very reactive and highly soluble. Its main source is dissolved NaCl from sea spray or ancient marine deposits. Sodium sulfates and sodium carbonates also yield sodium in solution during the wetting and drying of sediments. Many igneous rocks also contain sodium in feldspars, a group of rock-forming minerals that also contain calcium and potassium, and make up as much as 60% of the Earth's crust. Carbonic acid in rainwater reacts with some of these feldspars to generate forms of sodium carbonate or bicarbonate that typify the soda lakes of East Africa, but these sorts of lakes are not common in Australia. Instead, we have sodium-chloride dominated salt lakes, many of which harbour specialized biota able to thrive under high salinities.

Calcium (Ca^{2+}) occurs in many inland waters as $CaCO_3$ which, although relatively insoluble in water, is soluble as $Ca(HCO_3)_2$ in the presence of carbonic acid (Figure 3.6). Immense reserves of sedimentary calcium carbonate have been laid down by living creatures for aeons. When these reserves are immersed in water rich in CO_2, calcium is released for recycling. Calcite, the most common form of $CaCO_3$, can be deposited during photosynthesis through absorption of CO_2. The shores of many lentic waters are encrusted with marl, fine-grained calcareous material usually from dead charophyte algae that are able to biogenically precipitate $CaCO_3$. A good example of these is the mound springs above the Great Artesian Basin (Chapter 8). Deposition of calcium carbonate forms the 'mound' of these springs (Figure 3.11) by either cementing detrital sediments or providing the primary construction material. The carbonates are dominated by tufa, travertine and very fine-grained or crystalline limestone, and originate from the combined chemical precipitation of calcium carbonate out of the artesian groundwater and precipitation by algae and bacteria.

Magnesium (Mg^{2+}) is found in silicate and nonsilicate minerals and, like many abundant cations, is an alkaline earth metal (elements on the periodic table with similar properties to Be, Ca, Sr, Ba and Ra). It is an essential element for photosynthesis and forms the heart of the chlorophyll molecule. Magnesium is highly soluble and is the second most abundant cation in seawater. Consequently, sea spray delivers large amounts of Mg^{2+} to coastal waterbodies, and the sediments of inland evaporation basins have high levels of this cation.

Figure 3.11 Blanche Cup, a mound spring in northern South Australia. (Source: Jenny Davis.)

The ratio of Ca^{2+} and Mg^{2+} varies in response to evaporation and changes in pH and CO_2. Loss of carbon dioxide and a rise in pH favours precipitation of $CaCO_3$ while Mg compounds stay in solution. During evaporation, Mg salts stay in solution longer than calcium salts and therefore contribute to the salinity of many inland waters. A different form of Mg that is highly soluble and occurs in standing waters is epsomite or 'Epsom salts', a soft white sulfate of magnesium ($MgSO_4 \cdot 7H_2O$). Waters rich in epsomite, such as the thermal springs and spa waters near Moree, NSW, are reputed to relieve arthritis and muscular aches.

Potassium (K^+) in most standing waters mainly originates from weathering of some feldspars but does not remain in solution as much as sodium. Potassium also tends to form micas (layered minerals) that are insoluble, rendering this K unavailable to aquatic biota. Potassium accumulates in plants and plant biomass contains more K^+ than Na^+. An outcome of this is that herbivore dung is very high in K (reflecting the diet) and is a potential source of this cation in arid-zone waters. Potassium can also combine with chloride to make sylvite (KCl). Sylvite is one of the last evaporite minerals (formed by concentration and crystallization through evaporation) to precipitate out of solution. Consequently, this salt is found only in very dry saline areas.

Silicon (Si) is a metalloid or transition element (i.e. with properties in between those of metals and nonmetals) and is the second most abundant element in the Earth's crust. It enters aquatic systems mainly by weathering of abundant feldspars and as dust, and can reach concentrations of up to 25 ppm in waters as dissolved silica. Dissolved silica (also known as silicon dioxide, SiO_2) is essential to diatoms that build their beautiful cases (frustules) of this glassy material (Figure 3.12), and for freshwater sponges whose internal skeletons comprise spicules of silica. Diatoms (Bacillariophyta) take up dissolved silica and deposit it within the protective coating of their frustules. This has been referred to as the 'biological silica pump', and marine food webs and associated commercial fisheries

Figure 3.12 The beautiful frustule (outer shell) of this diatom *Cymbella* sp. (40 μm long) is made largely of silica. (Source: Darren Ryder.)

that ultimately rely on diatoms would collapse if not replenished by silica from rivers entering the ocean (Struyf and Conley 2009).

3.7 REDOX REACTIONS AND REDOX POTENTIAL

When dry sediments are inundated, they quickly become devoid of oxygen (**anoxic**) through microbial respiration. Conditions in the sediments thus change from being **oxic** (meaning free oxygen is present as O_2) to **hypoxic** (less oxygen than oxic) immediately after waterlogging, and finally **anoxic**. The term **hypoxia** is best used to denote an oxygen concentration less than saturation, especially where this deficiency affects some physiological or biogeochemical process. Many chemical processes in aquatic ecosystems are influenced by oxygen concentrations because this molecule is frequently involved in the transfer of electrons during what are called redox or reduction-oxidation reactions.

During redox reactions, electrons (e^-) are transferred from a donor (Fe^{2+} in the example that follows) to an acceptor (Fe^{3+}). One substance is **oxidized** (Fe^{3+}) by another which, in the process, is **reduced** (Fe^{2+}). The reduced material (Fe^{2+}) loses an electron to become oxidized while the electron acceptor (the oxidant Fe^{3+}) accepts electrons from the donor and becomes reduced.

$$Fe^{3+} + e^- \underset{\text{Oxidation}}{\overset{\text{Reduction}}{\rightleftarrows}} Fe^{2+}$$

Reduction and oxidation occur simultaneously because an ion gains electrons (reduction) only when another ion loses them (oxidation). Because the reactions are reversible, the reduced and oxidized forms constitute a redox pair. We have already seen one example of a redox reaction in photosynthesis and respiration; there are many others. Because the transfer of electrons also involves the transfer of energy, redox reactions are common in virtually all biological processes mediated by microorganisms, even under anaerobic conditions.

Redox potential (E_h) is the tendency of a solution to either oxidize or reduce. Redox potential is measured by detecting released electrons in a solution, and is expressed in millivolts (mV). In the laboratory, E_h is measured with a fragile but sensitive hydrogen electrode and is often standardized to a pH of 7 (E_7) because E_h declines as pH rises. In the field, we use platinum and calomel (Hg_2Cl_2, mercurous chloride) electrodes because these are smaller and more robust than laboratory electrodes. Redox is typically measured in sediments whereas DO meters are used in the water column.

In the sediments of standing waters, redox potentials dictate which redox reactions can occur and where. Approximate thresholds of E_h correspond broadly to the zones where different inorganic compounds are used as electron acceptors by sediment bacteria to oxidize organic matter (Figure 3.13). The sequence of these zones and their characteristic redox reactions are controlled largely by their relative reduction potential (Reddy and DeLaune 2008). When the oxidant with the greatest free energy yield (i.e. energy left over for respiration after the reaction is complete) is exhausted, oxidation continues using the next most efficient oxidant, and so on until the supply of organic material itself has been exhausted. Microorganisms compete for the oxidant (usually oxygen) that will yield the greatest net gain of energy. For example, nitrite is reduced at a redox potential between +200 and +300 mV, manganese (Mn^{3+} to Mn^{4+}) and nitrate at approximately +200 mV, Fe^{3+} at +120 mV, and SO_4^{2-} at −75 to −150 mV (Figure 3.13). By the time redox potentials are strongly negative (<−250 mV), only

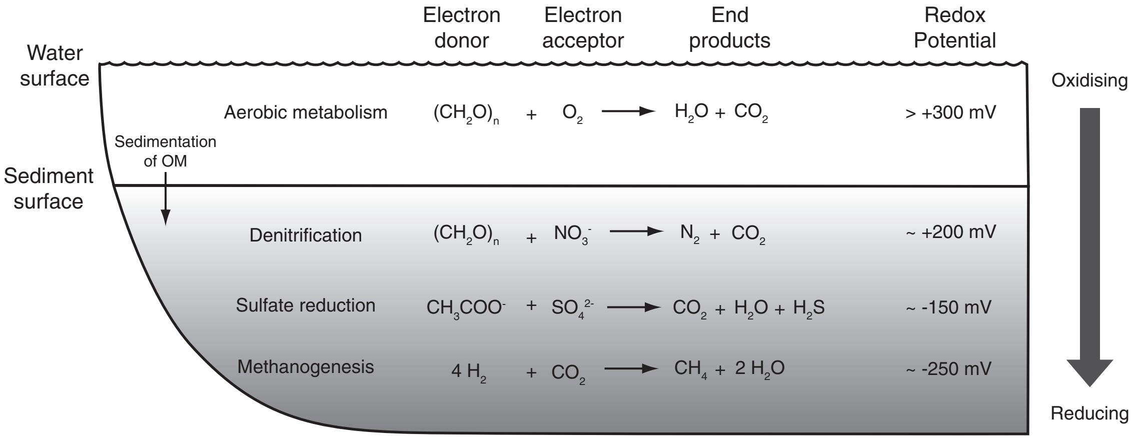

Figure 3.13 Changes in redox potential along a gradient from oxidizing to reducing conditions, with some examples of predominant redox reactions in a standing water and its sediments. OM = organic matter. (Source: Boulton and Brock 1999.)

methane and a few other compounds such as phosphine (PH_3) are generated.

3.8 REDOX REACTIONS AND SOME COMMON METALS

Many Australian inland waters contain large amounts of various metals such as **iron** and manganese. The solubility of both these metals (and indeed many other chemicals) is determined by the redox potential. For example, ferric iron (Fe^{3+}) is relatively insoluble when $E_7 > 300\,mV$ but, as E_h falls, the redox reaction yields soluble ferrous iron (Fe^{2+}). Soluble, reduced iron is found only in hypoxic waters where Fe^{3+} oxides are highly insoluble, such as the hypolimnia of eutrophic waters. When oxygen is added, such as when mixing occurs, the iron oxidizes and precipitates as yellow-brown $Fe(OH)_3$ (Figure 3.7). This also happens when groundwater containing reduced iron emerges at the surface, marking its exit point with a rusty residue (Chapter 8).

Because the reduction potential is so positive, iron is commonly used by microorganisms as an electron acceptor in respiration to oxidize a wide range of organic substrates. This reactive iron also binds with phosphorus, a significant macronutrient discussed later in this chapter, to form $FePO_4$ (ferric phosphate) or $Fe_3(PO_4)_2$ (ferrous phosphate). Consequently, the high concentrations of iron common in many Australian waters can reduce the phosphate available for primary productivity. Furthermore, iron also facilitates the formation of complexes of phosphorus with dissolved organic carbon in surface waters (Baldwin and Mitchell 2012), preventing two crucial elements from being involved in biogeochemical processes.

Another common metal, **manganese** (Mn) behaves like iron. Manganese oxides abound in the sediments of standing waters, have low solubility in water at pH 7, and precipitate readily under oxic conditions. Similarly, the reduction of Mn^{2+} is a biologically significant redox reaction that provides energy for processes such as the decay of organic matter. For example, specialized bacteria living in anoxic sediments and groundwater oxidize organic matter to CO_2 using metals such as manganese and iron as the only electron acceptor. When a waterbody stratifies, manganese (+200 mV) becomes soluble in the water before iron (+120 mV). However, when mixing occurs, iron precipitates out before manganese. Dissolved manganese is often carried in hypolimnetic water released from reservoirs, leaving tell-tale black stains of manganese dioxide (MnO_2) at the release point (Figure 3.14).

Another group of metals, although less common than iron and manganese, deserves mention. These are the '**heavy metals**' and are of interest because many of them are toxic, even in minute concentrations, to

Figure 3.14 The dark stains on the wall of this reservoir arise from oxidation and precipitation of dissolved manganese into insoluble manganese dioxide on contact with oxygen. (Source: Darren Ryder.)

humans and other organisms. Redox conditions in the water column and sediments govern the chemistry and bioavailability of these elements. Their solubility increases as the redox potential decreases, usually because of changes to the composition of complexes (e.g. with clays or organic matter) that release the metal ions into the overlying water. For example, the metalloid arsenic has several oxidation states regulated by the redox potential. Reduction of As^{5+} at approximately +100 mV produces As^{3+}, which is soluble and highly toxic.

We can now see how useful it is to know the redox potential when predicting the behaviour and bioavailability of ions in standing waters. This theme is revisited in Section 3.9 when we discuss cycling of phosphorus (P), nitrogen (N) and carbon (C). But first, let's define nutrients and nutrient limitation.

3.9 NUTRIENTS, NUTRIENT LIMITATION AND ECOLOGICAL STOICHIOMETRY

Many ions and metals are essential components of all aquatic organisms, and are termed nutrients. These comprise **macronutrients** (e.g. P, N, C, S, K, Mg, Ca), which comprise >0.1% of the dry weight of the organisms and **micronutrients** or trace elements (e.g. Fe, Mn, Cu, Zn, Si, Mo, V, Co) needed in only tiny amounts. In excess, many of these nutrients are actually toxic.

The productivity of all organisms is constrained by **limiting factors** that may be physical (e.g. light for producers), chemical (e.g. dissolved oxygen, Box 3.1), biological (e.g. prey availability for consumers), or any combination of these. Nutrient availability is a chemical limiting factor that often governs the distribution and activity of many aquatic organisms as well as controlling the rate of vital ecosystem processes such as primary production. For example, the concentration, availability and ratio of nutrients such as N and P can affect primary productivity of well-lit waters. If growth of an aquatic plant increases following addition of a nutrient, we refer to this as a **limiting nutrient**. The same applies to the total potential biomass of aquatic plants. Growth rate and total potential biomass may be limited by either different nutrients or the same one. Thus, it is necessary to state the exact type of nutrient limitation taking place. In most standing waters, phosphorus is the usual macronutrient limiting both growth rate and biomass, but sometimes, nitrogen is limiting instead. For example, growth and biomass of phytoplankton (photosynthetic organisms in the water column, Chapter 4) in tropical floodplain wetlands of the NT may be limited by nitrogen (Townsend and Edwards 2003).

Often the *ratio* rather than the absolute concentration of nutrients is more relevant to many biological processes. This underpins the field of **ecological stoichiometry**, the study of the balance of chemical elements in ecological interactions (Sterner and Elser 2002). Variation in supply and uptake of nutrients in inland waters alters the stoichiometry and affects fundamental ecological processes such as primary productivity and growth rates. In particular, deviations in concentrations of the macronutrients carbon, nitrogen and phosphorus from a molar ratio of 100:16:1 (C:N:P), the **Redfield ratio**, can decrease growth of phytoplankton in aquatic ecosystems (Elser *et al.* 2007). In a field experiment conducted in tropical NT,

Box 3.6 Linking photosynthesis and nutrient limitation with autotrophy and heterotrophy

Light, photosynthesis and nutrient limitation are all linked to support autotrophic (primary producers) and heterotrophic (microbial, invertebrate and vertebrate) production in aquatic systems. In the Daly River (Northern Territory) during the dry season when river flow is supplied by groundwater, nutrient concentrations are low. This nutrient limitation reduces the potential for photosynthetically fixed carbon to be incorporated into primary producer biomass (Webster *et al.* 2005). Photosynthesis increases during the dry season as primary producer biomass increases, although self-shading amongst benthic algae and other plants limits primary production. Much of the carbon provided by primary producers to aquatic food webs is dissolved organic carbon (DOC), which can be degraded by bacteria to contribute to whole-of-river respiration. In the Daly River, respiration increases in proportion to photosynthesis (Townsend *et al.* 2011). This relationship seems to result from the bacterial degradation of refractory DOC (which is normally resistant to degradation) being enabled by the concurrent degradation of photosynthetically derived DOC. Thus, light and nutrient availability control ecosystem processes such as photosynthesis that, in turn, controls microbial respiration of refractory carbon.

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Townsend *et al.* (2008) found the filamentous alga *Spirogyra fluviatilis* had an optimal molar C:N:P ratio of 1800:87:1. This substantially deviated from the Redfield ratio, suggesting the growth of the algae was limited by the ratio of available nutrients rather than absolute concentration of any one nutrient (Box 3.6). However, the Redfield ratio needs to be used cautiously; it was derived for marine phytoplankton and the optimal molar ratios of C, N and P are likely to differ for different types of producers in fresh waters.

In studies of nutrient limitation, the three macronutrients phosphorus, nitrogen and carbon receive special attention because these macronutrients are often considered to be needed in greatest supply and are most likely to be limiting in standing waters. Although N and P are the most likely culprits, always be aware that any of the other macronutrients or micronutrients may potentially limit algal growth, biomass or both when other environmental factors such as light and temperature are adequate (reviewed by Moss 2011). Furthermore, nutrient ratios rather than absolute concentrations often cause the limitation.

3.9.1 Phosphorus

Phosphorus (P) is often the nutrient in limited supply in inland waters, and even a modest increase can, under the right conditions, accelerate aquatic plant growth (Harris 2001). Phosphorus is essential to all life as a component of nucleic acids and in the universal energy-transfer molecule adenosine triphosphate (ATP). Natural sources of P include the atmosphere (e.g. as dust) or the catchment as organic matter from fringing and aquatic vegetation and in run-off containing organic matter and weathered sediments (Figure 3.15). Groundwater can also contribute small amounts. In natural waters, P exists as HPO_4^{2-} (hydrogen phosphate) or $H_2PO_4^-$ (dihydrogen phosphate), readily dissociating to release H^+ and PO_4^{3-}. However, most P is biologically unavailable, either bound to cations and sediment particles or within living organisms or buried detritus.

When collecting water samples for P, make sure that your sampling bottles have never been washed in commercial detergent because this may contaminate your samples. After filtering the water through a 0.45-μm filter to remove all particulates, soluble inorganic phosphate (PO_4^{3-}) is measured colorimetrically using a spectrophotometer. Reagents are added that intensify in colour according to the amount of soluble P in the sample. The intensity of this colour is then read at a specific wavelength on a spectrophotometer. To measure organic phosphorus, unfiltered water is digested with sulfuric acid to break down all P bound to detritus, organisms and sediments into soluble phosphate, which is then measured colorimetrically as described previously. This is called **total phosphorus**

(TP) and is all the phosphorus in the water. To determine particulate phosphorus (PP), you subtract the value from the filtered sample (dissolved P) from the value of TP. The same procedure is done for determining total nitrogen (Section 3.9.2).

Organic phosphorus (OP, Figure 3.15) is P that exists in dissolved and particulate detritus and in living organisms. Inorganic phosphate (**orthophosphate**, PO_4^{3-}) is the only form of P that can be used by aquatic plants. Aquatic plants take up dissolved inorganic P from the water column or sediments and convert it to OP when it becomes part of their tissues. Consumers get the OP they need by eating microorganisms, aquatic plants or other animals. Many microorganisms obtain theirs from decomposing plant and animal material.

When plants and animals excrete wastes or die, the OP they contain sinks to the bottom. Consequently, sediments are the major store of OP in standing waters and the usual location for the conversion of organic

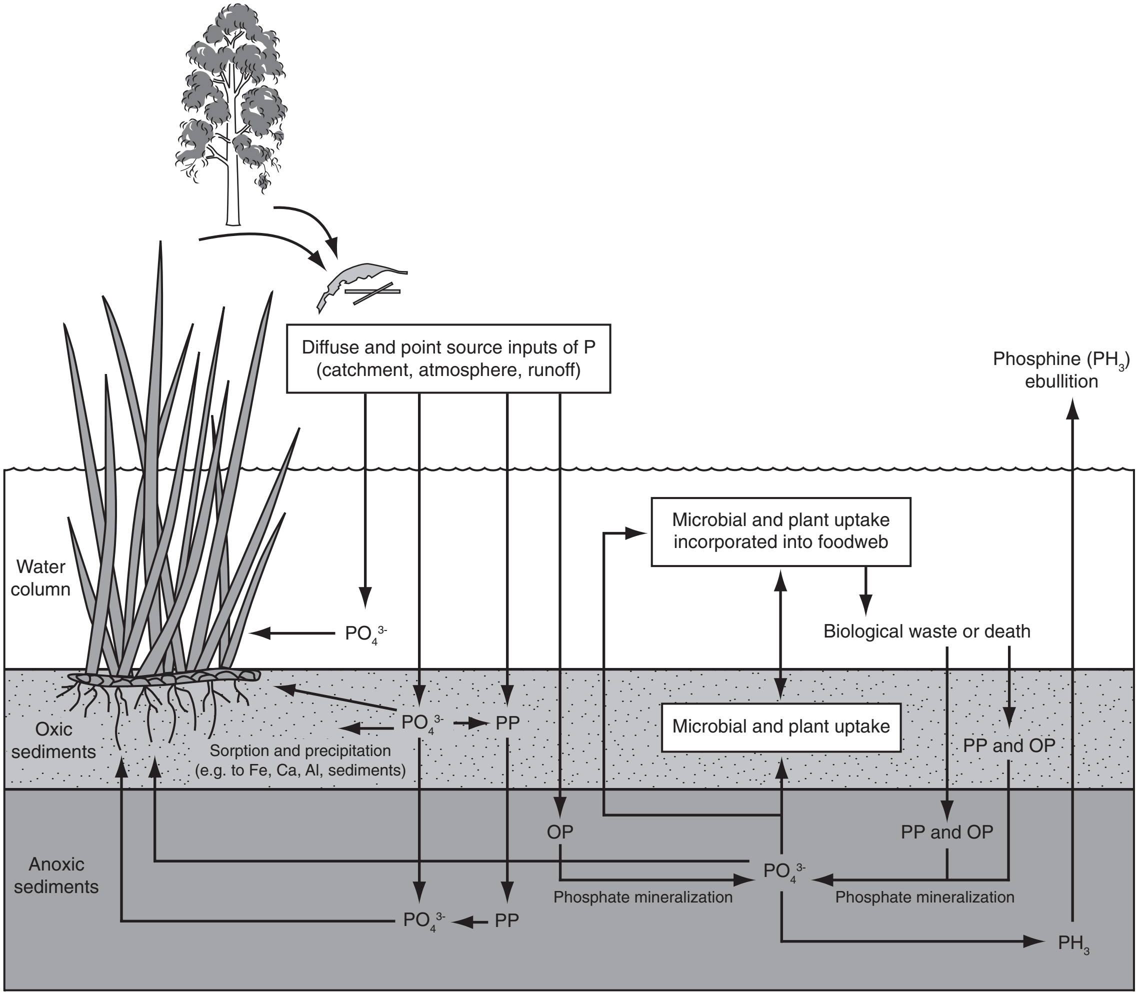

Figure 3.15 The cycling of phosphorus in standing waters. OP = organic phosphorus; PP = particulate phosphorus; PO_4^{3-} = phosphate. Minor amounts of P also enter and leave via groundwater (not shown here). (Source: Image drawn by Belinda Cale.)

phosphate to PO_4^{3-} through **mineralization** (Figure 3.15). Mineralization is the release of compounds and inorganic ions during decomposition, many of which can be used by plants or taken up by microorganisms. In the sediments, microbial decomposition mineralizes OP back to inorganic phosphorus, which re-enters the water column by diffusion and when sediments are disturbed by physical or biological activity. The resulting PO_4^{3-} is then taken up by plants and the cycle begins again, with P continually recycled through aquatic food webs, facilitated by microbial activity (Figure 3.15).

When photosynthesis occurs in waters with low concentrations of nutrients, only traces of PO_4^{3-} are found because it is swiftly taken up by algae and aquatic plants. Microorganisms are impressive competitors with algae and plants for this resource, and any P released into water by one organism is swiftly taken up by another. Movements of P in lentic environments include sorption (i.e. attachment) and exchange reactions with soils and sediments, chemical precipitation in the water column, processes of sedimentation and entrainment, and of course, the uptake and release by vegetation and biofilms. Soluble inorganic phosphorus can bind to a number of metals and ions. Bonding to metals (e.g. Fe, Mn, Al) is usually redox-mediated. Therefore, the cycling of these forms of insoluble inorganic phosphorus is affected by biological processes of respiration. In contrast, bonds to ions such as calcium often occur in dense lattices (e.g. calcium phosphate such as hydroxyapatite) that are unaffected by redox conditions and P is more permanently sequestered. The diversity of these linkages in the cycling of phosphorus is a prime example of one of the themes of this book: the importance of interactions among physical, chemical and biological components in aquatic systems and the ways that these rely upon each other.

One component of the P cycle that is commonly overlooked is phosphine (PH_3), a colourless gas that can bubble up from anoxic sediments (Figure 3.15). Phosphate is reduced to phosphine at a redox potential of >-250 mV, similar to that at which methanogenesis takes place (Figure 3.13). Phosphine therefore represents a gaseous phase for P (the absence of which is often cited as a major difference between N and P cycles). High P loads and the reducing conditions in constructed wastewater treatment wetlands often result in substantial phosphine fluxes (Han *et al.* 2010), but this process is poorly studied in natural standing waters. Phosphine is spontaneously flammable and has been suggested as the cause of strange lights and 'will-o'-the-wisps' alleged to occasionally occur over certain inland waters on spooky dark nights.

Human inputs of P arise from sewage outfalls, agricultural fertilizers and other sources, often leading to excessive primary production and blooms of nuisance or toxic aquatic plants and cyanobacteria (Chapter 11). The vulnerability of a waterbody to these problems can be estimated from equations involving its physical dimensions (depth, shoreline, volume and wetted area) and the annual water budget, but these equations have proved only partially successful in Australia (Davis and Koop 2006). Long after external inputs of limiting nutrients have ceased, '**internal loading**' (i.e. the release of nutrients from the sediments) continues to add nutrients to the water. In shallow standing waters, internal loading occurs when wave action resuspends material such as nutrient-laden sediments. In stratified waterbodies (particularly large impoundments), internally loaded nutrients from the sediments and the hypolimnion (Chapter 2) are circulated to producers in the euphotic zone during mixing, often causing blooms of producers soon afterwards. Internal loading can persist for decades after external inputs have been markedly reduced, and it requires careful management (Chapter 11).

3.9.2 Nitrogen

Like phosphorus, nitrogen (N) is essential for all life but it has a more complex biogeochemistry, is more labile and has more chemical species (i.e. oxidation states). Unlike P-cycling where the emphasis is on the cycling of organic and inorganic phosphate through microbial communities and aquatic food webs, the N cycle is best conceptualized by thinking about the changes in oxidation state and the effects of the physical and chemical environments associated with the various forms of N.

Seventy-eight percent of the atmosphere is **nitrogen gas** which is often the major source of N for aquatic systems. **Particulate** and **dissolved organic nitrogen (PON and DON)** in organic matter and **dissolved inorganic nitrogen (DIN)** enter from fringing and aquatic vegetation, other catchment sources, and groundwater (Figure 3.16). In the water column and oxic sediments, both forms of organic nitrogen are broken down by microorganisms into inorganic forms of nitrogen: ammonium,

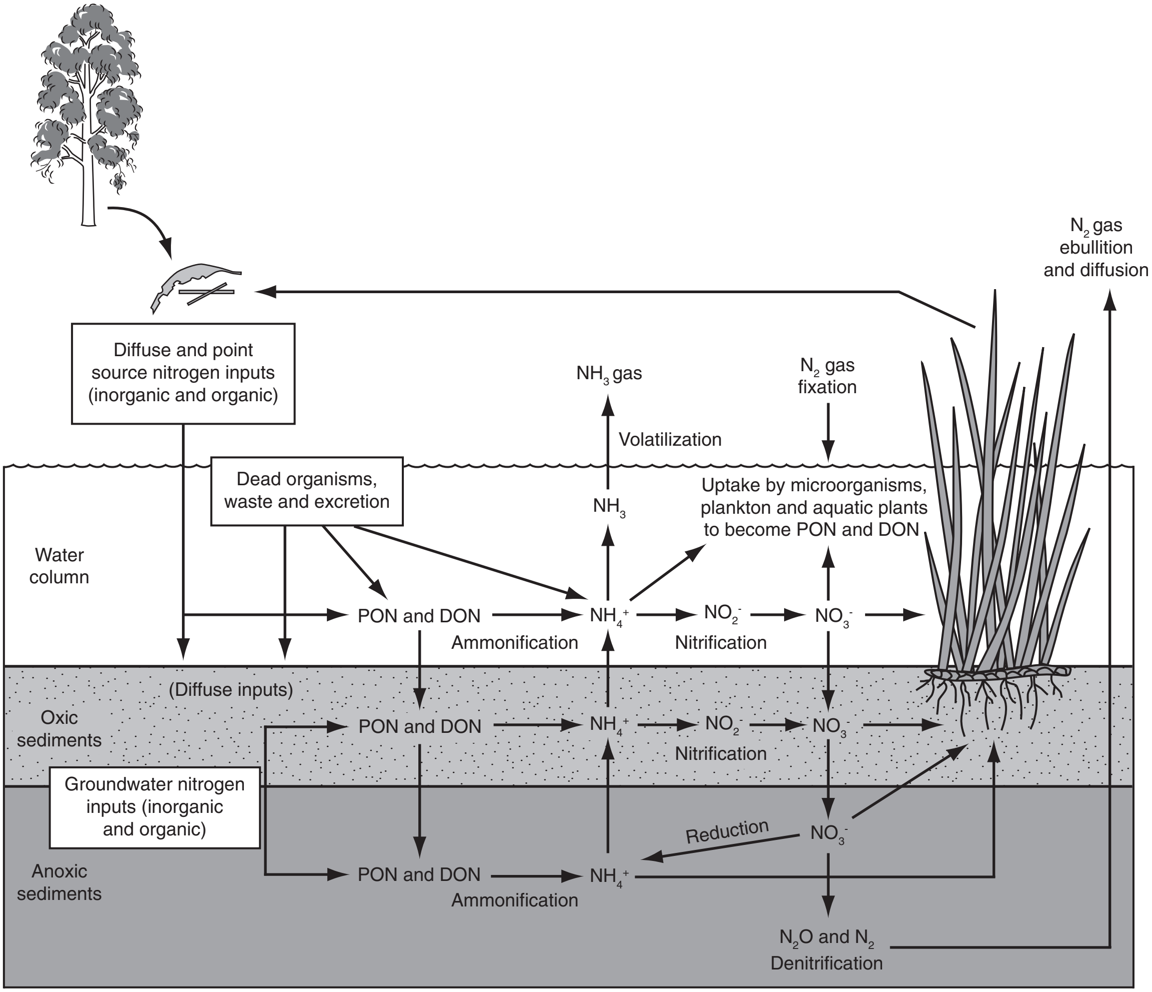

Figure 3.16 The cycling of organic nitrogen in standing waters. PON = particulate organic nitrogen, DON = dissolved organic nitrogen. See text for the other abbreviations. (Source: Image drawn by Belinda Cale.)

nitrite and nitrate (Figure 3.16). **Ammonification** is the conversion of organic nitrogen to ammonium (NH_4^+). In anoxic sediments, most of this ammonium is re-assimilated by microbes or diffuses into the overlying water or sediments. However, where oxygen is present, this ammonium is oxidized to nitrite (NO_2^-) and then to nitrate (NO_3^-) by a process called **nitrification**. This oxidation is completely microbial, and provides substantial energy for the microorganisms.

The nitrate, produced by nitrification, can be reduced to nitrogen gas via **denitrification** and exported from the system as a gas. Alternatively, it can be reduced back to NH_4^+. During denitrification, the denitrifying bacteria use NO_3^- as an alternative electron acceptor (i.e. the oxidant) instead of O_2. The reduction back to NH_4^+ can be either assimilatory or dissimilatory (Figure 3.16). In assimilatory reduction, only small amounts of nitrate are taken up by microbes or plants. Conversely, in dissimilatory reduction (predominantly occurring in sediments), large amounts of nitrate are reduced to NH_4^+ by microbes in a process resembling respiration (Reddy and DeLaune 2008).

The loss of nitrogen via denitrification can be balanced by its gain via nitrogen '**fixation**'. Although molecular N dissolves readily, a few groups of organisms can 'fix' N_2 by using specific enzymes to break its powerful triple bonds. Nitrogen fixation uses the enzyme nitrogenase and usually occurs in special cells (heterocysts) that provide anoxic micro-environments where the enzyme can function. Nitrogen-fixing organisms include free-living heterotrophic bacteria and cyanobacteria (Section 4.5) commonly found in the water column. When N in the water column begins to limit primary production, cyanobacteria produce their own directly from atmospheric nitrogen. The cyanobacterium *Anabaena azollae* fixes atmospheric nitrogen and lives in a symbiotic relationship with the floating fern *Azolla* (Figure 3.17): the cyanobacterium provides nitrogen to the water fern that, in turn, provides a special chamber within its fronds to house the cyanobacterium in an optimal location for nitrogen fixation and exchange (Lechno-Yossef and Nierzwicki-Bauer 2002) where it is protected from sinking by the buoyant fronds.

Almost all the N-cycling processes described so far involve microorganisms occurring in specific redox conditions. Other organisms also play key roles. For example, nitrate and ammonium can be assimilated by algae and other aquatic plants. When algae are eaten by zooplankton (Chapter 4), the excess nitrogen is excreted, usually as NH_4^+, which enters the nitrogen cycle once again. This cycling of N between algae and zooplankton, much like the cycling of N among sediments, microorganisms and food webs, is called 'internal cycling' because it does not rely on external inputs of N.

Standard chemical methods are used to measure concentrations of nitrate, nitrite, ammonium and organic nitrogen. For nitrite and nitrate, filtered water samples are passed through a column of copper-coated cadmium, which reduces the dissolved nitrate to nitrite. Nitrite plus nitrate (sometimes expressed as NO_x) are then analysed chemically (diazotization) to produce a pink dye whose concentration can be read using a spectrophotometer. To measure nitrite alone, the water is analysed as before but not passed through a reduction column first. Organic nitrogen is digested with sulfuric acid using the Kjeldahl method to produce ammonia that is then analysed by various chemical methods, the most common of which is a phenol-hypochlorite method. There are also automated analysers for all these forms of N (Wetzel and Likens 2000).

Ammonium (NH_4^+) is the ionized form of ammonia gas (NH_3), and so the two words should not be used interchangeably. Ammonium and ammonia shift in equilibrium with each other according to pH, and the different forms can have major ecological consequences. For example, at high pH (>9), ammonia is the more common form. However, ammonia is highly toxic

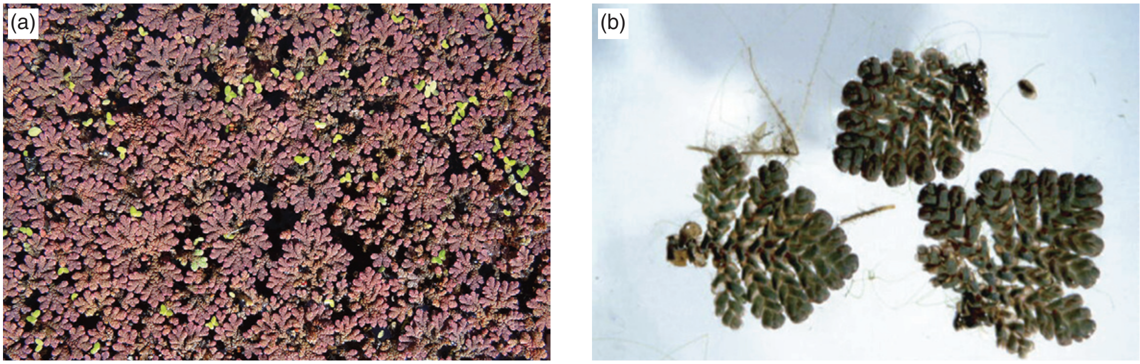

Figure 3.17 The water fern *Azolla* floats on the water surface (a) and its fronds (b) house populations of the cyanobacterium (*Anabaena azollae*) that fixes gaseous nitrogen. (Source: Jane Chambers.)

Box 3.7 Sources and trophic role of dissolved organic carbon in Australian aquatic ecosystems

Dissolved organic carbon (DOC) plays a vital trophic role in aquatic ecosystems, supplying energy for metabolism and secondary production. Microbes such as bacteria and fungi are the principal heterotrophs that can directly utilize DOC. These organisms are subsequently consumed in the water column and in biofilms by invertebrates. Microbes mediate detrital breakdown and nutrient transformations, gaining their energy by respiration. The rate of microbial respiration depends on the ease of breakdown (bioavailability) of the DOC constituents. DOC composition varies according to its origin. Allochthonous sources from leaf litter, soil and tree roots typically dominate the DOC pool. These molecules are predominantly humic substances, such as fulvic acids, which have low bioavailability. Algal and other plant exudates are the major autochthonous sources of DOC, and comprise mostly carbohydrates, carboxylic acids and amino acids. These smaller molecules are more bioavailable and are rapidly recycled through the microbial loop. Disturbances that reduce the bankside vegetation, including agriculture and urbanization, are likely to increase the proportion of bioavailable DOC in aquatic ecosystems, which may then alter food web dynamics.

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and when pH levels approach or exceed 9, fish kills often occur because of the shift from the relatively harmless ammonium to the deadly ammonia.

3.9.3 Carbon

Carbon (C) is the chemical basis of all life on Earth because it occurs in all living organisms, usually in large amounts. It is cycled in almost all aquatic ecosystems, involving transformations and movements of organic matter. Organic matter occurs in both dead and living organisms, and contains a diverse array of compounds such as celluloses, tannins, lignins, proteins, lipids and sugars, all of which contain carbon as well as other elements. When discussing all these compounds collectively, we use the term ‘organic matter’. However, when only the carbon fraction is of interest (e.g. when using the Redfield ratio), the term ‘carbon’ is used, referring only to that elemental part of the total organic matter.

Sources of organic matter are either **autochthonous** (within the waterbody) or **allochthonous** (outside the waterbody), although this distinction can sometimes be uncertain near the water’s edge. Arbitrarily, organic matter is categorized into three size classes: **particulate organic matter (POM)**, further divided into coarse (CPOM, >1 mm) and fine (FPOM, 0.045 – 1 mm) fractions, and **dissolved organic matter (DOM**, <45 μm). Particulate organic matter comprises living organisms, varying in size from huge trees down to minute bacteria, and dead material, such as bits of leaf and wood, collectively termed **detritus**. In most aquatic ecosystems, the majority of organic matter is the dissolved fraction, a complex array of organic compounds and a crucial source of carbon and energy (Box 3.7).

During analyses, dissolved organic matter is commonly separated from POM by filtration, either with glass-fibre filters (pore size of about 1 μm) or with membrane filters with a pore size of 0.45 μm. However, these filters do not retain all bacteria, which clearly are particulate matter, leading to some discrepancy between what is measured and the real situation. Amounts of POM and DOM are usually expressed in units of their carbon content, stated as **particulate organic carbon (POC)** and **dissolved organic carbon (DOC)**, respectively. Methods for measuring DOC are described in Box 6.4.

We have already come across the inorganic forms of carbon as carbon dioxide, carbonates and methane in our discussions of chemical processes in standing waters. It is time to tie all these together with the organic forms in the carbon cycle (Figure 3.18). The flux of carbon dioxide across the water surface and its generation through aerobic respiration drive most of the primary production (i.e. photosynthesis) of autochthonous organic matter. This organic matter, plus allochthonous inputs from the catchment and the

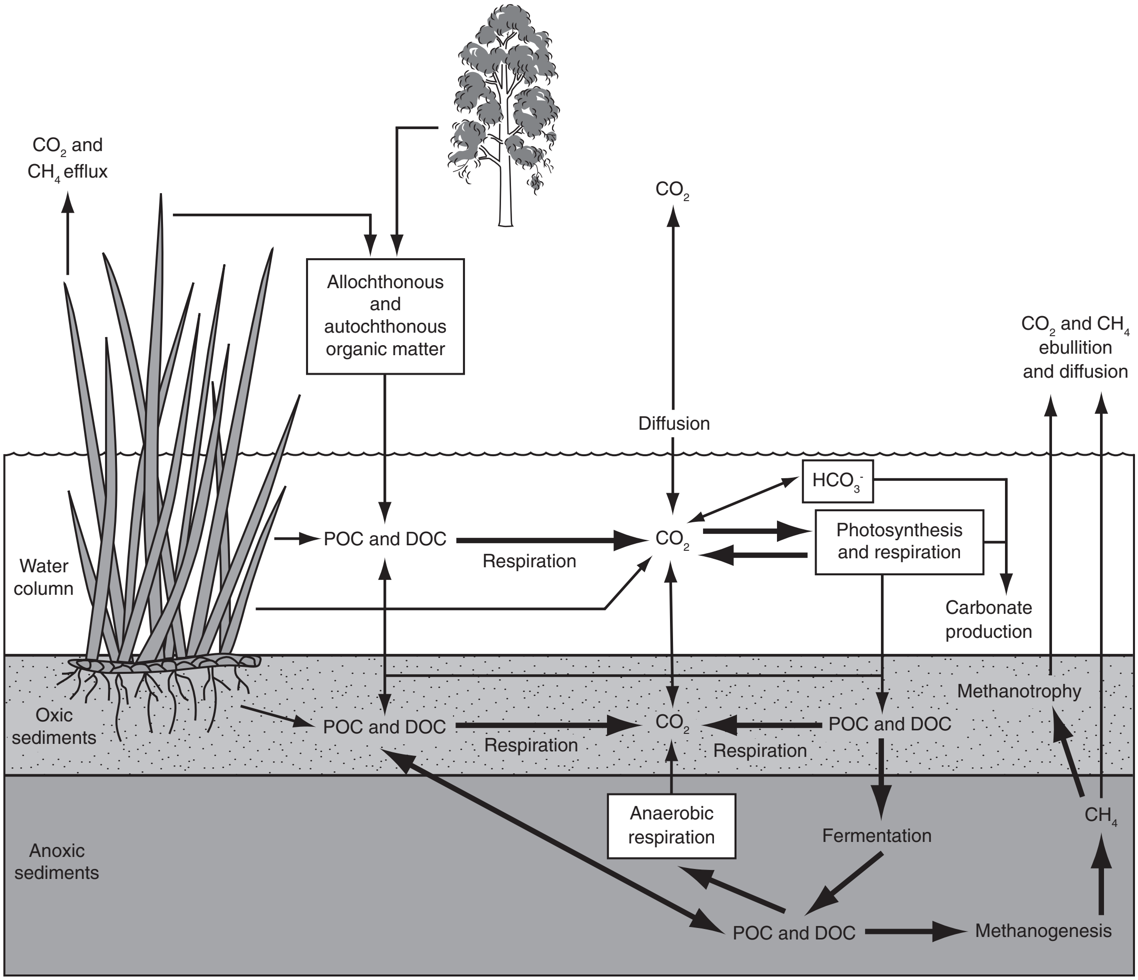

Figure 3.18 The cycling of carbon in standing waters. Thick arrows indicate biological transformations; thin arrows show physical or chemical transformations. POC = particulate organic carbon, DOC = dissolved organic carbon. See text for other abbreviations. Other sources of C (including inorganic forms) include weathering, runoff and groundwater (not shown). (Source: Image drawn by Belinda Cale.)

groundwater, is eaten by consumers or broken down microbially (i.e. respired) in the water column and the sediments. Carbon leaves the system as carbon dioxide from aerobic respiration, methane from anaerobic respiration, or as POC or DOC in emigrating biota and water outflows at the surface or into the groundwater.

Concentrations of DOC in Australian natural waters usually range from about 1–10 mg L^{-1}, but can exceed 25 mg L^{-1} in poorly flushed systems or those with high loadings of organic matter. These include, for example, waters stained deep brown with tannins and lignins leached from terrestrial and riparian vegetation. As well as being a major carbon source, dissolved organic matter can alter the physical environment by reducing light penetration (Section 2.2.2). In addition, certain forms, especially the polyphenols, can inhibit enzymes secreted by aquatic microbes (Kobayashi *et al.* 2009b), impairing respiration rates. DOM also influences the biogeochemical cycling of heavy metals because they

Box 3.8 Nutrient release from dried sediments

Desiccation causes many fundamental changes to sediment properties, in turn, altering nutrient dynamics after re-inundation. When sediments are exposed to the atmosphere, two different effects can be expected. First, the oxygen content of the sediment will increase. Second, the moisture content of the sediment will be substantially reduced (Baldwin *et al.* 2000). Combined, these two processes can increase the crystallinity of mineral phases (i.e. the formation of crystal structures such as Fe^{3+} oxides within the sediment matrix), and reduce the sediment's capacity to adsorb nutrients such as phosphorus. Drying increases the mineralization rate of organic N and C, and may kill a large proportion of the sediment microbiota (Rees *et al.* 2006). As a result, significant amounts of N and, to a lesser extent, P may be released on re-wetting. Re-wetting of desiccated soils and sediments will result in an initial flush of available N and P (which can then be incorporated into biomass of bacteria or aquatic plants), coupled with an increase in aerobic bacterial activity, particularly nitrification. However, nutrient cycling within the re-wetted sediment may be impaired until sediment microbiota recover.

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can be kept in solution by forming complexes with DOM. This makes them more readily transported or taken up by organisms (McCullough and Horwitz 2010).

3.10 WATER REGIME, DRYING AND WATER CHEMISTRY

How do water regime and hydrological variability affect water chemistry, especially in temporary lentic waters? When filled, chemical processes in a temporary waterbody resemble those in nearby permanent ones of equivalent size, depth and shape. However, while the water volume declines during drying, water chemistry may fluctuate more widely. Chemical extremes occur either just before the water dries completely (owing to concentration by evaporation and the small remaining volumes) or soon after filling (because of the first flush of dissolved materials and release from the sediments). Changes in water quality during drying and filling depend on many factors including sediment properties, the mode of water drawdown (gravity or evaporative), the process of drying (e.g. proportion of area drying, timing, severity and rate of drying), and the conditions of refilling (e.g. origin of water, timing).

Sediment properties have a major effect on nutrient transformations and exchanges between sediments and the overlying water. Two major processes drive the increase in nutrients often observed soon after rewetting. The first is physicochemical, primarily as sorption of P onto the sediments. The second is biological, primarily the uptake and release of P by microbes (Box 3.8). The actual process of drying also alters the sediment itself. For example, during drying the particles often aggregate and become compacted, and organic matter is mineralized. There are also changes to the sediment porosity, which can affect fluxes between pore water and the overlying water (Baldwin *et al.* 2000, 2006). As the waterbody dries, pore water initially moves up through the sediments to the surface and then evaporates. Remaining solutes become concentrated, and chemical changes occur because of exposure to oxygen, high temperatures and solar radiation.

3.10.1 What happens to water chemistry during a wetting-drying cycle?

Despite the variability in water regimes in temporary waters (Chapter 1), there are likely to be broad parallels in the principal changes in water chemistry during a generalized wetting-drying cycle Figure 3.19). Using depth as a surrogate for volume and related physical features of a temporary standing water, we can predict the relative changes in water temperature, dissolved oxygen, conductivity, pH and nutrients in the water column upon re-wetting and later, drying.

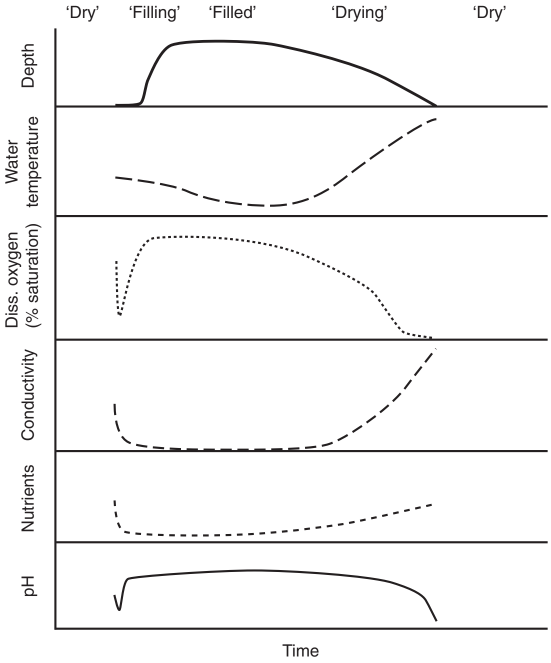

Figure 3.19 Likely changes in several physical and chemical features in a temporary waterbody during a wetting-drying cycle. The time axis may span days to years but the trends are probably broadly similar. (Source: Boulton and Brock 1999.)

Water temperature will likely track air temperatures although the range of temperatures will be buffered by the high specific heat of water (Section 1.5.1). In Australia's temperate southern regions, drying usually occurs as air (and water) temperatures rise, and with the dwindling volume, the variation in water temperature over 24 hours will also probably increase. When standing waters first fill, dissolved oxygen concentrations may be initially high from the turbulence of filling by rain, surface runoff or both. However, if the waterbody fills from recharged groundwater when the water table rises after rainfall, the dissolved oxygen concentration will probably be lower. Soon after re-wetting, the previously desiccated and aerated sediments become waterlogged and devoid of oxygen (Boon *et al.* 1997) owing to high oxygen demand by benthic microbial respiration and poor mixing of the water column (Page and Dalal 2011). Eventually, dissolved oxygen concentrations rise as aquatic photosynthesis becomes established, and soon the conditions resemble those of nearby permanent waters of equivalent dimensions. When drying begins and the water becomes shallow, rising water temperatures reduce the percentage dissolved oxygen saturation and accelerate biological processes such as the decomposition of stranded dead and dying aquatic plants and even animal carcasses. The final puddle before the water dries completely is often almost anoxic (Figure 3.19).

Early runoff from the catchment or groundwater inflow through bed sediments usually contain elevated levels of dissolved salts, leading to an initial peak in conductivity (Figure 3.19). The newly wetted sediments are also likely to release nutrients, causing a brief peak in dissolved macronutrients, particularly N and P. The phenomenon of a large flush of nitrogen mineralization shortly after rewetting of dry soil was first reported by Birch (1958). Since then, the increase in N availability has been known as the 'Birch effect'. After the waterbody has filled, trends in N and P concentrations are less clear but their organic forms probably increase in concentration as primary and secondary production become established.

Most temporary waters dry during summer in southern regions of Australia. Native eucalypt and paperbark forests typically dominate the fringes of these waters, and the peak leaf fall in summer leads to an accumulation of leaf litter in the basin. The dissolved organic matter leached from this litter may cause pH to initially decline during the filling phase (Figure 3.19), especially as rainfall runoff is usually poorly buffered. Eucalypt oils and other organic acids continue to leach from fallen leaves in the receding pools, also reducing pH (Petrone *et al.* 2009). As the water temperatures rise, the percentage saturation of dissolved oxygen falls depending upon the rates of algal photosynthetic activity in the water. Reduced light caused by the dissolved organic acids in the water may restrict photosynthesis and, with the decay of organic litter in the pools, conditions can become anoxic over time. Evaporation causes conductivity to rise, and just before the pool dries, water quality is often extremely poor (Figure 3.19).

In Australia, most of these general trends have been described in temporary waters in arid zones (Bunn *et al.* 2006), warm temperate climates (Sommer and Horwitz 2009) and the tropics (Townsend 2002). This broad consistency in physical and chemical responses of standing waters to wetting and drying may help scientists and managers predict likely trends under climate change scenarios of reduced rainfall and runoff (Chapter 12). However, always be aware that there may also be system-specific features and feedback mechanisms (especially biological ones, Chapters 4 and 7) that could yield unexpected patterns and responses.

3.11 SYNTHESIS

We have seen how the chemistry of standing waters is intimately linked to physical processes occurring within the waterbody, as well as the atmosphere and surrounding catchment. Physical features such as depth, light, temperature and water regime influence almost all features of water chemistry. In particular, changes to redox potential, resulting from stratification or wetting and drying, will produce different conditions that favour different chemical transformations. Increasingly, concepts such as the role of nutrient stoichiometry in regulating the productivity of aquatic ecosystems are increasing our understanding of the linkages between chemical and biological processes. More details about water chemistry and its links to ecological processes are in specialized texts such as Batzer and Sharitz (2006) and Reddy and DeLaune (2008).

Despite the diversity of waters across the continent (Chapter 1), there are broad parallels in physical processes such as the penetration of light and heat or the effects of the shape of a waterbody on its tendency to stratify. Similarly, aspects of the water regime such as wetting and drying cycles in temporary waters elicit broadly parallel trends in physical and chemical features across a diverse array of climatic zones. In the next chapter, we review how aquatic biota influence and are influenced by their physical and chemical environment, and how energy and materials traverse food webs and trophic levels in standing waters.

CHAPTER 4

Biological processes in standing waters

4.1 BIOLOGICAL PLAYERS ON A PHYSICAL AND CHEMICAL STAGE

In Chapters 2 and 3, we saw how physical processes in lentic environments arise primarily from interactions among the penetration of water by light and heat, the depth, volume and location of the basin, and sometimes water chemistry (e.g. salinity). Many of these features relate to how the basin formed and to the geology and land use of the catchment. Arising from these interacting physical processes is a complex chemical landscape whose conditions in the water column and sediments are influenced by redox potentials, microbial activity and other factors. These factors, operating at multiple scales of space and time, produce diverse environments, ranging from anoxic, lightless ones deep in the sediments through to oxic and well-lit habitats in the upper water.

Occupying these diverse habitats are organisms, collectively termed **aquatic biota**, whose activities both influence and are influenced by the physical and chemical features. This chapter reviews the microorganisms, plants and animals that comprise the aquatic biota, how they interact with each other and their environment, and how they are involved in fundamental ecosystem processes such as organic matter processing and energy transfer. In lentic environments (e.g. Figure 4.1), these biological processes and the aquatic biota interact closely with the water regime (Chapter 1) and physical (Chapter 2) and chemical processes (Chapter 3).

Before we start, let's revisit the concept of scales in time and space. Aquatic biota and biological processes occur across wide spatial (micrometres to global) and temporal (milliseconds to millennia) scales. Different processes dominate at different scales, often within a hierarchy of levels of organization (Table 4.1). For example, at fine scales within body cells, tissues and organs, physiological processes govern how an **individual** organism obtains its nutrition, reproduces and moves. All individuals of a single species within a habitat patch comprise a **population**, and a set of populations linked by dispersal is called a **metapopulation** (Leibold *et al.* 2004). Changes in abundance and age or size structure of populations usually affect the availability of resources such as food or living space, often altering metapopulation dynamics within and among waterbodies.

Individuals in populations of different species within a habitat patch interact as a **community**, usually through biological processes such as predation and competition (Table 4.1). Sets of local communities linked by dispersal of multiple interacting species form **metacommunities** (Hanski and Gilpin 1991; Leibold *et al.* 2004). The significance of dispersal is discussed later (Sections 4.3–4.6) and in Chapter 7; at this stage, it is enough to acknowledge its importance as yet another ecological linkage at the scales of populations and communities.

The final level of organization (Table 4.1) is the **ecosystem** where communities and their environments are linked by pathways of energy transfer and

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Australian Freshwater Ecology: Processes and Management, Second Edition. Andrew J. Boulton, Margaret A. Brock,
Belinda J. Robson, Darren S. Ryder, Jane M. Chambers, and Jenny A. Davis.

Companion Website: www.wiley.com/go/boulton/freshwater

Figure 4.1 Around and beneath the mirror-like surface of Narawntapu wetland, Tasmania, aquatic biota influence and are influenced by physical and chemical processes in the waterbody and its catchment. (Source: Jenny Davis.)

Table 4.1 Biological processes can be considered within a hierarchy of levels of organization. Processes at one scale influence those at higher and lower scales.

Level of organization	Biological processes (examples)
Individual	Dispersal, respiration and feeding
Population	Changes in numbers of individuals, age or size structure, competition within a population
Community	Trophic interactions such as predation and competition among species
Ecosystem	Ratio of photosynthesis to respiration (P:R), biogeochemical cycling of nutrients

biogeochemical processes. On the landscape scale, ecosystems interact and exchange nutrients, energy and water. No one scale is the most important, and processes at one scale influence those at larger and smaller scales. For example, colonization by microbes of a dead leaf that falls into a waterbody will affect the rate of decomposition of that leaf and hence the rate of carbon cycling through the ecosystem. Activities such as agriculture and forestry, which occur at the landscape scale, can alter the inputs and types of dead leaves and this may affect the community composition and population structure of the organisms that break down the leaves. Understanding how processes interact across a range of scales in time and space is one theme of this book.

4.2 MAJOR ECOLOGICAL ZONES AND HABITATS

Aquatic ecologists recognize several major ecological **zones** in standing waters. Although their boundaries may be ‘blurred’ (Section 4.3), the zones are useful when we discuss and compare different standing waters. Within, and sometimes across, these zones are **habitats** occupied by characteristic assemblages of plants and animals. These different habitats provide different resources and conditions because the zones vary in heterogeneity, stability, water chemistry and physical features – again, at multiple scales of space and time.

The upper region of the water column, where plants receive enough light to photosynthesize, is the **euphotic zone** (Figure 4.2). Below it is the poorly lit **profundal zone** (Figure 4.2). The entire bottom of the waterbody is the **benthic zone** (benthic = ‘bottom’). Wherever the euphotic zone extends down to the bed is the **littoral zone** and this includes the bottom and the water above it. The water column directly above the profundal benthic zone is called the **open water** (or limnetic or pelagic) **zone**. Finally, extending from the shoreline of the littoral zone out to the edge of the vegetation beyond the influence of the waterbody is the **fringing zone** (Figure 4.2). This zone is ecologically equivalent to the riparian zone bordering running waters (Section 7.2 and 10.4).

The **air-water interface** provides support for floating plants and animals (**pleuston**) because of the high surface tension of water caused by the hydrogen bonds that link water molecules (Section 1.5.1). Below this interface, the open water and the water column of the littoral zone is inhabited by **nekton** such as fishes and mobile invertebrates, and the **plankton**, which are

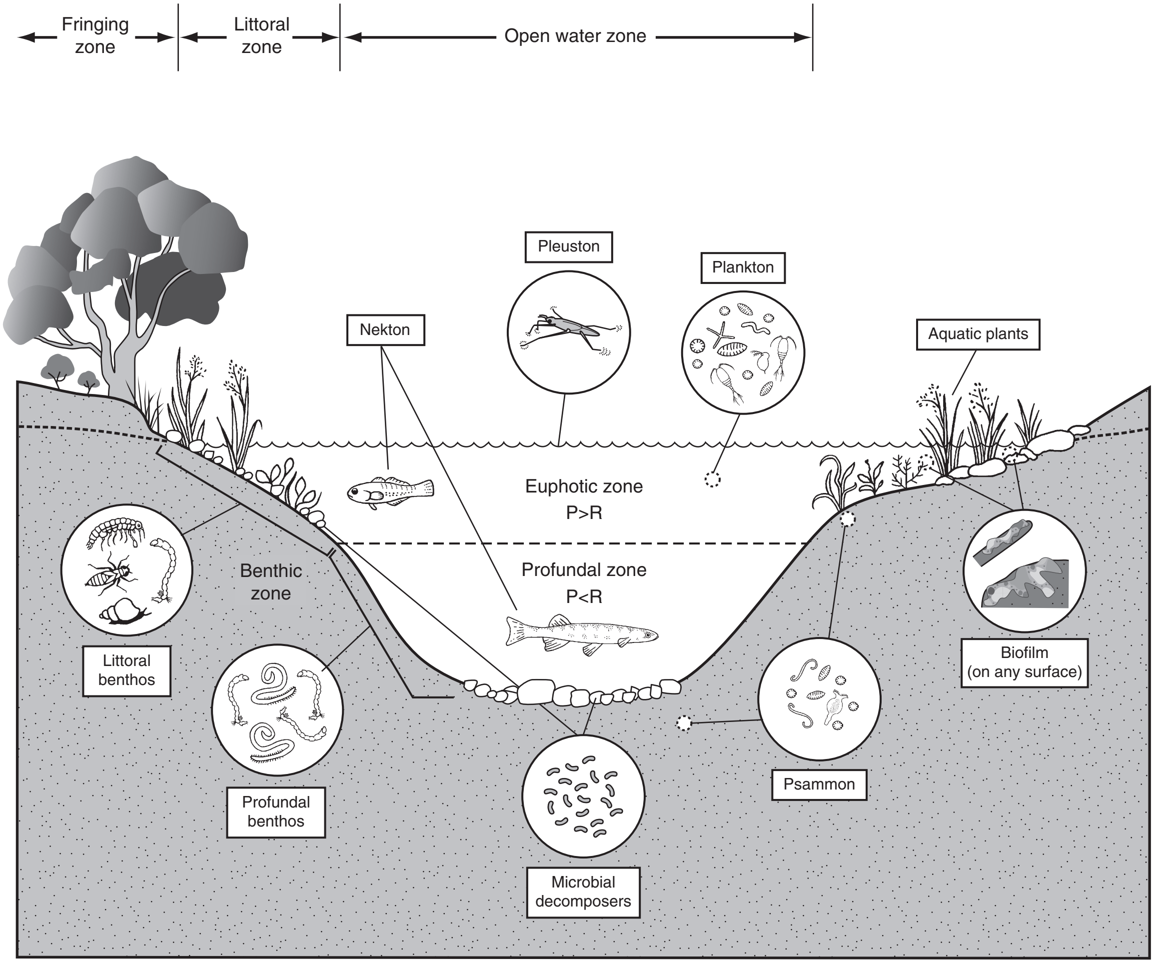

Figure 4.2 Biological assemblages (boxes) associated with the major zones and habitats of standing waters. P = photosynthesis; R = respiration. (Source: Adapted from Chambers *et al.* 2009. Reproduced with permission of Cambridge University Press. Image drawn by Belinda Cale.)

often less mobile. Plankton are further divided according to whether they are plants (**phytoplankton**) or animals (**zooplankton**). There are also smaller forms such as bacterioplankton and nanoplankton, discussed later in this chapter.

Organisms that live in the benthic zone are collectively called the **benthos**. They are often further divided into littoral benthos and profundal benthos – two broad groups of organisms able to exploit the very different conditions in these two zones. In both zones, the benthos includes the **psammon**, the microscopic plants and animals inhabiting the saturated spaces among the sediment particles. **Decomposers**, organisms that break down or eat dead and decaying plant and animal material, are common in the benthos, probably because that is where most of their food settles. Many underwater surfaces in the benthic zone and of aquatic plants in the water are coated in **biofilms**, a complex matrix of fine organic matter and small organisms including algae, microbes and fungi.

The plants in these biofilms are termed **periphyton** when attached to any submerged surface and **epiphytes** when attached specifically to plants.

These zones typically differ in their predominant biological processes. For example, in the littoral zone, rates of photosynthesis exceed those of respiration (P > R, Figure 4.2) whereas the converse occurs in the profundal zone (P < R) where there is far less light. Shallow waterbodies can be very productive because both the open water and the benthic zones receive enough light for plants to grow. In deeper waterbodies that stratify (Section 2.5), the profundal benthic zone is often hypoxic or anoxic and the sediments are usually finer and more homogenous than those within the littoral benthic zone. Consequently, fewer species live in the profundal zone than in the littoral zone where the habitat is more physically complex and well-oxygenated. While you read the following sections about the biota that use these different zones and the different processes that take place there, keep thinking about what sorts of constraints are imposed on them by the physical and chemical conditions within each zone. How might these conditions vary over time and across different types of lentic environments?

4.3 BLURRED BOUNDARIES AND MOBILE ASSEMBLAGES

Many texts discuss the assemblages of plants and animals specific to ecological zones but we prefer to avoid the implication that there are *always* distinct assemblages that typify each zone. Not only are the boundaries between the zones indistinct at fine and intermediate spatial scales, but many aquatic organisms cross them readily using multiple zones as their habitat. For example, nekton can live in both euphotic and profundal parts of the open water zone but also swim into the littoral zone to feed.

Despite these blurred boundaries, this classification into zones is conventional and helps us think about the different processes occurring in them. It also guides our methods for collecting lentic organisms because different equipment is typically used to sample in different zones, and even different habitats within zones. For example, a long-handled dip net (Figure 4.3a) is used to collect fast-swimming littoral invertebrates, whereas a grab sampler (Figure 4.3b) would be appropriate for sampling soft profundal sediments. A plankton net (Figure 4.3c) towed through open water captures swimming and drifting zooplankton and phytoplankton. Where quantitative samples are needed, the use of a corer will provide invertebrate densities by sampling a known area of shallow sediments. Similarly, a stovepipe sampler (Figure 4.3d) will collect littoral or open water invertebrates from a known volume of shallow water.

There are two other points to make. The first is that lentic (and lotic) aquatic ecosystems do not stop at the water's edge. The fringing zone (Figures 4.1 and 4.2) is an integral part of a lentic ecosystem, providing a dynamic interface or **ecotone** between the wet and dry components. This ecotone is an important habitat for many organisms and is the site of much of the nutrient and organic matter cycling that fuels food webs and energy subsidies of aquatic and terrestrial components of all lentic ecosystems. Consequently, it must be recognized in management and conservation (Chapters 9–12), and not overlooked simply because it appears dry for much of the time.

The second point also relates to spatial context. At the landscape scale, **mosaics** of waterbodies of different types and sizes are interconnected and interspersed with terrestrial environments and their assemblages. These mosaics support populations of species that can disperse between waterbodies when conditions are favourable (Gibbs 2000). For example, dispersal by fully aquatic species, such as fishes, is promoted by the hydrological connectivity among floodplain wetlands during high flows (Fullerton *et al.* 2010). Conversely, many isolated basin wetlands are not connected by surface flows (e.g. the numerous shallow waters across the arid inland) and are occupied by aquatic plants and animals that can cross dry land or disperse actively or passively by air. Many of these plants and animals can also persist in the dry sediments of temporary waterbodies (Section 4.7). When studying the assemblages and biological processes of standing waters, we must always consider their landscape context and their linkages with surrounding terrestrial, groundwater, estuarine and marine ecosystems.

4.4 TROPHIC GROUPS AND SOURCES OF ENERGY

Aquatic food webs encompass three major trophic groups: **producers**, **consumers** and **decomposers**.

Figure 4.3 Different sampling equipment used to collect organisms from different habitats: (a) sweep-net sampling with a pond net (here, held above the water to show the collecting bag on the frame); (b) a benthic grab sampler, spring-loaded in the 'open' position and triggered shut when the heavy weight ('messenger' to the left) is released to slide down the cord and hit the top of the sampling box; (c) a plankton net, with a sample-jar screwed to the apex, about to be cast out into the water and towed back to shore; (d) a stove-pipe sampler (the middle person is using a bilge pump to evacuate the contents of the sampling box (right) into a collecting net (left). (Source: (a) and (b) Darren Ryder, (c) and (d) Jenny Davis.)

Most producers convert energy from sunlight via photosynthesis into chemical energy stored as carbohydrates. Consumers are organisms that cannot make their own food (i.e. fix carbon) and so they rely on producers or other consumers for their nutrition. They include **herbivores** feeding directly on living plant material, **carnivores** feeding on other consumers, and **omnivores** eating both producers and consumers (either dead or living). Conversely, **detritivores** and **decomposers** only consume dead and decaying plant and animal material, collectively termed **detritus** (Section 3.9.3). Throughout this book, we use 'decomposers' as a general term for all organisms that break down or eat detritus whereas detritivores are a subset of decomposers that feed directly on detritus. Unlike fungi, bacteria and other microbial decomposers, detritivores do not actually mineralize the detritus but their feeding activities often expose greater surface areas for microbial decomposers.

Broadly, there are two major pathways by which energy flows and matter cycles through aquatic systems: a producer–consumer (**autotrophic**) pathway and a detritus–decomposer–consumer (**heterotrophic**) pathway (Figure 4.4). In the autotrophic pathway, solar energy powers photosynthesis by producers (i.e. autotrophs) such as phytoplankton and attached algae, as well as plants at the water's edge. Herbivores feed directly on this living plant material and, in turn, are fed on by other consumers and, ultimately, decomposers. Plant tissue that is not eaten by herbivores will eventually die and be decomposed via the heterotrophic pathway. In the heterotrophic pathway, dead organic matter enters the food web from terrestrial sources, groundwater and fringing vegetation as well as from aquatic sources. This dead organic matter is colonized by microbes and fungi or consumed by detritivores that are then eaten by carnivores. Remember, this is only a general model and the pathways are seldom so clear cut. Nonetheless, Figure 4.4 is a handy conceptual framework to help us think about how trophic groups rely on different sources of energy and how changes to water regime, physical structure and water chemistry might affect these two pathways in different types of standing waters.

Building on this conceptual model, standing waters can be classified into either **net autotrophic** or **net heterotrophic** systems, depending on which pathway is dominant. Dominance can be measured by comparing the amount of primary production (P) to the amount of respiration (R), and is often done by measuring changes in the uptake and release of oxygen as an indication of the relative amount of photosynthetic activity (which produces oxygen) to respiration (which consumes oxygen). The ratio of P to R provides valuable information about the way organic matter is processed, nutrients are cycled, and energy is transferred in aquatic ecosystems. Light availability influences the relative dominance of autotrophy versus heterotrophy. Typically, the well-lit euphotic zone is autotrophic ($P > R$) whereas the dark profundal zone is heterotrophic ($P < R$) (Figure 4.2). Extensive shading by fringing vegetation or steep banks also favours heterotrophy. Highly turbid conditions in many Australian inland waters imply heterotrophy because light penetration is limited by suspended sediments, although autotrophy may also occur (e.g. some turbid waterholes along Cooper Creek in western Queensland, Burford *et al.* 2008).

Another benefit of this conceptual model is that it helps us think about the number of links along a trophic pathway in a particular system. Energy is dissipated at each link, limiting the number of links possible and consequently, the lengths of food-chains and networks (Box 4.1). Food web analysis has always been a challenging task, involving gut content analyses and delicate dissections. More recent techniques such as DNA-based dietary analysis provide better taxonomic resolution of diets at much shorter timescales and are becoming more widely used as costs fall and technology improves (Pompanon *et al.* 2012).

Finally, this conceptual model invites us to determine the sources of carbon in a food web and how much of that carbon is taken up (i.e. assimilated) during each link along the pathway. One powerful technique for this is stable isotope analysis, where the ratios of different isotopes of nutrients such as carbon and nitrogen are measured in a variety of consumers and their potential food sources, and then compared to assess the likely pathways by which the nutrients travelled (Box 4.2). When trying to distinguish carbon produced within the aquatic ecosystem (**autochthonous**) from that produced externally (**allochthonous**), we can use isotopic ratios and various 'mixing models' to test hypotheses about the dominance of one source versus the other. In reality, the distinction is blurred by the difficulty in deciding whether carbon produced by a plant in the fringing zone, for example, is autochthonous or allochthonous and because many animals are dietary generalists. Most ecologists now address these issues by using techniques such as stable isotope

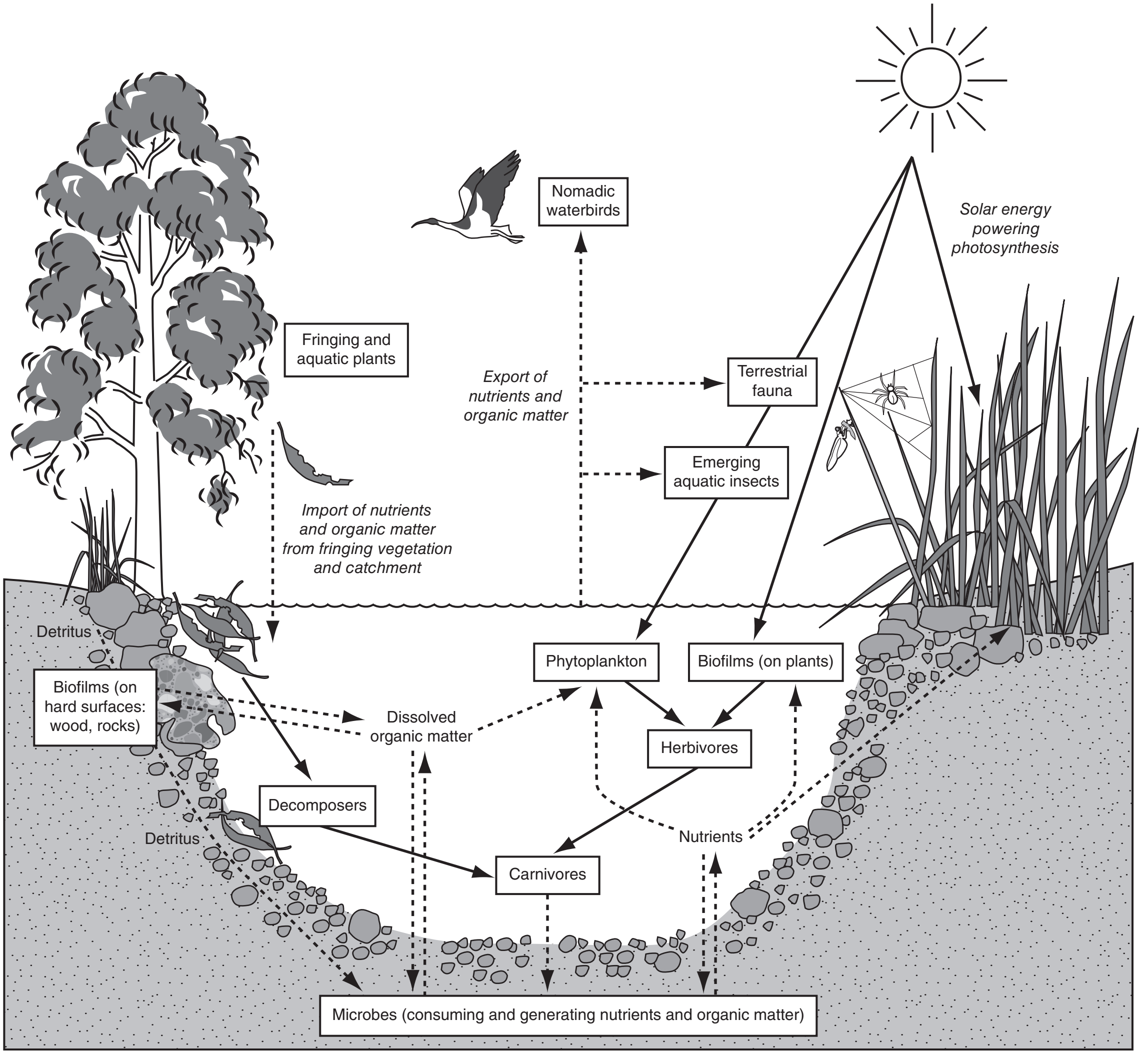

Figure 4.4 The two major pathways by which energy flows (solid arrows) and organic material and nutrients cycle (broken lines and arrows) through standing waters: a heterotrophic detritus–decomposer–consumer food chain (left-hand side of figure) and an autotrophic producer–consumer food chain (right-hand side). All decomposers and consumers excrete nutrients and, when they die, decompose to become detritus (pathways not shown). (Source: Image drawn by Belinda Cale.)

analysis to specifically identify sources of carbon and other nutrients.

4.5 PRODUCERS

Producers occupy every aquatic habitat where there is sufficient light, nutrients and gases for photosynthesis. They are diverse in size and shape (Figure 4.5), and represent all evolutionary plant groups, including cyanobacteria (blue-greens), microscopic algae (e.g. diatoms, desmids), macroscopic algae (e.g. charophytes and filamentous algae), and larger plants, including bryophytes (mosses and liverworts), ferns (e.g. *Azolla*) and flowering plants. Some Australian aquatic plant species

Box 4.1 Food chain lengths and networks in standing waters

Food webs encompass all component species in an aquatic habitat and the feeding links between them. The study of food webs has been particularly active in fresh water, and some of the largest, most highly resolved and complex food webs have been described from streams and lakes (Thompson *et al.* 2012a). The main strength of food web studies is that they incorporate patterns of biodiversity and the processes that underpin those patterns, including fluxes of energy (Thompson *et al.* 2012b). Seminal research from lakes and streams showed that decreasing the amount of energy entering the base of a food web (as either primary production or detritus) led to the loss of top predators, resulting in shorter food chains. Understanding food webs also allows predictions of the effects of removing particular species or increasing rates of harvesting. Models based on food webs, such as Ecopath (Christensen and Pauly 1992), have been widely applied in the management of lake fisheries. Detailed, long-term datasets on food webs from standing waters can also show the direct and indirect consequences of stresses such as climate change and invasive species.

Ross Thompson, University of Canberra

Box 4.2 Stable isotope analysis in standing waters

Recent advances in food web ecology have relied heavily on stable isotope analysis (SIA), a relatively quick and cheap method of assessing ‘who eats whom’ within systems. SIA provides powerful insights into trophic relationships, particularly when used in combination with gut analyses. I used both these techniques to explore the trophic overlap and the potential for competition between the invasive small-bodied eastern gambusia *Gambusia holbrooki* and the native carp gudgeon *Hypseleotris* in floodplain wetlands of south-eastern Australia. Stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope signatures and gut contents of both species revealed they often shared similar trophic positions. They both fed predominantly on larval chironomids and small crustaceans called chydorids in summer and spring, when allochthonous resources (leaves of river red gum *Eucalyptus camaldulensis*) were primarily fuelling food webs. However, seasonal flooding increased the variety of basal resources in the wetlands, causing *G. holbrooki* to shift towards assimilating consumers of filamentous algae. These insights into the effect of seasonal flooding and changing food web structure on the potential for competition between these two fish species would not have been as revealing without SIA.

Susie Ho, Monash University

occur world-wide such as the reed *Phragmites australis*, which occurs in both hemispheres from the equator to 70° latitude (Roberts and Marston 2011). Although many of the aquatic flowering plants and freshwater algal groups are cosmopolitan at the generic level, they are often regionally or locally endemic at the species level. Consequently, some are threatened and require special protection and conservation (Chapter 12).

In this book, all producers, whether microscopic (i.e. invisible to the naked eye) or macroscopic, are referred to as **aquatic plants**. To minimize confusion, we avoid the term ‘macrophyte’ because many references unfortunately use the term loosely, sometimes to mean all aquatic plants, sometimes only submerged aquatic plants and sometimes only the larger plants. While on terminology, we follow Huisman and Saunders (2007) in using the term ‘**algae**’ (singular is ‘alga’) to include all macroalgae, unicellular and multicellular microalgae and cyanobacteria. This last group will be referred to as ‘cyanobacteria’ or ‘blue-greens’ (and not

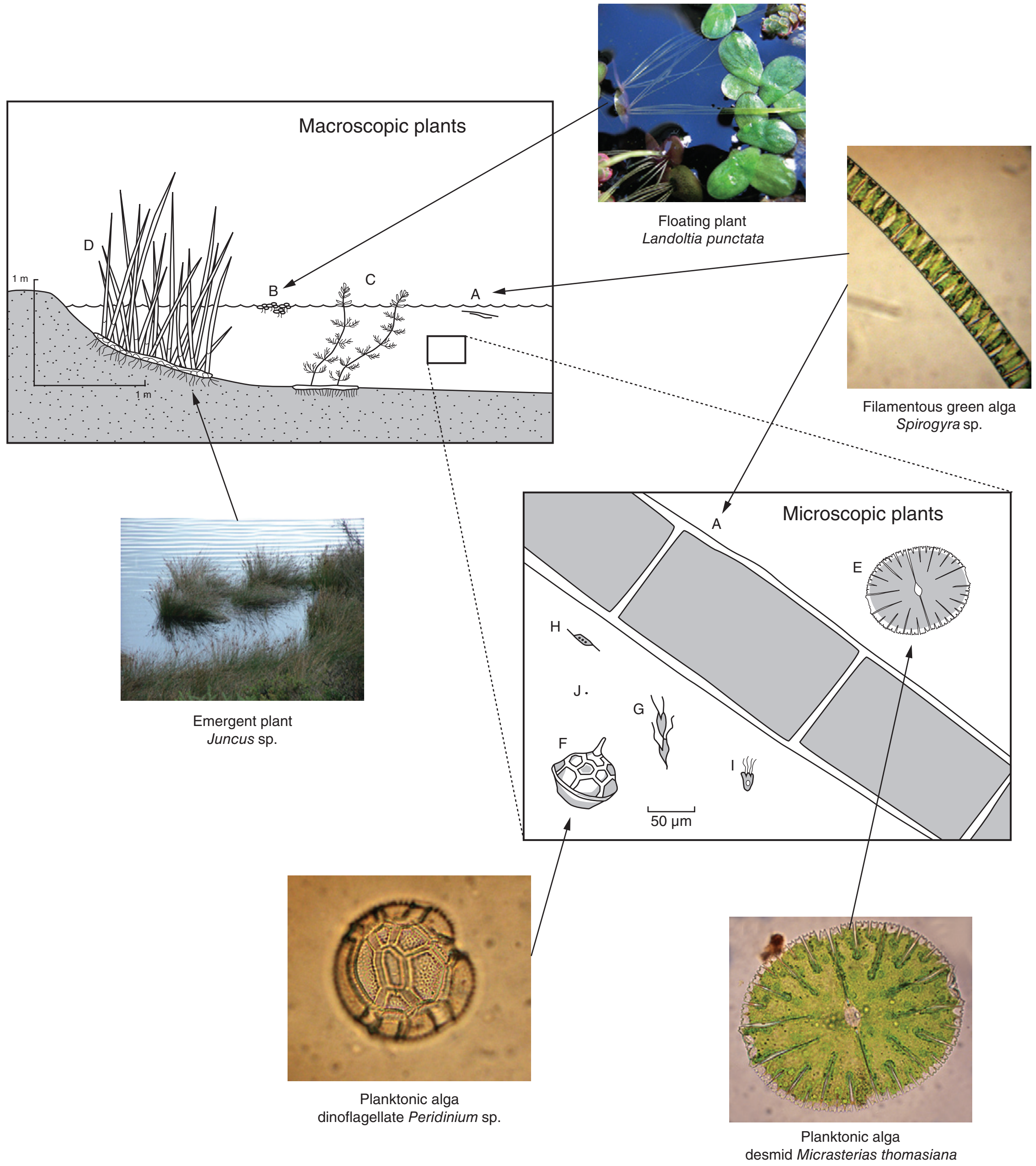

Figure 4.5 Relative sizes of some lentic producers. Macroscopic plants include the filamentous green alga *Spirogyra* (A), floating plants such as duckweed *Landoltia punctata* (B), submerged plants such as *Myriophyllum* (C) and emergent plants like *Juncus* (D). Microscopic plants (with a close-up of *Spirogyra*: A) include phytoplankton such as the desmid *Micrasterias thomasiana* (E), dinoflagellates like *Peridinium* sp. (F), golden-brown algae (G), diatoms (H), and green unicellular algae (I). Many bacteria (represented as a small dot, J) are also producers. (Source: Adapted from Brock 1994 and reproduced with permission of Cambridge University Press. Images: *Landoltia punctata* – Mark Wapstra; algae – Joan Powling; emergent plant – Margaret Brock.)

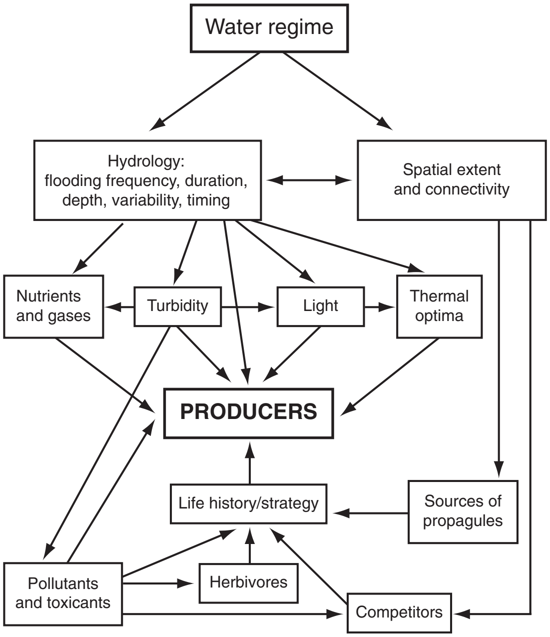

Figure 4.6 Water regime plays a major role in governing the ecology of producers in aquatic ecosystems. Arrows indicate direction of effect. (Source: Boulton and Brock 1999.)

'blue-green algae') in recognition that they are actually bacteria (prokaryotes).

Water regime (Figure 4.6) governs the availability of resources such as nutrients, gases and light (Chapters 2 and 3), which are all crucial to photosynthesis. It also interacts with climate and geography to affect landscape-scale factors such as the hydrological connectivity within and among mosaics of standing waters over time, which influences biological processes such as colonization and dispersal. Other biological processes that affect the ecology of producers include competition and herbivory (Figure 4.6) and these are reviewed later in this chapter.

4.5.1 An ecological classification of producers

Producers in and around waterbodies may be aquatic or terrestrial. Of the aquatic ones, some are completely aquatic, some use both water and air, and some alternate between complete submersion and desiccation. Aquatic plants can be divided into microscopic or macroscopic (Figure 4.7), and may live suspended, free floating or attached to surfaces. Macroscopic aquatic plants rooted in or attached to the sediments have their photosynthetic parts such as leaves either floating, submerged or emergent, and many are amphibious (able to live both on land and in water) or semi-terrestrial (able to grow in damp but not flooded places). This functional group classification provides a framework for thinking about how different groups of producers exploit habitats and cope with different water regimes (Brock and Casanova 1997). It also facilitates intra- and inter-system comparisons and predictions, even when species differ taxonomically. For example, amphibious species thrive in unpredictable water regimes of many temporary wetlands in Australia but rarely establish in the predictable twice-daily water fluctuations in US freshwater tidal wetlands (Leck and Brock 2000). This functional approach has also been used to predict vegetation response to changes in inundation depth, duration and frequency (Casanova and Brock 2000).

4.5.2 Microscopic aquatic plants

Microscopic aquatic plants range in size from less than a micron to clearly visible colonies and filaments. Taxonomically, they include the prokaryotic blue-greens (Cyanobacteria), and a range of eukaryotic groups dominated by the green algae (Chlorophyta), diatoms (Bacillariophyta), euglenoids (Euglenophyta), cryptomonads (Cryptophyta), dinoflagellates (Dinophyta) and golden-brown algae (Chrysophyta). Cyanobacteria, green algae and diatoms are often dominant so we shall describe them in a little more detail.

Cyanobacteria (blue-greens) are prokaryotic photosynthetic bacteria that lack structures such as chloroplasts and nuclei, yet often have functional features such as gas vesicles that aid buoyancy (Brookes *et al.* 2000). They can be single cells, colonies or filaments, and reproduce asexually. As their name suggests, they appear blue-green. The **green algae** appear grass-green and are a diverse group that includes solitary forms such as *Chlamydomonas* and *Micrasterias* (Figure 4.5) and colonial forms that may number thousands of cells (e.g. *Volvox*). In *Volvox* colonies, outward-directed flagellae propel the gelatinous mass along like a miniature, spinning green golf ball. Some flagellate

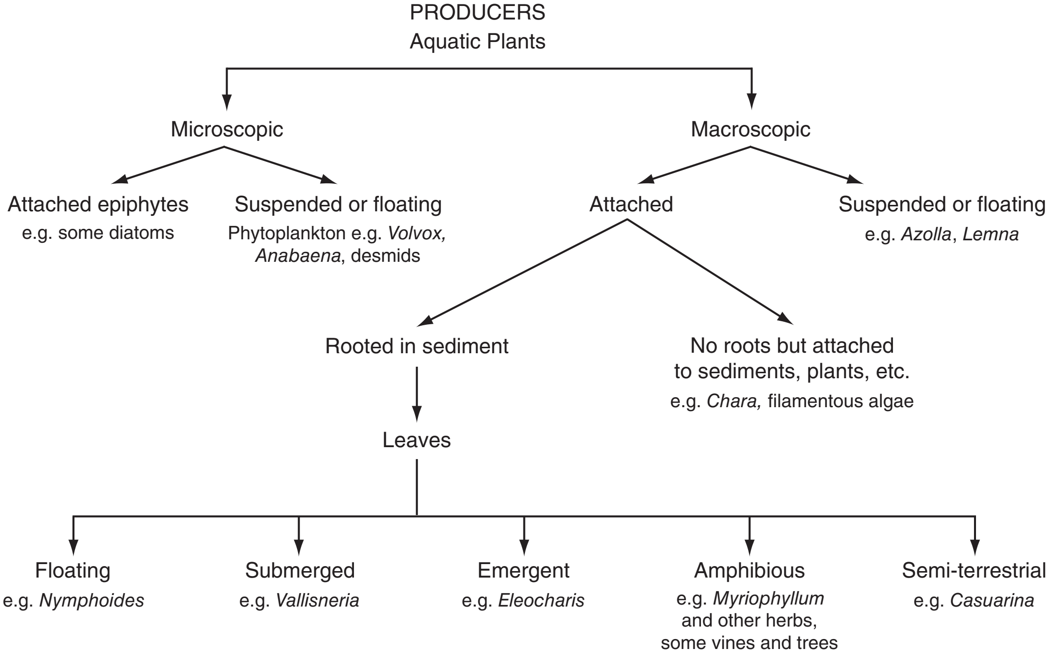

Figure 4.7 Functional-group classification of the growth forms of microscopic and macroscopic aquatic plants based on where they grow in relation to water regime (i.e. when, where and to what extent water is present). (Source: Boulton and Brock 1999.)

algae have an 'eye spot' as part of the chloroplast that serves to detect the direction of light. Most **diatoms** are yellow to light brown, and occur as single cells, filaments or colonies. They are characterized by their silica cell wall, which is often intricately beautiful (Figure 3.12). Australian freshwater algae can be identified using Entwisle *et al.* (1997, 2007) and the online algal key ALGKEY (Yee and Entwisle 2013).

Ecologically, microscopic aquatic plants occur as phytoplankton in the open water zone, periphyton growing attached to all substrata including plants (epiphyton) and rocks (epilithon), and microphytobenthos (part of the psammon) living where sufficient light reaches the sediments. The main functional distinction is whether they are attached or suspended (Figure 4.7), because this affects their capacity to respond to changes in water regime as well as light levels and other essential resources.

Phytoplankton are often categorized by size (Figure 4.5): femtoplankton (0.02–2 μm – virus-like particles), picoplankton (about 2 μm – some algae and cyanobacteria), ultraplankton (2–5 μm), nanoplankton (5–20 μm), microplankton (20–60 μm) and net plankton (>60 μm). In waterbodies with low nutrient concentrations (i.e. oligotrophic), picoplankton and ultraplankton probably carry out much of the photosynthesis. Many smaller phytoplankton such as cryptomonads, dinoflagellates and golden-brown algae consume bacteria as well, thus blurring trophic boundaries (Moss 2010). Reliant on light, phytoplankton live in the euphotic zone in shallow lakes and in the epilimnion of stratified lakes. The activity and distribution of different species vary during the day, seasonally and from year to year, usually in response to variations in light, nutrients, turbidity, temperature, competitors and grazers (Brookes *et al.* 1999).

Phytoplankton blooms occur naturally but are now more frequent because of human activities that increase the concentrations of nutrients (Section 11.3). Although blooms of green algae or diatoms occur (e.g. the diatom *Aulacoseira granulata* in the Murray River: Hötzel and Croome 1996), the blooms that attract

Box 4.3 Microalgae in arid-zone standing waters: diversity, dynamics and ecological significance

The diversity of microalgae in the arid zone (e.g. the Lake Eyre Basin in 2000–2012) is impressive. From first wetting to final drying and in between, phytoplankton diversity fluctuates according to local flows, rainfall and salinity (Costelloe *et al.* 2005). It peaks immediately after the arrival of floodwaters when bacteria and diverse assemblages of flagellates and other picoplankton develop and are readily devoured by newly hatched rotifers and microcrustaceans. Around the shoreline of some of the large lakes, benthic cyanobacteria, green algae and diatoms form ‘bathtub ring’ mats, important components of the food web for many macroinvertebrates and wading birds. However, it is the truly planktonic cyanobacteria that command attention because of their vivid appearance during a bloom and their potential toxicity to animals, including humans. Diversity changes over time and with salinity. Species such as *Anabaena circinalis* and *Cylindrospermopsis raciborski* are present early in the cycle. As salinity increases, the large episodic lakes support tens of thousands of waterbirds feeding in self-sustaining blooms of *Anabaena aphanizomenoides*, *Nodularia spumigena* and species of *Spirulina* and *Anabaenopsis*. Eventually, the lakes dry ... until the next ‘boom-and-bust’ cycle begins again.

Joan Powling

most attention are cyanobacterial (e.g. *Anabaena*, *Microcystis*) because they can render water toxic to livestock and humans. Conditions for cyanobacterial blooms vary with factors such as salinity and light (Oliver *et al.* 2010), and understanding more about the physiological responses of cyanobacteria to these factors guides prediction and management of future blooms, especially in water storages (Oliver *et al.* 2012). Phytoplankton are also conspicuous in many arid-zone standing waters (Costelloe *et al.* 2005), especially temporary ones where large populations develop swiftly soon after re-wetting (Box 4.3).

Periphyton, often dominated by green algae and diatoms, forms part of the biofilm on submerged surfaces such as rocks and plant leaves at appropriate depths for photosynthesis. Submerged parts of most flowering plants, mosses and liverworts are often densely colonized by epiphytes. In sediments where light is sufficient for photosynthesis, there may be different suites of algae, usually dominated by single cells, filaments or colonies of diatoms. Microscopic algae also grow inside plants but are seldom host-specific. An exception is the symbiotic relationship between the cyanobacterium *Anabaena azollae* and the floating fern *Azolla filiculoides* (Section 3.9.2). Microalgae also grow on animal substrata such as turtle shells, crocodiles, snails and crustaceans, and are referred to as epizoic (literally ‘on’ + ‘animal’) algae.

Before we discuss macroscopic aquatic plants, we should emphasize the importance of microscopic aquatic plants to lentic **primary productivity**. Primary production is a function of plant biomass and productivity. **Biomass** is how much material there is at a given time (often measured as g m^{-2}). Individual producers with the highest biomass are usually macroscopic plants such as sedges and trees; in comparison, microscopic algae have very little biomass. **Productivity** is the rate of generation of this biomass (often measured as g m^{-2} y^{-1}). Although microscopic algae such as phytoplankton have low biomass, they are short-lived and so their rates of generation and turnover are high. Thus, primary production by microscopic aquatic plants can rival that of the larger and more obvious macroscopic plants, and even temporarily exceed it in nutrient-enriched systems. Other factors affecting the contribution of different types of plants to aquatic primary production include the shape of the basin, the composition of the sediments, water chemistry, biotic interactions and changes in climate and hydrology.

4.5.3 Macroscopic aquatic plants

Ecologically, macroscopic aquatic plants tend to be described by where their photosynthetic parts (e.g.

leaves) sit in relation to the water (Figure 4.7). This is more than simply for convenience; it also relates to how the plants cope with a variable water regime, how they exploit resources in different parts of the waterbody, their relative rates of production and the habitats that they provide for other aquatic organisms.

Floating plants have the whole plant, or just their leaves, at the water surface. The smallest flowering plants, the duckweeds (e.g. *Wolffia australiana*), the liverwort *Ricciocarpus natans* and the fern *Azolla* all float at the surface. Many floating plants must get all their nutrients from roots or rhizoids (root-like structures) suspended in the water. Therefore, they flourish in nutrient-enriched conditions while enjoying the competitive advantage of access to light at the water's surface. Floating plants provide microhabitats for epiphytes, invertebrates and fishes, and cope easily with rapid changes in water level, especially if the whole plant floats.

Submerged plants, such as ribbon weed *Vallisneria*, photosynthesize mostly under water. Although submerged and usually rooted in the sediments, most of these plants must flower at the water surface. To do this, some species employ a coiled spring-like stalk (Figure 4.8) to maintain the flower's position at the water surface for pollination. Submerged plants grow as deep as light and, in especially clear lakes, water pressure will allow. Bryophytes and charophytes often occur deeper than flowering plants because they do not need to reach the surface to reproduce. Although submerged plants may suffer from light shortage when screened by phytoplankton or suspended particles, they benefit from growing in sediments that are generally much richer in nutrients than the over-lying water. Submerged plants provide a complex physical habitat for attached biofilms, algae and aquatic animals as well as a food supply for some waterbirds (Section 4.6.5).

Figure 4.8 The submerged plant *Ruppia tuberosa* uses a coiled spring-like stalk (lower right) to hold its flowers at the water surface and then retracts them under water after pollination. (Source: John Porter.)

Emergent plants are rooted in the sediments with a major proportion of their photosynthetic parts above the water. They include aquatic grasses, rushes, sedges, and some trees and shrubs (Figure 4.7). Emergent plants are limited to water shallower than about 2 m unless they have specialized internal aeration to move gases between sediment and surface (Sorrell and Hawes 2010). These plants play a key role in nutrient cycling and provide habitat for nesting and foraging waterbirds, calling places for breeding frogs, and upright stems for the emergence of aquatic insects such as dragonflies. Although the tubular or strap-like architecture of most emergent plants creates less complex habitat than other plant groups for littoral invertebrates, the attached assemblage of microalgae, bacteria, fungi and small invertebrates such as freshwater limpets, is often rich and diverse.

Around the edge of the shoreline where the littoral zone wets and dries, we find a species-rich and highly productive community of **amphibious** plants. Some trees, shrubs, sedges, rushes and grasses tolerate changes in water level whereas many herbs respond to water level change by varying growth form or leaf shape (Brock and Casanova 1997, Section 4.5.4). The upper shoreline is occupied by **semi-terrestrial plants** such as rushes (e.g. *Juncus* spp.), herbs (e.g. *Gratiola peruviana*), shrubs and trees (e.g. some *Casuarina* spp.) that cannot tolerate extended flooding. These plants in the fringing zone (Figure 4.2) usually dominate the wet-dry ecotone between aquatic and terrestrial ecosystems.

Texts on State or regional floras, and online keys from State herbaria, can be used to identify aquatic flowering plants and ferns, liverworts and mosses. Specialized references for macroscopic aquatic plants include Aston (1973) and Sainty and Jacobs (2003). Be careful when using older texts (because scientific names often change) and where possible, confirm the names with the Australian Plant Names Index (www.anbg.gov.au/apni/) or using web-based herbarium lists from individual states and territories.

4.5.4 Plants living in water: benefits and constraints

Living in water has benefits and constraints for plants. On the positive side, water is usually readily accessible for metabolic processes and to provide structural support in the water column. On the negative side, gases and light are less available in water than in air (Chapters 2 and 3). Biological processes such as reproduction are also problematic for submerged flowering plants and ferns, and it is fascinating to see how different ecological groups have solved the problems of living in water.

To **grow underwater**, the photosynthetic parts must obtain sufficient light and a reliable supply of gases and nutrients. Submerged flowering plants maximize capture of gases and light by suspending their thin (for gas absorption) and large or finely divided (for maximum surface area) leaves in the euphotic zone. Their stems have large air spaces and little woody tissue, yet provide adequate support in the buoyant water with a low investment of energy.

Phytoplankton also need access to light so they must maintain their position in the water column without sinking. Some, such as various cyanobacteria, are buoyed up by gas vesicles or oil droplets. However, most are denser than water and would sink if not for wind-generated water movements or the action of flagellae. Many diatoms, desmids, dinoflagellates and other aquatic plants have cell or colony sizes and shapes that slow rates of sinking. For example, long spines on many desmids (Figure 4.9) slow their rate of sinking and also make them more difficult for zooplankton to consume. In contrast, periphyton must stay attached and avoid being eaten while still obtaining their requirements for metabolism. Most filamentous algae have a holdfast cell to hold them in place, and rapid growth of filaments soon renders them too large for most herbivores.

To **reproduce sexually under water**, gametes must meet to fertilize and this is a special challenge for some groups. Algal groups evolved in water so have little problem releasing gametes into the water where they fertilize. However, flowering plants, which evolved on land, have gametes that cannot swim and must rely on wind or insect pollination in air or at the air-water interface. Elongated flower stalks or shoots often elevate flowers to or above the water-surface for pollination. Ribbon weeds (*Vallisneria*) have separate male and female flowers. Female flowers reach the surface on long flower stalks; male flowers break off and float to the surface where the petals act as a keel and a sail as each flower disperses its pollen. After pollination, the spiral stalk draws the female flower back underwater where seeds develop and disperse. Most salt-lake and estuarine plants (e.g. most *Ruppia* and *Lepilaena* species) also rely on pollination at the water surface, with flowers then withdrawn underwater on spiral stalks (Figure 4.8). However, *Ruppia maritima* pollinates underwater by releasing an air bubble from the vascular system, and the pollen and egg meet on this submerged air-water interface. For many flowering plants, vegetative spread by rhizomes, stolons or overwintering buds (turions) supplements sexual reproduction.

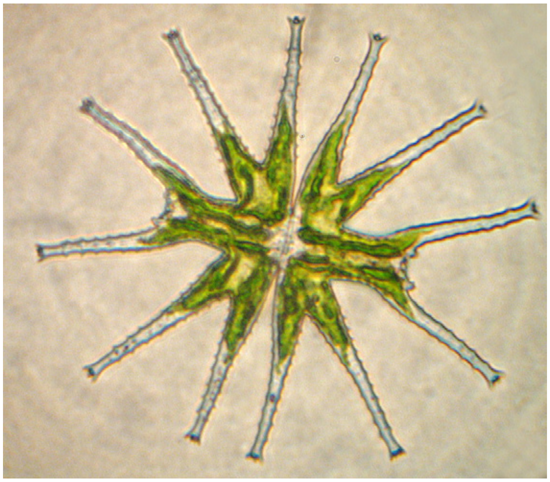

Figure 4.9 The imposing spines of this phytoplanktonic desmid *Micrasterias hardyi* (diameter 160 μm) slow its rate of sinking and deter predators. (Source: Joan Powling.)

To **live in both flooded and dry conditions**, amphibious plants lead a dual life of submersion then emersion. Many have evolved complex combinations of morphological plasticity and reproductive flexibility to cope. For example, when stranded on mud, the water milfoil *Myriophyllum variifolium* grows prostrate and has entire leaves and roots at each node. When inundated, the plant has long internodes, grows upright and has divided underwater leaves that maximize light capture. A single plant can change its form within days between being stranded and flooded. Water milfoil can also reproduce asexually or sexually, further broadening its options.

Figure 4.10 Modified leaves of the submerged bladderwort *Utricularia australis* trap small planktonic organisms that are digested, providing nutrients to the plant. (Source: Hans and Annie Wapstra.)

Many aquatic plants in temporary waters have long-lived desiccation-resistant seeds or spores that can survive in the sediments when drying occurs. Not all these seeds germinate on first flooding, and this helps insure against local extinction in a waterbody with a variable water regime (Brock 2011). Most attached algae in standing waters have physiological mechanisms to survive drying, similar to those of algae in temporary streams (Chapter 7).

To **live in low-nutrient waters**, common in Australia, some plants have become consumers and decomposers as well as producers to increase their access to nutrients. Bladderworts such as *Utricularia australis* (Figure 4.10) derive additional nutrients from catching and digesting small planktonic organisms in hundreds of traps (modified leaves) where digestive enzymes and mutualistic bacteria decompose the prey to soluble nutrients. Carbon assimilated from photosynthesis helps support the mutualistic bacteria whose secretions apparently attract zooplankton into the traps (Albert *et al.* 2010).

4.5.5 Alternative states: changes in plant dominance in shallow waterbodies

We have seen that the composition of different assemblages of producers in standing waters is governed by water regime, the availability of light, nutrients and gases, and biological interactions such as competition and herbivory. But what happens to entire communities of aquatic plants at a whole-lake level when there is a sustained shift in one of these governing factors such as, for example, nutrient supply?

Aquatic ecologists have long known that nutrient-enriched, shallow, permanent lakes in Europe and elsewhere typically exist in either of two **alternative states**: a clear-water state dominated by macroscopic plants or a turbid-water state dominated by microscopic phytoplankton (Scheffer 1998). In European lakes where phosphorus rather than nitrogen is limiting, macroscopic plants typically dominate when total phosphorus (TP) is less than $50\,\mu g\,L^{-1}$ and phytoplankton dominate when total phosphorus exceeds $150\,\mu g\,L^{-1}$ (Figure 4.11). Between those two thresholds, it is harder to predict whether phytoplankton or macroscopic plants will dominate. Much depends on the lake's recent state, as feedback mechanisms make it difficult for macroscopic plants to invade a phytoplankton-dominated system and *vice versa* (Figure 4.11).

Understanding the dynamics and drivers of such alternative states is crucial for successful management. If, say, a clear-water state dominated by macroscopic plants is desired but the waterbody is turbid and phytoplankton-dominated, then nutrients must be reduced well below the lower threshold to overcome the feedback mechanisms maintaining the phytoplankton state. This is known as a **hysteresis effect**. The key issue is that there is not a simple linear relationship between nutrient concentration and abundance of phytoplankton or macroscopic plants but that there are thresholds where one state of plant dominance can abruptly change to the other state. These thresholds and the feedback mechanisms must be overcome to change the state.

Scheffer and van Nes (2007) extended the initial two-state concept, describing several states along a gradient of eutrophication: domination by free-floating plants, submerged charophytes, submerged flowering plants, green algae or cyanobacteria. Species replacements along this gradient seem to be a continuum that is interrupted at critical points by an abrupt change to a contrasting alternative regime dominated by different species. The switch between a clear-water state and a turbid-water state is one such change but others may happen where there are marked changes in water regime, salinity or organic matter loadings.

Do either the dual or multi-state alternative-states models apply to Australian standing waters? The dual

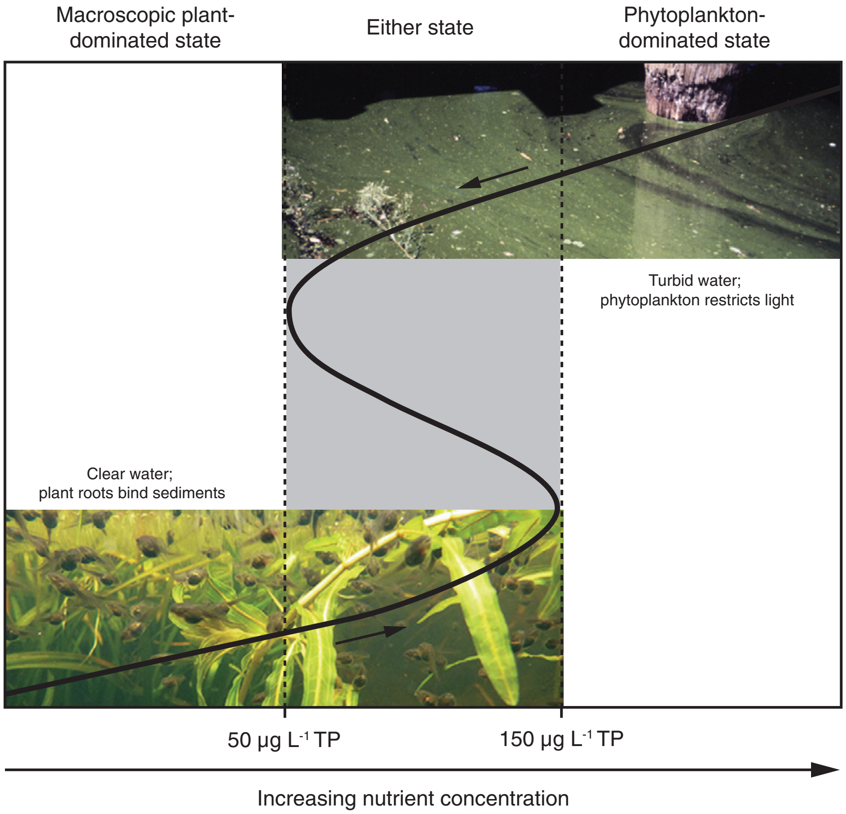

Figure 4.11 The alternative states model suggests that at low nutrient concentrations (e.g. below 50 µg L^{-1} TP, lower left), macroscopic plants dominate. At high nutrient concentrations (e.g. above 150 µg L^{-1} TP, upper right) phytoplankton dominate. Either state may exist at intermediate concentrations (shaded, 50–150 µg L^{-1} TP), depending on the strength of the feedback mechanisms that act to maintain different states. The solid black line illustrates the non-linear relationship between nutrient concentration and state where the state cannot be readily predicted at intermediate concentrations. (Source: Macroscopic plants – Jane Chambers; phytoplankton – Wasele Hosja.)

state model did not seem to pertain to wetlands with a seasonal water regime (Sim *et al.* 2009) but a multi-state model did apply to perennial salinized wetlands in WA where salinity, rather than nutrient concentration, was the driver of state change (Davis *et al.* 2003, Sim *et al.* 2006). Increasing salinization caused a shift from freshwater plant assemblages to ones dominated by plants such as *Ruppia*, *Lepilaena* and *Lamprothamnium* normally associated with saline conditions. When salinity and nutrients were both high, the system became dominated by salt-tolerant phytoplankton such as *Dunaliella*. With further increases in salinity, these systems then became dominated by benthic microbial communities composed mostly of cyanobacteria and halophilic bacteria (Figure 4.12).

The stability of these states seems to be maintained by **feedback loops**, a defining feature of alternative states (and why the model is sometimes called 'alternative stable states'). In clear-water, permanent, shallow lakes where submerged plants dominate, the plants take up nutrients from the sediments, promote sedimentation and provide refuges for the herbivores that

Figure 4.12 In the WA wheatbelt, shallow lakes of differing salinity exist in different states that are either dominated by submerged plants, by phytoplankton or by microbial mats. These lakes may occur close to each other yet have very different assemblages. (Source: Jenny Davis.)

eat phytoplankton. However, when nutrient concentrations exceed the plants' assimilative capacity, the state shifts to one where different feedback loops operate. Now, phytoplankton rapidly recycle the nutrients so that they remain in the water column. High turbidity created by the high densities of the phytoplankton reduces light transmission, thereby impeding the establishment of submerged plants. When phytoplankton blooms collapse, their biomass accumulates as flocculent organic sediment that is frequently anoxic and easily resuspended, maintaining high nutrient concentrations in turbid water (Chapter 3). At high salinities ($>45\,\mathrm{g\,L^{-1}}$), benthic microbial mats become established and bind the sediments, suppressing wind resuspension of fine sediments.

Models like this are a powerful tool for integrating data on physical, chemical and biological features of standing waters into concepts that generate testable predictions. Further, given the management implications of this conceptual model for biomanipulation of aquatic plants in shallow standing waters, more testing is needed in diverse systems, particularly in tropical and subtropical areas. We shall come across other conceptual models in later sections on trophic cascades (Section 4.6.7) and biomanipulation (Section 4.6.8).

4.6 CONSUMERS

Producers provide food for the consumers in aquatic food webs (Figure 4.4), either as dead and dying organic matter (detritus) for decomposers or as living plant material for herbivores. In turn, these two groups of consumers are eaten by carnivores. In this section on consumers, we distinguish **vertebrates** (amphibians, reptiles, fishes, birds and mammals) and **invertebrates** because this taxonomically conventional division also has ecological relevance. Most aquatic vertebrates are larger, more mobile and longer-lived than invertebrates. They are better known (some might say more 'charismatic') but, as we shall see, vertebrates rely on the activities of microbes and invertebrates in all aquatic food webs.

Invertebrates are typically the major trophic link between producers and vertebrate consumers. They contribute greatly to the biodiversity of most standing waters, and are frequently sampled as indicators of ecosystem 'health' (Section 11.8.1). Major families of aquatic invertebrates of both standing and flowing waters can be identified with an online guide provided by the Murray-Darling Freshwater Research Centre (www.mdfrc.org.au/bugguide), which includes helpful taxonomic terminology, distribution data and feeding-group classifications. Books by Hawking and Smith (1997), Davis and Christidis (1997) and Gooderham and Tsyrlin (2002) provide additional help. Keys to aquatic vertebrate groups are reviewed in Section 7.4.4.

4.6.1 Decomposers: the importance of microbes and fungi

Microbes, fungi and tiny invertebrate decomposers account for the majority of the breakdown and mineralization of dead or dying organic material. Large populations of non-photosynthetic bacteria (bacterioplankton) that feed on particulate or dissolved organic matter inhabit the water column of most lentic environments. Bacterioplankton are extracted from water samples using centrifugation and membrane filtration, and artificially classified into the same size groups as phytoplankton (Section 4.5.2).

In the food webs of standing waters, bacteria provide the link between dissolved organic carbon and higher trophic groups in a process termed the **microbial loop**. Heterotrophic aquatic microorganisms such as bacteria and fungi decompose the complex organic compounds, thus recycling the inorganic nutrients and mediating the transfer of dissolved organic carbon to higher trophic groups (Figure 4.13) through the incorporation of the carbon into microbial biomass. This biomass is then consumed, and these consumers become food for subsequent ones, transferring organic carbon up the food chain.

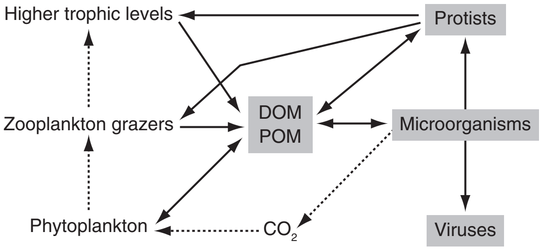

Figure 4.13 The microbial loop includes various forms of organic matter (DOM and POM), microorganisms and consumers (shaded boxes) that directly (solid lines) or indirectly (dotted lines) contribute to aquatic food webs. Arrow direction indicates movement of carbon. DOM = dissolved organic matter; POM = particulate organic matter.

In food webs of the open water zone, most particulate detritus sinks to the bed to become unavailable to planktonic bacteria unless stirred by water circulation. However, **soluble detritus** composed of dissolved organic matter (DOM) and very fine organic particles (POM) remains suspended for long periods. This detritus originates from algal exudates, microbial decomposition and animal excretion and feeding, and is eaten by bacteria and protists (a diverse group of organisms that are either unicellular or multicellular without specialized tissues). These microbial communities are more than simply decomposers; they form a critical link between detritus and consumers in most aquatic food webs.

Aquatic fungi are also potentially important in detrital food chains, both in nutrient and carbon cycling as well as providing a trophic link between detritus and consumers (Box 4.4). Although little studied, fungi are common in standing waters. They either are primarily adapted to life in water (Chytridiomycetes) or have reinvaded water from land (e.g. aquatic hyphomycetes and yeasts). Their diversity, abundance and colonization are influenced by organic and inorganic nutrients as well as land-use practices such as the removal of veg-

Box 4.4 Fungal decomposition processes in freshwater ecosystems

Aquatic hyphomycetes dominate fungal decomposion of detrital leaves worldwide, from alpine, temperate and tropical areas in both the Northern and Southern Hemispheres and across leaves from a range of species. Dynamics and diversity of fungal colonization processes are well known from measurements of fungal biomarkers and microscopic examination of sporulation. More recently, 454-pyrosequencing DNA techniques are revealing further details about their community composition. However, spatial distribution of fungal biomass within leaves and the mechanism of interaction between fungal and leaf tissue is less well understood. The combination of classical histological staining and synchrotron light-source Fourier-transform infrared (S-FTIR) microspectroscopy allows us to study the spatial distribution of fungi during leaf decomposition. These techniques show that significant decomposition of the leaf substrate can occur during terrestrial processing, and that such leaves entering waterways are largely recalcitrant (lignified) carbon and fungal tissue. Under aquatic conditions, fungi can de-polymerize the lignified tissue, accessing the bound carbohydrate (Kerr *et al.* 2013) and returning part of the leaf carbon to the aquatic carbon cycle. This process likely contributes to the higher nutritional value of fungal-colonized leaves.

Stephanie Suter, Gavin Rees and Ewen Silvester,
LaTrobe University and CSIRO

etation and changes in water quality (Bärlocher *et al.* 2012). Further development and application of molecular identification methods will greatly increase our understanding of fungal diversity (only 7% of total estimated species are described) and their ecological contribution to trophic processes in standing waterbodies (Wurzbacher *et al.* 2010). In Australia, fungi have been found in upland (Thomas *et al.* 1992), alpine (Suter *et al.* 2011) and lowland waters (Bärlocher *et al.* 2012).

Aquatic fungi are often also classified morphologically into filamentous fungi that dominate the littoral zone and unicellular fungi that dominate the open water zone. Filamentous fungi scavenge nutrients after their hyphae penetrate dead leaves and other coarse particulate detritus, accelerating breakdown into fine particulate organic matter. This fine material then becomes a substrate for unicellular fungi that break it down further. Thus, the ecological roles played by fungi include the decomposition of particulate organic matter as well as the transfer of nutrients to higher trophic levels via the microbial loop.

4.6.2 Invertebrate detritivores

Fungal colonization of organic matter increases the palatability and nutrient content of detritus for invertebrate detritivores in running waters (Canhoto and Graça 2008, Section 7.5), and this probably also occurs in Australian lentic waters. Although this group inhabits the littoral zone, they are especially abundant in the profundal benthic zone where they feed on organic matter that settles to the bottom. Little light penetrates down there so producers and herbivores are rare or absent.

Common invertebrate detritivores include nematodes (roundworms), bivalve molluscs, oligochaetes (true worms) and larval chironomids ('bloodworms' and other midge larvae). Those that live in the hypoxic profundal zone, such as tubificid worms and bloodworms (Figure 4.14), possess forms of haemoglobin to facilitate the uptake of dissolved oxygen. Some oligochaetes also have extensive gills along their tail segments that they oscillate in the overlying water to enhance access to the scant dissolved oxygen. Meanwhile, many chironomid larvae build mud tubes that project some millimetres above the sediment surface, also improving access to oxygenated water and perhaps providing a refuge from predators.

Although there may be few invertebrate species in the profundal benthos, productivity can be high because of the relatively high food and nutrient supply. Microbial and fungal colonization of profundal organic matter such as detritus and faecal pellets (Section 4.6.1) likely enriches this food supply for invertebrate detritivores. As most profundal species either emigrate from the sediments or become inactive during summer

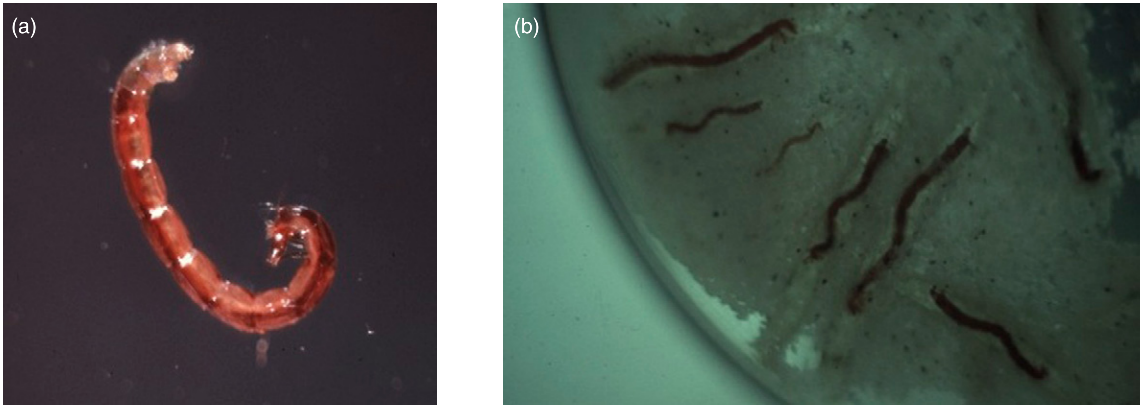

Figure 4.14 Some larval chironomids are called ‘bloodworms’ (they are insects, not true worms) because they possess haemoglobin (a red pigment), which increases their ability to take up oxygen in hypoxic sediments: (a) *Chironomus* larva; (b) larval chironomids in burrows constructed in sand in a petri dish. (Source: Jenny Davis.)

when the hypolimnion becomes anoxic (Section 3.2.1), productivity in the profundal zone may be least over summer, a time when it is high in the littoral zone.

In the littoral zone where physical habitat complexity and dissolved oxygen concentrations are higher, there are more species of invertebrate detritivores. One way to classify invertebrate detritivores (and we shall explore this in more detail in Sections 7.4.9 and 7.4.10) is according to how they feed and the size of the organic matter particles that they eat. Detritivores that eat large (>1 mm) bits of organic matter are called **shredders** and include crustaceans (e.g. yabbies, shrimps, amphipods and isopods) and some insects, mainly several species of larval caddisflies. Detritivores that eat smaller (<1 mm) detritus are termed **collector-gatherers** if they feed by browsing on surfaces or within sediments, or **collector-filterers** if they filter-feed on suspended fine particulate organic matter. Collector-gatherers include many true fly larvae and oligochaete worms; collector-filterers include mosquito larvae, bivalve molluscs such as freshwater mussels, and some species of zooplankton.

Some microcrustacean detritivores such as ostracods may reach very large numbers in the benthos of shallow freshwater and salt lakes, and appear to be an important link in this detrital trophic pathway. Similarly, a major role as decomposers is played by nematodes and protists such as ciliates, flagellates, testate amoebae and other microfauna. Their activity, rapidity of turnover and total biomass might mean that they contribute more to decomposition than the more obvious macrofauna.

4.6.3 Invertebrate herbivores

In the open water zone, phytoplankton are an abundant and rapidly assimilated food resource for herbivorous zooplankton, including rotifers, copepods (Calanoida and Cyclopoida) and cladocerans. Many cladocerans such as *Moina* (Figure 4.15) consume bacteria and phytoplankton by using their beating legs to create currents that draw food particles into the body cavity where they are trapped by fine combs of setae (hairs) and passed to the mouth.

Most zooplankton feed selectively. Planktonic grazers prefer diatoms and small green algae (Ganf *et al.* 1983), and densities decline when phytoplankton communities shift to a dominance by large green algae, cyanobacteria or dinoflagellates. The presence of cyanobacteria can actually suppress feeding by cladocerans, probably because of toxins. The dietary specificity of grazing zooplankton underpins their potential use in biomanipulation to control nuisance algal blooms (Section 4.6.8).

Gastropods (aquatic snails) are the main grazers of periphyton and biofilms on rocks and wood. Several species of caddisfly larvae and mayfly nymphs also eat

Figure 4.15 A cladoceran *Moina micrura* (approximately 500 μm long) feeds by beating its legs (arrowed) to create a current of water that carries bacteria and phytoplankton into its food cavity. (Source: Russ Shiel.)

this material although most are partly detritivorous (Gooderham and Tsyrlin 2002). Direct herbivory on aquatic plants by invertebrates is considered rare although aquatic moth caterpillars and several adult and larval beetles (e.g. some weevils) eat living plant material. A few species of weevils have been used in biological control of invasive aquatic plants (Section 7.4.5).

4.6.4 Invertebrate carnivores

In standing waters, invertebrate carnivores are diverse and occupy all the main zones and habitats described earlier. In the open water, species of cyclopoid and calanoid copepods eat other zooplankton. Some are even cannibals, with smaller males at risk of being eaten by large females. Predation may promote **cyclomorphosis** in some rotifers and cladocerans, a process whereby body shape varies seasonally, apparently in response to predation pressure. This often involves the development of spines or crests that complicate the handling of prey by potential predators (Dzialowski *et al.* 2003).

Also in the open water are actively swimming invertebrate carnivores such as back-swimmers (Notonectidae) and diving beetles (Dytiscidae). Larval hydrophilids and dytiscids, with the evocative common name of 'water tigers', have highly specialized mouthparts (Figure 4.16a) for seizing their prey. These predators

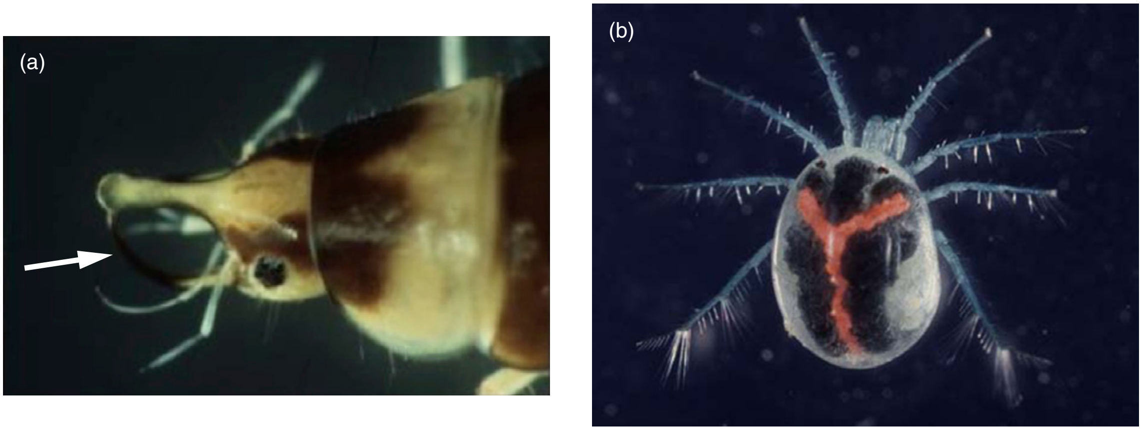

Figure 4.16 Some larval diving beetles (a) have an elongated rostrum protruding from the top of the head that enables them to hold prey items against their scythe-like mandibles (arrowed). Many water mites, such as *Piona murleyi* (b), are distinctively coloured, possibly to warn potential predators that they are not palatable. (Source: Jenny Davis.)

also venture into the littoral zone whose structural complexity harbours diverse prey as well as providing cover for 'sit-and-wait' ambush predators such as dragonfly and damselfly nymphs (Odonata). Other predators such as water mites (Hydracarina, Figure 4.16b) have piercing mouthparts to suck the body fluids from their prey.

At the air-water interface, invertebrate predators in the pleuston (Figure 4.2) include water striders and veliids (Hemiptera) that scurry across the surface looking for prey. These bugs can run on the surface because of their light bodies and the way their broad limbs, coated in water-repellent wax or hairs, spread their weight over as great an area as possible (Lancaster and Downes 2013). Also at the water surface but capable of diving down into the water to pursue their prey are whirligig beetles. Intriguingly, these beetles have each eye divided into a lower part that can see down into the water and an upper part that looks into the air above – an elegant feature for life at the interface between two media with different refractive properties.

In the profundal zone, dissolved oxygen concentrations are limiting for most invertebrates and only a few predators seem able to persist. The most common are tanypod chironomid larvae (Diptera). Other dipteran larvae, such as rat-tail maggots (hoverflies – Syrphidae) and marsh flies (Sciomyzidae) are also found in this habitat, and some of these taxa are carnivorous.

4.6.5 Vertebrate herbivores

Two groups of vertebrates are conspicuous herbivores in Australian standing waters: tadpoles and waterbirds. In littoral zones, many species of **tadpoles** feed on periphyton, often leaving grazing scars where they have scraped algae from the rock surfaces with their complex mouthparts. Tadpoles can be seasonally abundant and as they comprise considerable biomass, their productivity may be high at certain times of the year. For example, in drying temporary waters, a 'soup' of wriggling tadpoles is common, often attracting terrestrial predators such as snakes and birds.

Many Australian **waterbirds** (such as swans, coots and ducks) graze on sedges and grasses in the littoral zone. Black swans, *Cygnus atratus* (Figure 4.17), grub for starch-rich rhizomes and the submerged leaves of plants in shallow wetlands and forage on fringing herbs and grasses. Magpie geese *Anseranas semipalmata*, abundant in tropical waterbodies, depend upon the corms of spike rush *Eleocharis*. Within standing waters, herbivorous waterbirds partition resources by eating different plants or plant parts. For example, Eurasian coots *Fulica atra* feed mainly on submerged aquatic plants whereas magpie geese and Australian wood ducks *Chenonetta jubata* eat seedheads, leaves and other parts of both aquatic and terrestrial vegetation.

Waterbirds can travel long distances and exploit food and other resources as they become available, even in

Figure 4.17 Adult black swans use their long necks (a) to feed on submerged plants but their young offspring, cygnets, lack this advantage and feed on zooplankton. Plant material is also used for nests (b). Making nests as small islands within the waterbody restricts access by terrestrial predators such as foxes. (Source: Jenny Davis.)

unpredictably filled waters of the arid inland (Kingsford *et al.* 2010). Water regimes and availability largely govern the distribution of many aquatic plants (Section 4.5). Consequently, food availability for most herbivorous waterbirds is closely linked to spatial and temporal changes in rainfall and runoff. Waterbirds exploit the 'boom' periods when floods inundate vast areas and promote immense primary production. However, the 'bust' periods that follow when the water dries and aquatic plants die off signal the departure of most waterbirds to wetter places. Kingsford *et al.* (2004) found lower densities of herbivorous waterbirds on lakes whose hydrological variability had been reduced, especially by removal of natural dry periods, than on nearby lakes with naturally variable hydrology. This difference was ascribed to reduced food availability, and is an excellent example of why protecting the natural variability of water regime in Australia's 'boom-and-bust' ecosystems is crucial (Box 4.5).

4.6.6 Vertebrate carnivores

Most Australian native fishes occur in lotic (Section 7.4) rather than lentic waters. Those that do occur in standing waters are usually small-bodied predators such as galaxiids (native minnows), pygmy perch and freshwater smelt. These fishes eat aquatic invertebrates as well as terrestrial and aerial insects that fall into the water from the fringing vegetation (Stoffels 2013). Sadly, the most common fish now found in the littoral zone of almost every temperate Australian standing water is the introduced *Gambusia*. This was an unnecessary introduction (to control mosquitoes) and has been implicated in the displacement of small native fishes and tadpoles that also occupy the littoral zone (Section 12.8.1).

Many waterbirds in Australian standing waters are carnivores, including pelicans, kingfishers, darters, cormorants, ospreys, herons and egrets. Some, like herons, stalk or ambush their prey (Figure 4.18), swiftly grabbing unsuspecting morsels from above. Others, such as ospreys, fly to swoop and seize their prey with sharp talons. Yet others, such as cormorants and darters, swim after their prey below the water. Although water is not an easy place to feed as an air-breathing vertebrate, carnivorous and herbivorous waterbirds have some fascinating solutions to this challenge (Box 4.6).

Some waterbirds such as straw-necked ibises also feed on terrestrial prey in pastures, such as grasshoppers, crickets and caterpillars, and this has encouraged pastoralists to support environmental watering (Section 9.5) to sustain the waterbodies where these species breed. This is only one example of an important trophic link between all aquatic and terrestrial ecosystems whereby a **subsidy** of energy or organic material is transferred by mobile predators and herbivores

Box 4.5 Waterbird ecology in a boom-and-bust environment

There are about 90 species of waterbirds in Australia, consuming different organisms such as plants, invertebrates and fishes. Each of these consumers has specialized ways of catching and feeding on their specialized prey. Darters swim fast underwater, projecting their neck and bill to catch fishes. The various duck species forage in different parts of the habitat depending on their prey. Black swans graze on submerged plants in shallow lakes and estuaries while pink-eared ducks eat invertebrates. All Australian waterbirds capitalize on the 'boom' in resources provided by rivers and their wetlands during floods and often extending for years afterwards. These floods increase productivity enormously, providing sufficient food that is usually a catalyst for waterbirds to breed. Inevitably, dry or 'bust' periods force the waterbirds to fly to nearby persistent lakes or more reliable waters near the coast. Sometimes, they are unable to do so and die from starvation. Cycles of 'boom' and 'bust' are critical for viability of many Australian waterbirds but these natural cycles have often been disrupted by water extraction and damming of rivers, primarily for irrigation.

Richard Kingsford, University of New South Wales

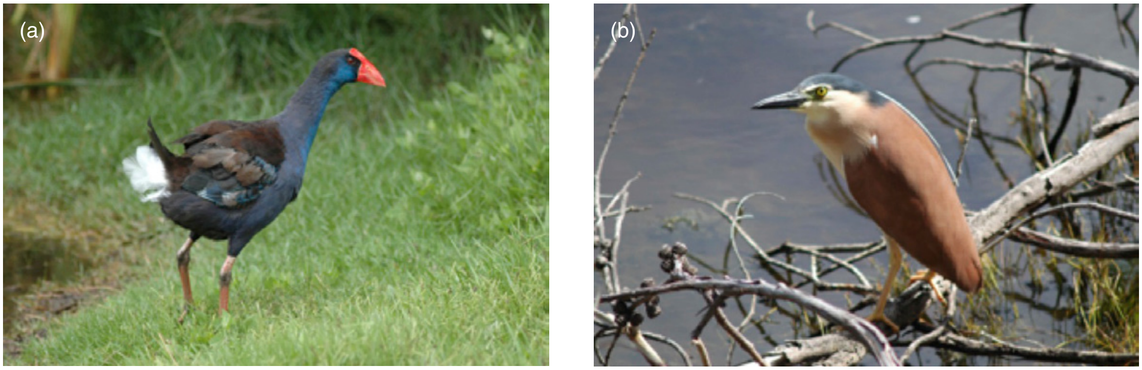

Figure 4.18 The purple swamphen *Porphyrio porphyrio* (a) is common in many Australian waterbodies, feeding on leaves of plants in the littoral zone, invertebrates, and sometimes eggs, ducklings and small fishes. The rufous night heron *Nycticorax caledonicus* (b) is a 'sit-and-wait' predator that eats insects, small fishes and reptiles. Despite its name, it can often be seen during the day, hunched on vegetation, overlooking a wetland. (Source: Jenny Davis.)

Box 4.6 Challenges for birds feeding in water

Birds find water dense and unbreathable. Diving for prey, musk ducks and grebes hold their breath and swim with short, stiff wings and webbed feet. Long-legged ibises, spoonbills, and egrets have nostrils set high on long bills that probe for submerged prey. Waterbirds must separate food from excess water, processing large items above water. A black swan plucks submerged plants, then raises its head, beak downwards, to drain off water. Being dense, water will carry a small food item away from the thrust of a closing beak. Pink-eared ducks suck plankton-rich water in through the front of the bill, then force it out at the side through finely separated, stiff lamellae that retain the plankton but release the water. Leathery flaps along the sides of the upper bill close over the filters as water is sucked in, but lift to let water out. The Australian pelican, lunging at a fish, de-fuses the thrust of its closing beak by inflating a bag below its flexible lower jaw to surround the water containing the fish. Then the pelican drains off the water, swallowing just the fish.

Peter Jarman, University of New England

(Figure 4.4). Frogs, bats, snakes and other mobile organisms all act as conduits between aquatic and terrestrial environments, supplementing the same activities by mobile invertebrates and physical processes such as flooding and wind.

4.6.7 Predation and trophic cascades

So far, we have dealt mainly with how physical and chemical processes (Chapters 2 and 3) influence organisms and ecological processes in standing waters. However, biological interactions within and among populations and communities (Table 4.1) can also be powerful structuring forces. Competition for resources, for example, is often intense among similar-sized individuals of the same species, when they share the same needs for a scarce resource. Competition also occurs between different species although this process, if sustained over time, usually results in either the local disappearance of one of the competing species or divergence in the habits or requirements of the two species.

Predation is another powerful biological interaction that can affect the distribution and abundance of different species in standing waters. When predators reduce the abundance of their prey, thereby releasing the next lower trophic level from predation, the abundance of this next level usually increases in a process termed a **trophic cascade** (Pace *et al.* 1999). One classic example of this was shown in a study by Brooks and Dodson (1965) in northern Connecticut, where fishes were introduced into a lake that previously lacked them, causing a dramatic shift in the size structure of the zooplankton. Prior to fish introduction, most individuals in the zooplankton were 0.7–0.9 mm long, but after about 10 years of size-selective predation, most zooplankton individuals were 0.3–0.5 mm long.

This shift in size occurs because the fishes select the more visible, large zooplankton, allowing an increase in abundance of smaller species. When fishes are absent, large zooplankton dominate because they have a lower ratio of basal metabolism to overall respiration than do small zooplankton, they can eat a larger range of food, and their size protects them from invertebrate predators such as cyclopoid copepods and back-swimmers (Notonectidae). Larger zooplankton are more efficient at grazing phytoplankton and so will reduce algal biomass, whereas smaller species have less impact. Therefore, removing the larger herbivorous zooplankton sets off a cascading effect that potentially results in greater abundances of phytoplankton.

In theory, trophic cascades can be either ‘top-down’ or ‘bottom-up’ (Figure 4.19). In top-down cascades, removing a top predator such as a fish-eating (i.e. piscivorous) fish will favour the next lower trophic level that increases, intensifying its predatory pressure on the next lower level, and so on. Alternatively, a decline in the abundance of producers caused by, say, a reduction in nutrients, will induce a bottom-up cascade in which the abundances of higher trophic levels also decline. Thus, trophic cascades may be controlled by biological interactions such as predation, environmental factors such as nutrient supply, or possibly both.

4.6.8 Trophic cascades and biomanipulation

When persistent trophic cascades can be demonstrated, they might be used to manage issues such as the control of nuisance algae by promoting the abundance of particular herbivores or the optimal stocking of fishes for recreational angling. This process of **biomanipulation** has proven popular for managing some standing waters in the Northern Hemisphere (e.g. Mehner *et al.* 2004). However, there has been far less work on it in Australia, despite reviews encouraging research on assessing the potential of native fishes such as Murray cod *Maccullochella peelii* to improve water quality in lakes and reservoirs (Sierp *et al.* 2009).

As noted earlier, plant dominance in standing waters can switch between alternative states. In some shallow permanent European lakes, biomanipulation at a whole-lake scale has been used to change a turbid, phytoplankton-dominated state to a clear-water one dominated by submerged plants (Scheffer 1998). For biomanipulation to be successful in reducing phytoplankton, numbers of planktivorous fishes (feeding on the zooplankton that eat phytoplankton) must be drastically reduced, followed by a clear-water regime stabilized by extensive stands of submerged plants. However, this is unlikely to succeed consistently in the temporary waterbodies common across much of Australia because these waters seldom support persistent populations of fishes. Furthermore, sustained herbivory on the phytoplankton depends upon the presence of abundant large-bodied zooplankton grazers such as cladocerans. These either do not occur in all systems or their presence is limited to specific times. For example, populations of *Daphnia* often peak in spring and wane as water temperatures rise in summer, the time when nuisance algae are likely to flourish.

Nonetheless, in permanent and managed waters such as reservoirs, biomanipulation continues to attract attention and warrants research to further assess its potential as a tool to improve water quality. Biomanipulation of densities of native and introduced fishes in experimental enclosures in Emigrant Creek Dam, a subtropical reservoir in northern NSW, indicated that removing exotic fishes such as common carp would improve water quality (Akhurst *et al.* 2012). However, before biomanipulation becomes routinely used in Australian water storages, large-scale trials are needed to assess how long the beneficial effects will persist and whether there are any unwanted side-effects.

4.6.9 How vertebrates use waterbodies: linkages and subsidies

Earlier in this chapter, we referred to the importance of **linkages** and **subsidies** of energy, nutrients and food between aquatic and terrestrial ecosystems, the significance of considering standing waters in a landscape

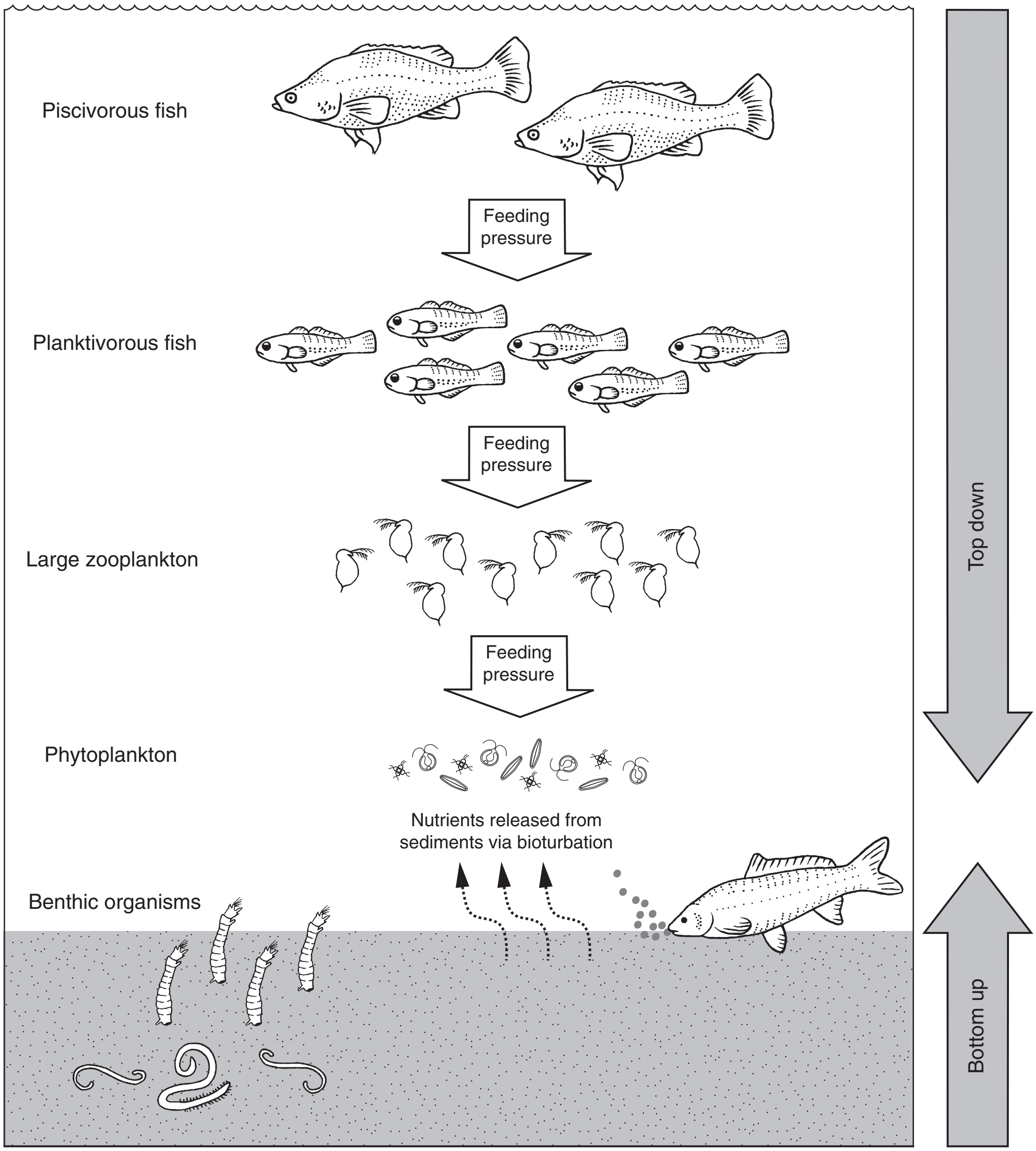

Figure 4.19 Trophic cascades can be considered as either 'top-down' where changes in the abundance of the top consumers (e.g. golden perch) cascade down the food chain to influence the abundance of lower trophic levels, or 'bottom-up' where changes in factors such as nutrients released from the sediments through bioturbation (i.e. biological disturbance by worms burrowing or fishes such as common carp feeding in the sediments, etc.) influence the abundance of producers and cascade up the food chain, ultimately affecting the abundance of top predators. (Source: Image drawn by Belinda Cale.)

context, and the ways by which organisms relying on Australian waterbodies cope with naturally variable water regimes in time and space. Let's explore these features by looking at how vertebrates use inland waterbodies.

Vertebrates use standing (and running) waters in multiple ways, including as a food and water source, a refuge from predators or desiccation, and a place to nest and reproduce. Usage can be constant or occasional, and can vary with size, age or sex. Despite this variation, each time an animal enters or leaves a waterbody, it transfers nutrients, organic matter and energy. When an aquatic insect emerging from a swamp is eaten by a bat, which then flies into a cave and defecates, energy is transferred from the waterbody to the cave ecosystem. If that same bat then flies to another swamp nearby and dies there, part of the energy from the terrestrial and aquatic insects that it has eaten enters the aquatic ecosystem via the decomposer pathway and is transferred through the levels of the aquatic food web. Thus, a landscape context is crucial to understanding linkages (e.g. among metapopulations and metacommunities, Table 4.1), as well as trophic pathways across wetland mosaics or river networks. Significant subsidies occur via all these linkages and blur boundaries even further.

Mobile waterbirds travel readily among waterbodies, but many species breed in or near water and, for a time, the parents are obliged to return to the nesting site to brood eggs or feed their young. In contrast, most water-associated reptiles leave the water to breed. For example, Australia's two crocodile species lay their eggs in nests above water in heaps of aquatic vegetation (estuarine or saltwater crocodiles *Crocodylus porosus*) or in sandy banks (freshwater crocodile *C. johnstoni*). Freshwater turtles spend their juvenile and adult life in the water, emerging only to bask or to lay their eggs in a nest chamber dug in dry ground away from water. However, some south-eastern Australian turtles (e.g. the eastern long-necked turtle *Chelodina longicollis*) can move up to 1.5 km overland from seasonally drying wetlands to ones that are permanently wet (Roe and Georges 2007). They return to breed near the temporary wetlands when they refill from floods or heavy rains. Filling stimulates a pulse of productivity, which provides the extra food needed by breeding turtles and their hatchlings. The western long-necked or oblong turtle (Figure 4.20) in WA also copes with seasonal drying. Although capable of walking overland to find suitable habitats, this species appears to survive drying by aestivating within the bed. This strategy is also used by the endangered western swamp turtle *Pseudemydura umbrina*, restricted to ephemeral swamps within two small nature reserves (Section 12.7).

In the north, the Arafura file-snake *Acrochordus arafurae* is entirely aquatic, even giving birth to live young in the water. File-snakes live in freshwater systems that connect to the sea during floods. Also in the tropical north, several species of colubrid snakes,

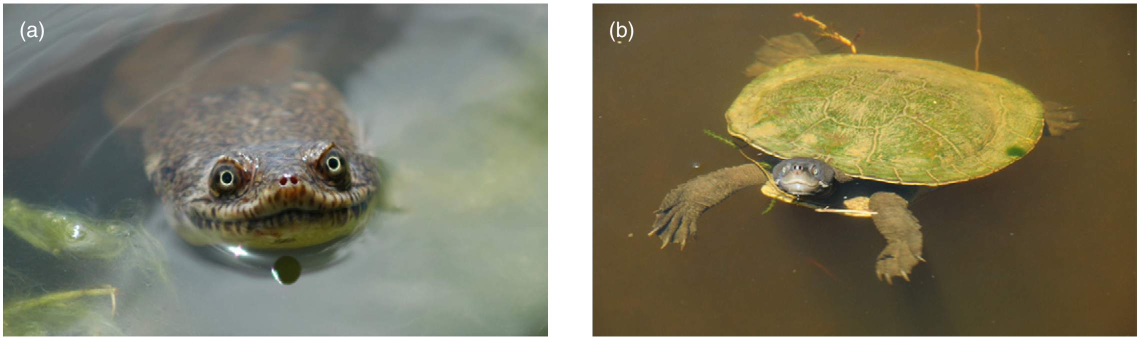

Figure 4.20 The western long-necked or oblong turtle (a) in waterbodies near Perth, WA, is vulnerable to the impacts of urbanization (e.g. isolation of waterbodies by housing and roads) and predators such as foxes. The Murray turtle *Emydura macquarii* (b) occurs in rivers and permanent wetlands in the Murray-Darling Basin. As it cannot traverse dry land, it relies on swimming and floods for dispersal. (Source: Jenny Davis.)

one python and one or two goanna species are at least semi-aquatic, swimming well and finding much of their prey in water. The water monitors (goannas) and the eastern water dragon *Physignathus lesueurii* (an agamid lizard) bask on trees and logs overhanging water, dropping into water and swimming away if disturbed. Thus, they use water as a refuge as well as foraging in it. Most snakes are also good swimmers. Some species (e.g. tiger snakes *Notechis* spp., red-bellied black snakes *Pseudechis porphyriacus*) are common around the edges of standing waters where they feed on invertebrates and small vertebrates such as frogs and mice.

Many frogs live as adults well away from water, but mate and lay eggs in or next to water where the juveniles (tadpoles) swim and feed. Two families of Australian frogs occur near standing waters: the Hylidae or tree frogs (e.g. *Litoria*) and the Myobatrachidae or southern frogs (e.g. *Limnodynastes*) (Tyler and Knight 2011). Tree frogs respond to rain by moving to waterbodies to lay eggs in or on the water where their young will develop (Tyler and Davies 1993). Some myobatrachids lay eggs in low-lying areas where temporary wetlands are likely to appear following rain events. Learning more about how frogs and tadpoles use different waterbodies (Box 4.7) better equips us to stem the declines in abundance and distribution of many of our amphibian species.

4.7 BIOLOGICAL PROCESSES IN TEMPORARY STANDING WATERS

We conclude by reviewing biological processes in two types of standing waters common across much of Australia: temporary waters and salt lakes (many of which are also temporary). Most of the assemblages and biological processes discussed earlier in this chapter also occur in temporary and saline systems. In particular, these systems exemplify the significance of extremes in water regime and water chemistry as major drivers of biological processes at scales from individual organisms to ecosystems (Table 4.1).

In all temporary lentic (and lotic) waters, the types of ecological processes and responses by the biota differ between the phases of re-wetting, drying, damp and completely dry (Brock and Jarman 2000, Table 4.2). Transitions across these phases are usually gradual although the final disappearance of surface water, for example, rapidly leads to the disappearance of all but the desiccation-resistant stages of fully aquatic organisms. Because the duration, timing, frequency and extent of the dry and wet phases all vary over time and among waterbodies, there is a corresponding diversity of responses and ecological outcomes. Nonetheless, some generalizations are possible (Table 4.2).

During drying by evaporation, dissolved salts become concentrated in the remaining water and may even

Box 4.7 Use of floodplain wetlands by frogs and tadpoles in the Murray-Darling Basin

Frogs and their tadpoles can account for a significant proportion of vertebrate biomass in floodplain wetlands. Frogs have several ways to cope with variable water regimes. Burrowing and aestivation during dry periods are common, enabling species in genera such as *Cyclorana* and *Neobatrachus* to persist between flow events by remaining dormant. Other species, such as the southern bell frog *Litoria raniformis*, move to permanent refuge habitats during dry periods, but must disperse across the floodplain in wet years to recruit (Wassens *et al.* 2008). Extended reductions in flow will prolong dry periods, potentially threatening dormant stages. The number and extent of refuge habitats will decrease, ultimately excluding sensitive species and reducing species richness. Most frogs in the Murray-Darling Basin have a fully aquatic tadpole phase. Watching them feed around the shallow edges of wetlands is fascinating, and many species can be identified by their unique behaviours. Tadpoles of some species in the Murray-Darling Basin develop faster in response to wetland drying (Anstis 2007). However, juvenile frogs that develop faster are often smaller and have lower survival rates than those with an extended tadpole phase.

Skye Wassens, Charles Sturt University

Table 4.2 How aquatic biota respond to re-wetting, drying, damp and completely dry phases in temporary standing waters.

Biotic component	Re-wetting phase	While drying and damp	When dry
Microorganisms	Mediate biogeochemical processes to recycle nutrients and organic matter	Open-water processes decline	Assemblages change from anaerobic to aerobic; resistant stages persist in sediments
Cyanobacteria	Photosynthesize, reproduce, bloom	Fix nitrogen	Persist as resistant spores in sediments
Phytoplankton	Photosynthesize in water column, reproduce, bloom	Concentrate in density to ultimately become stranded and die	Propagule bank of resistant sexual and asexual spores persists in sediments
Aquatic plants:			
– submerged	Germinate, grow and reproduce in water	Seeds into seed bank	Seed bank in sediments
– amphibious	Aquatic form or seed bank	Survive declining water	Seed bank in sediments
– semi-terrestrial	Survive as seed bank	May tolerate drying and damp conditions	Persist in damp or dry areas
Zooplankton	Eggs hatch, hatchlings feed and reproduce	Concentrate in density to ultimately become stranded and die	Propagule bank of resistant eggs in sediments
Benthic invertebrates	Larval and adult stages grow, adults reproduce and disperse	Migrate from drying waterbody or concentrate in density to ultimately become stranded and die	Persist as terrestrial adults or resistant eggs in sediments
Frogs	Tadpoles mature in water; adults leave and return to spawn	Tolerate or use damp areas to move between wet and dry habitats	Adults spawn briefly resistant eggs in edge vegetation; some adults aestivate
Turtles	Grow, feed and mature in water; move between wetlands, eggs laid on land	Move to wet waterbodies	Eggs laid in adjacent terrestrial habitats; some adults aestivate in lake bed sediments or under vegetation; others leave to find water elsewhere
Waterbirds	Feed, breed and nest when habitat available	Tolerate or respond to declining water	Disperse to other waterbodies
Aquatic mammals	Feed and, in some cases, breed	Tolerate declining water or disperse	Refuge in suitable habitats
Terrestrial mammals	Opportunistic feeding in fringing zone	Opportunistic feeding over large areas of bed	Opportunistic feeding over entire bed

precipitate. This, coupled with high water temperatures, reduces the capacity for oxygen to dissolve in the remaining water, stressing aerobic organisms and impairing biogeochemical transformations that use dissolved oxygen as an electron-acceptor (Section 3.2). Receding water levels strand aquatic plants attached in the littoral zone while competitive interactions intensify in the diminishing free water. Ultimately, a 'predator-prey soup' results as consumers tolerant to the declining water quality capitalize on the high densities of prey concentrated by the drying (Lake *et al.* 1989). When the pool finally dries, a terrestrial 'clean-up crew' of ants, scavenger beetles and other animals consumes the aquatic remnants, as described for drying rivers by Steward *et al.* (2012). This represents a major subsidy from aquatic to terrestrial ecosystems in arid and semi-arid parts of Australia.

Meanwhile, many vertebrates leave the drying water-body. Some will aestivate near the edge whereas others will travel to permanent waters or other refuges (Table 4.2, Chapter 7). Soon, only a dry bed exists where nutrients lie locked in the sediments, aerobic microbial processes predominate and the seeds, eggs and other resting stages of plants and animals await suitable cues to germinate, hatch or emerge (Brock *et al.* 2003). Some terrestrial vertebrates graze on the abundant grasses and herbs that grow after water recedes and dries because the dry bed is now a habitat for terrestrial organisms until the water returns.

On re-wetting, the swift transformation back to a fully functional aquatic ecosystem can seem miraculous. Fuelled by the pulse of nutrients released from the newly inundated sediments (Section 3.10.1), there is soon a bloom of microscopic aquatic plants whose desiccation-resistant propagules have either survived in the sediments or have blown in (Table 4.2). The seeds of macroscopic plants also germinate. However, their long-term persistence depends on the extent and duration of wetting as well as herbivory pressure and other challenges (Brock 2011). Numerous invertebrates, mainly a diverse group of rotifers, protozoans and microcrustaceans, such as ostracods, copepods and cladocerans (Box 4.8), emerge quickly from resting stages and eggs. Some, such as shield shrimps (*Notostraca*), clam shrimps (Conchostraca) and fairy shrimps (Anostraca), seldom occur in permanent ponds but appear in newly filled puddles and rockholes throughout semi-arid and arid Australia. Although some of these early arrivals can be predators (e.g. the shield shrimp, *Lepidurus*), almost all the microcrustaceans are herbivores or detritivores.

Mobile invertebrates such as dragonflies and water beetles (dytiscids and hydrophilids) soon fly in and either lay eggs or start to feed on the burgeoning aquatic life. Many invertebrate species in temporary waters have aquatic stages that develop rapidly, depending on water temperature and food quality. For example, the dragonfly *Hemianax papuensis* can complete its larval stage in 8–12 weeks in temporary waters compared to its relatives in permanent waterbodies that may take almost a year. Waterbirds that eat larger invertebrates, fishes or the foliage of aquatic

Box 4.8 The dynamics of seed and egg banks in temporary waters

When we think about wetlands, we picture water teeming with life. We don't usually think of dusty dry floodplain soils as equally biodiverse places. Yet this is where many aquatic organisms spend most of their lives in temporary wetlands. Within hours of water inundating a dry floodplain, protozoans and algae emerge, followed by rotifers, crustaceans and larger plants. Although most dormant propagules (seeds, spores, eggs, drought-resistant adults) are long-lived, they are most productive and diverse when wetlands dry and flood frequently. When drying increases, either naturally or through river regulation or climate change, propagule density and diversity of plants and animals decline (Jenkins and Boulton 2007), along with carbon stores. The pattern of flooding and drying in temporary wetlands produces a landscape mosaic, with some wetlands flooding yearly while others may flood only once every decade or two. Frequently flooded wetlands are hot-spots of microinvertebrate biodiversity and productivity in the landscape. Products of the seed and egg banks of these hot-spots provide a rich food supply to higher trophic levels such as fishes, frogs, waterbirds and bats.

Kim Jenkins, University of New South Wales

plants are the last to return because their resource base takes the longest to reach levels high enough to sustain populations. Waterbirds also differ in their times to initiate breeding after reflooding. Ducks, herons, ibises, spoonbills and others that nest in trees standing in flood waters can nest as soon as flooding under the trees protects nests from non-flying, non-swimming predators. However, grebes or whiskered terns that nest in or on emergent or floating plants must delay until those plants have grown.

Highly mobile waterbird species use many wetlands in a lifetime, flying hundreds or thousands of kilometres. For these species, the Lake Eyre Basin, usually one of the driest regions on the continent, offers the greatest amount of habitat under wet conditions, and this region's wetlands are linked by broad flyways to the wetlands of south-eastern Australia (Kingsford *et al.* 2010). Dispersal of waterbirds across the arid zone also passively disperses cosmopolitan aquatic plants, including species of *Lemna*, *Typha*, *Myriophyllum* and *Nitella* (Green *et al.* 2008).

At first sight, environmental variables and water regime would appear to be the main drivers of ecological processes and assemblage composition in temporary waters. For the most part, this is true. However, biological interactions can also be important at certain times. In isolated temporary waters not associated with rivers, fully aquatic vertebrate predators such as fishes are seldom found, creating opportunities for other predators, usually invertebrates like water beetles (Dytiscidae and Hydrophilidae) and back-swimmers (Notonectidae), to take their place. Predation pressure by invertebrates can be a potent force structuring the assemblages of temporary standing waters, especially when water has persisted for some months. Similarly, competition can be intense, especially when resources decline as water recedes.

Within days or weeks after re-wetting, most of the ecological processes typical of permanent standing waters will occur. Depending on detrital inputs, shading and turbidity, these ecosystems may be autotrophic, heterotrophic or both. During the 'boom' times, productivity can be immense, accelerated by the high water temperatures and rich nutrient loads. However, all good things must end and long periods of 'bust' eventually occur when the water disappears.

Our temporary standing waters range from vast freshwater and salt lakes (e.g. Kati Thanda – Lake Eyre) through to small clay pans and isolated rockholes. These temporary waters provide many ecosystem goods and services such as fresh water (e.g. in rockholes and gnammas, Box 4.9, Figure 4.21) in the arid zone, pulses of aquatic productivity that support palatable species such as some fishes and waterbirds, feed for stock during the dry phase, and substantial cultural, aesthetic and scientific values. Viewing an expanse of dry lake bed under a brilliant blue sky can be an emotional experience, especially for urbanites

Box 4.9 Ecosystem processes and invertebrates of Australian gnammas

The quintessential temporary freshwater habitat on Australian rocky, arid surfaces is the modest-sized, Nyungar-named *gnamma*: a flooded rockhole. They are either shallow pans or deeper pits (Figure 4.21). For both types of micro-ecosystem, the main allochthonous sources of energy are decaying terrestrial plants, pollen, dead terrestrial insects, and marsupial, lizard and bird faeces – all supplying detritus and bacteria. Especially for the longer-lasting pits, there may be a significant autochthonous energy contribution via algal photosynthesis. Over 100 invertebrate taxa have been recorded from granite gnammas in WA. The vast majority of these taxa, typified by microcrustaceans, spend their entire life-cycle within the gnamma, desiccation-resistant eggs/embryos being crucial for dry periods. Fly-in insect predators such as notonectids and dytiscids may exert a structuring influence on community composition. The longer-lasting pits have fewer (mainly generalist) species than the short-lived pans (Bayly *et al.* 2011). In pans, the water column is short and typically highly transparent, and the invertebrates darkly pigmented for UV protection. The diversity of Australian rock-pool species apparently exceeds that of rock-pool faunas of all other continents (Jocque *et al.* 2010).

Ian Bayly, Killiecrankie, Flinders Island

Figure 4.21 A pit-gnamma on Pildappa Rock, upper Eyre Peninsula, SA. (Source: Ian Bayly.)

Figure 4.22 Like a string of huge pearls, this chain of salt lakes on the upper Avon River, WA, stretches to the horizon. Mosaics and chains of salt and freshwater lakes, dry for most of the time, span the vast inland expanses of the continent where their boom–bust cycles have occurred for millennia. (Source: Jenny Davis.)

unused to such uncrowded splendour. Unfortunately, temporary waters have seldom been as valued as permanent ones for protection and conservation. However, their conservation significance is being acknowledged as they become recognized as providing important ecological refuges and 'stepping stone' habitats of varying duration across the landscape.

4.8 BIOLOGICAL PROCESSES IN SALINE STANDING WATERS

Naturally saline standing waters abound across over three-quarters of Australia. Most of them periodically dry out, some for decades. The biota of these waters must be able to cope with not only high salinity but also massive fluctuations in salinity as well as in water level and availability. For most freshwater aquatic organisms, these extremes are too much, and the biota of most saline lakes is far less diverse than that of nearby fresh waters (Bayly and Williams 1966). However, productivity by the few species that can tolerate the conditions in saline waters can be very high, fuelling huge abundances of consumers all the way up to waterbirds and other top predators.

In temporary saline standing waters, we see parallels with the patterns described earlier. When dry saline lakes are re-wetted, resistant propagules of decomposers, producers and consumers in the sediments soon germinate or hatch. Producers such as cyanobacteria, algae and larger aquatic plants must complete their life-cycles while the salt lake is flooded, which may be only for a few weeks. Productivity is usually high. For example, the unicellular alga *Dunaliella salina* may be prolific enough to turn many salt lakes a characteristic pink as salinity increases after re-wetting. Other producers such as the charophyte *Lamprothamnium* and flowering plants of two submerged genera *Ruppia* and *Lepilaena* also flourish in the open water and littoral zones of saline lakes, while salt-marsh species (e.g. samphire *Sarcocornia* and seablite *Suaeda*) grow along the fringing zone.

Resting stages in the sediments yield a fairly diverse zooplankton and nekton on re-wetting. Common species include rotifers (e.g. *Brachionus*), anostracan brine shrimps such as *Artemia* and *Parartemia*, cladocerans (e.g. *Daphniopsis pusilla*), calanoid copepods (*Calamoecia*) and ostracods (*Mytilocypris*). Sometimes, mobile air-breathing insects such as dytiscid beetles (*Necterosoma*) and corixid (*Agraptocorixa*) and notonectid waterbugs (*Anisops*) also colonize newly filled salt lakes to feed on the high productivity. Spectacular larval populations of the chironomid *Tanytarsus barbitarsis* construct feeding tubes on the bottom of some salt lakes where they comprise the most abundant macrofaunal decomposer. In many salt lakes, the isopod *Haloniscus searlei* and the snail *Coxiella* also occur in large numbers (Bayly and Williams 1966, Box 4.10).

Box 4.10 A requiem for salt lakes in Victoria

Salt lakes are archetypal Australian wetlands. They are ubiquitous, but in western Victoria there is an exceptional cluster of lakes that span the range from fresh water to crystallizing brine. Some are ghosts of what they were, but all did much to foster the emergence of limnology as a discipline in Australia. Two pioneers who inspired many young researchers were Ian Bayly and Bill Williams – they described the lakes and speculated about the evolutionary origins of *Brachionus*, *Calamoecia*, *Coxiella*, *Diacypris*, *Haloniscus*, *Parartemia* and other iconic fauna (Bayly and Williams 1966). They showed that with progress along a salinity gradient, species diversity declines but the abundance of individuals (hence productivity) escalates, often to astonishing levels. The beaches of Lake Corangamite, for example, had rolling dunes of snail shells (*Coxiella striata*). Nearby lakes had water sometimes like green paint, setting records for algal productivity. Here then was a canvas for ideas about the physiological and ecological nature of animals and plants living in harsh, changeable environments, and the roles of physical, chemical and biological factors in the structure and dynamics of ecosystems (e.g. Walker 1973). For those keen to know more, Williams (2002) and Timms (2005) provide windows on our salt lake heritage and its future.

Keith Walker, University of Adelaide

Microbial processes also re-activate upon wetting. The sediments of most saline lakes are coated in cohesive benthic microbial mats, dominated by photosynthetic producers (bacteria and algae) but also containing complex assemblages of heterotrophic bacteria. These assemblages recycle nutrients locked in the sediments and contribute to the peak in nutrients often seen in reflooded wetlands (Section 3.10). As we saw earlier, these mats also play a role in governing the nutrient status of some saline waters, stabilizing the lake bed and promoting water clarity.

Coping with fluctuations of salinity and drying requires appropriate physiological, morphological and life-cycle features. For example, *Dunaliella salina* varies in morphology at different salinities and produces desiccation-resistant spores. It also produces glycerol to protect it from extremes of osmotic and temperature stress, and carotenoids as a ‘sun block’. The aquatic plant *Ruppia* accumulates proline as an inert osmotic substance that prevents salt entering the cytoplasm. This plant also differs in morphology in different environments, and produces prodigious numbers of seeds and asexual propagules that persist on the dry salt crust until the wetland refills (Brock 1986). A common group of plants in salt lakes, the samphires (e.g. *Sarcocornia quinqueflora*), accumulate salt in swollen leaf bases that then fall off, removing the excess salt. Most salt-lake crustaceans have physiological ways to cope with salt. For example, brine shrimps *Artemia* appear red because they have haemoglobin, which gives them an adaptive advantage at high salinities as well as at low dissolved oxygen concentrations (Mitchell and Geddes 1977), and the copepod *Calamoecia salina* produces an organic osmotic protector similar to that in *Dunaliella* (Bayly and Boxshall 2009).

Salt lakes are a crucial component of the chains and mosaics of standing waters in the Australian landscape (Figure 4.22). They attract immense numbers of waterbirds (e.g. >600 000 in Lake Eyre, Kingsford and Porter 1993) that feed or breed there. Saline lakes provide vital breeding and feeding habitats for the endemic banded stilt *Cladorhynchus leucocephalus*. They, and red-capped dotterels *Charadrius ruficapillus*, seek snails and crustaceans along the edges of ephemeral salt lakes. Out in the open water of larger lakes, pelicans can form massive fishing fleets. As most of these waterbirds fly among fresh and saline standing waters across the landscape, they link the systems with subsidies of energy, nutrients and propagules of colonists. Even an apparently isolated saline lake in the middle of the Australian desert is linked to other aquatic ecosystems as well as the adjacent terrestrial ones.

4.9 SYNTHESIS

Water regimes and physical, chemical and biological processes all interact at multiple scales, a theme repeated in a diverse array of standing waters. These interactions influence all levels of organization from individual organisms to mosaics of aquatic ecosystems at the landscape scale. Processes at one scale have major implications for smaller and larger scales.

Aquatic linkages are common but the linkages are also mediated by metapopulations and metacommunities of mobile organisms such as flying insects or waterbirds that provide pathways for subsidies of energy, nutrients and organic matter between aquatic and terrestrial ecosystems. In standing waters (and running waters, Chapter 7), energy is transferred across trophic levels via two broad pathways: an autotrophic producer–consumer one and a heterotrophic detritus–decomposer–consumer one. Different pathways predominate in different types of standing waters, at different times, and sometimes in different zones within a waterbody. Although this framework is simplistic, it helps us assess conceptual models (e.g. alternative states and trophic cascades) and to consider their application as tools (such as biomanipulation) to address management issues.

Many gaps remain in our knowledge about lentic environments. Unfortunately, natural history studies and fundamental limnological surveys have become unfashionable, and this means we often lack the empirical data needed to assess the validity of conceptual models. Long-term studies are particularly rare and struggle for on-going funding. Microbial processes, although fundamental to all aquatic ecosystems, are poorly known in most Australian waters, especially those that experience extremes in water quality, water availability or both.

In the next three chapters, we explore the parallels and contrasts between standing and running waters. The focus is on how unidirectional flow affects the physical, chemical and biological processes discussed so far. We also introduce several conceptual models developed to deal with networks of linked channels, instead of mosaics of standing waters, and consider how lentic and lotic waters interact within the Australian landscape.

CHAPTER 5

Physical processes in running waters

5.1 FLOW AND THE DIVERSITY OF RUNNING WATERS

The defining feature of all running waters is that they have **unidirectional flow**. Throughout this chapter, we build on what we learned about physical processes in standing waters (Chapter 2) and see how these processes are modified by the presence of flow. Not all rivers flow all of the time, and many flow laterally out onto their floodplain as well as longitudinally down their course (Section 1.5.2). Therefore, we need to know more about where flow goes and when, how to measure it, what and how much it carries, and what the implications of all this might be for chemical and biological processes. Diverse running waters occur across Australia, ranging from alpine streams fed by snow-melt through to ephemeral channels that flow only after unpredictable rain, and from steep and turbulent streams with rocky beds through to meandering lowland rivers dominated by fine sediments (Figure 5.1). There are also numerous streams and rivers that dry to isolated pools (Figure 5.1d), often only connected by water flowing below the bed of the channel.

In this book, the term 'running waters' is used to collectively encompass this diversity, along with the adjectives **lotic** (= flowing) and **fluvial** (= associated with running waters). We use the common term '**streams**' when the waters are relatively narrow and shallow enough to wade across them most of the time; wider and deeper ones are '**rivers**'. Of course, this division into streams and rivers is as arbitrary as our earlier distinction between deep and shallow lakes (Chapter 2), but will be familiar to most readers. Finally, to emphasize altitudinal aspects, we sometimes contrast **upland streams** with **lowland rivers**. The main themes of this chapter are how the physical processes of flow vary across different types of running waters and the effects of this variation on other processes such as the transport of sediments.

We begin by exploring issues of scale and hierarchies in physical habitats before discussing flow regime and how to measure flow and estimate discharge. Australian running waters have particularly extreme flow variability, and we review that before looking at one of the most characteristic physical processes in lotic environments – the interaction of flow and sediments – and how this affects the shape and profile of the channel and associated floodplains. The chapter concludes with a catchment-scale perspective of longitudinal changes in running waters, emphasizing the themes of connectivity, patchiness and variability.

5.2 SCALE, ECOLOGICAL HIERARCHIES AND NETWORKS

Lotic ecosystems are dynamic, changing through time and space, and connected by flowing water. As in lentic environments, processes in running waters occur at different spatial and temporal scales, usually considered as a hierarchy (e.g. Biggs *et al.* 2005). Hydrologists and fluvial geomorphologists describe lotic physical processes as occurring over time scales of present time (1–10 years, e.g. channel expansion and contraction),

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Australian Freshwater Ecology: Processes and Management, Second Edition. Andrew J. Boulton, Margaret A. Brock,
Belinda J. Robson, Darren S. Ryder, Jane M. Chambers, and Jenny A. Davis.

Companion Website: www.wiley.com/go/boulton/freshwater

Figure 5.1 Some examples of the diverse running waters in Australia: (a) upland sub-tropical stream, (b) cobble-bed coastal lowland river, (c) inland lowland river meandering over fine sediments, (d) remnant pool in an arid-zone sand-bed river (note the high-water mark on the rock walls indicating the water level when flowing). (Source: (a), (b) and (c) Darren Ryder; (d) Belinda Robson.)

modern time (10–>100 years; e.g. channel movement and formation) and geologic time (>1000 years; altered drainage patterns at the catchment scale) (Richards and Clifford 2011). Spatial scales, matched with these time scales, range from individual sediment particles to entire fluvial networks across the landscape. Physical processes of flow, erosion and deposition occur across all these scales to influence ecosystem processes in running waters.

Lotic waters and their catchments form **directionally nested networks**; 'directional' because downstream reaches are connected to upstream ones via unidirectional flow and 'nested' because smaller parts lie within larger ones (Section 5.3). Although there are many ways to describe these networks, one of the most popular is to describe how smaller streams link up to form larger ones and so on, referred to as **stream order**. The method proposed by Strahler (1952) is still widely used. The smallest (usually temporary) streams at the top of the catchment are called 'first-order' streams. When two first-order streams merge, they form a 'second-order' stream, and so on (Figure 5.2a). However, a limitation of this method is that a large number of first-order tributaries may join a larger channel (see left-hand branch of Figure 5.2a), increasing its discharge but not changing its order according

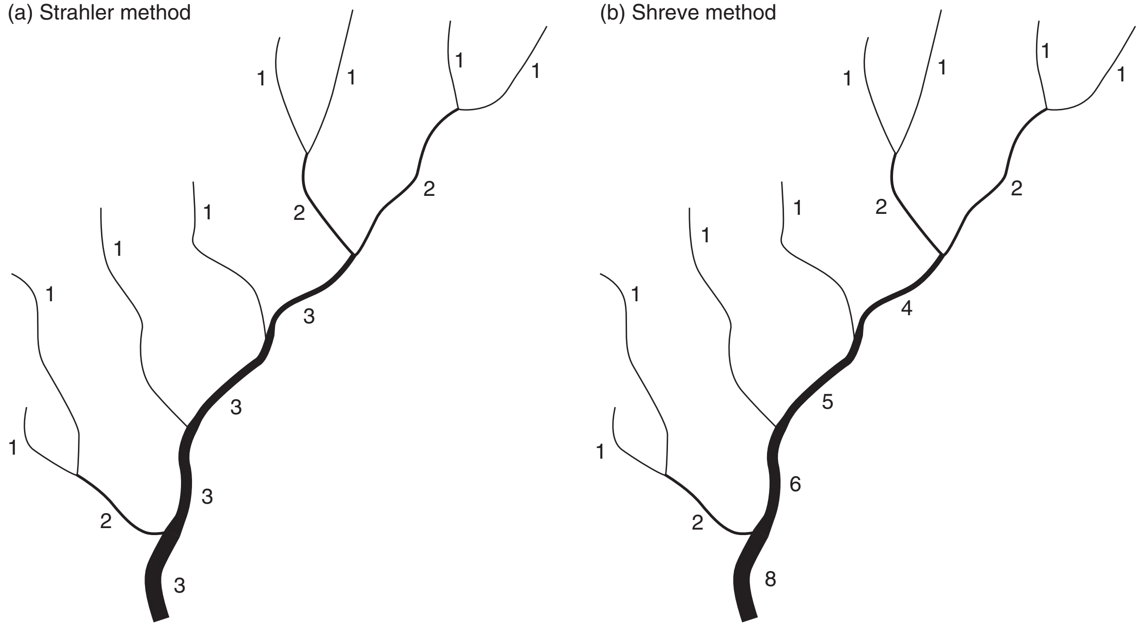

Figure 5.2 Depictions of stream order (where numerals represent order: 1 = first order, 2 = second order, etc.) classified by the Strahler (a) and Shreve (b) methods. (Source: Boulton and Brock 1999.)

to the Strahler method. To overcome this, Shreve (1966, 1967) suggested that stream order be calculated as the sum of the tributaries (Figure 5.2b). This system gives a classification that better matches discharge patterns but is cumbersome to compute for large streams. Both methods depend heavily upon the scale of the map used to determine stream order, and so the map scale as well as the method used should be specified when reporting the work.

The stream-order approach is a convenient estimate of channel and network size, is relatively easy to determine, and correlates well with empirical measurements of catchment drainage area, discharge volume and channel dimensions (Murphy *et al.* 2007). Consequently, it has been extensively used in the conservation planning and restoration of running waters (review in Melles *et al.* 2012).

A second approach to describe stream size is by **drainage area**. Drainage area can be determined for single tributaries up to entire river networks, and is also spatially nested like stream order. Increasingly, this measure is being used to represent stream size because it facilitates the creation of rainfall-runoff models and more precise calculations of discharge (Vaze *et al.* 2010). Technological advances in remote sensing and digital elevation models (Box 5.1) make information on drainage area readily available. Nonetheless, Strahler's stream-order approach will probably continue to be used widely as a convenient and simple estimate of stream size. Furthermore, many of Australia's river catchments receive such spatially uneven rainfall and have such complex patterns of evaporation and seepage down their length, especially in dryland (i.e. arid and semi-arid) regions, that relationships of drainage area with discharge are highly variable.

5.3 A HIERARCHICAL CLASSIFICATION OF PHYSICAL FEATURES

As well as using measures such as stream order and drainage area, many river ecologists think of physical features in running waters as being arranged in a

Box 5.1 Using digital elevation models to define river networks

The availability of high-resolution satellite imagery with sub-metre pixel sizes has opened up opportunities to map riverine landscapes at greater spatial and temporal resolutions. Detail visible in high-resolution satellite imagery approaches that of aerial photography. We can also now generate detailed three-dimensional digital elevation models with sub-metre horizontal resolution and vertical resolution of just a few centimetres using LiDAR (also known as Airborne Laser Scanning) to investigate channel and floodplain features and their hydrological connections over extended reaches. For example, Frazier *et al.* (2012) developed digital elevation models of habitat features of the Namoi River, NSW, by using a combination of LiDAR and image-based discrimination of habitat features assessed by object-oriented approaches. This technique was successful for mapping reach-scale geomorphic features such as channels and lateral bars, but less effective at discriminating large woody debris because of poor spectral and vertical resolution. Consistent technological improvements in high-resolution remotely sensed data will enhance the power of this tool for mapping and understanding the spatial and temporal distribution of reach-scale geomorphic features within drainage networks.

Paul Frazier, EcoLogical Australia

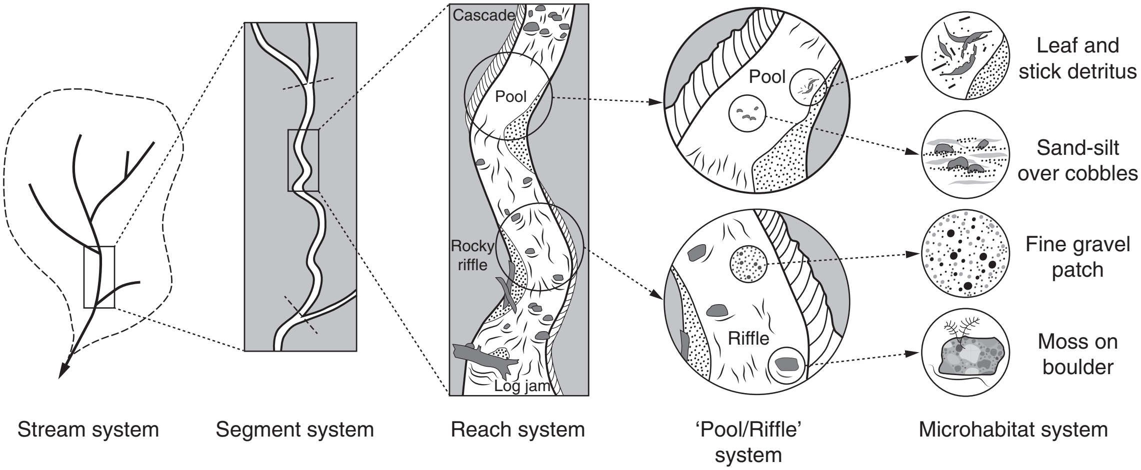

Figure 5.3 Running waters can be described spatially as a nested hierarchy of different 'systems'. (Source: Frissell *et al.* 1986. Redrawn with permission of Springer, New York LLC. Image drawn by Belinda Cale.)

spatially nested hierarchy that is longitudinally connected. One of the most widely used classifications is that by Frissell *et al.* (1986). In this classification (Figure 5.3), the **stream system** is the entire network of flowing surface water draining the catchment and leads down to a given point such as its confluence with a larger river, a terminal wetland or the ocean. Stream **segments** are typically bounded by tributary junctions whereas most **reaches** within stream segments are defined by breaks in stream slope. Within stream reaches, the most common habitats are erosional **riffles**, depositional **pools** and **runs** (whose water surface is smooth but where flow is faster than in pools), along with cascades, waterfalls and other habitats. Finally, within these different habitats lie various **microhabitats** such as patches of fine gravel and packs of leaves and sticks (Figure 5.3). Chapter 7 gives more details on these different microhabitats and their biota.

Like all such classifications, this one imposes artificial boundaries on what is really a continuum, albeit a patchy one. Furthermore, there are other features that could be included as microhabitats and we can envisage situations where pool-riffle systems are absent (e.g. most lowland rivers). Nonetheless, as a starting point in considering the physical features of running waters, this is a useful spatial framework. For example, it can be extended into the 'network dynamics hypothesis' proposed by Benda *et al.* (2004), which highlights the key roles that channel confluences (where two channels meet) play in water and sediment flux that then trigger changes in channel and floodplain morphology. By describing a river network as a population of channels and their confluences, predictions can be made about how basin size, basin shape, drainage density and network geometry interact to regulate the spatial distribution of physical habitats throughout a river basin.

The framework also has the advantage of reminding us how space and time are associated at different levels in the hierarchy (Figure 5.4, Biggs *et al.* 2005). Various geomorphological processes are likely to occur as scales of time and space decrease (Frissell *et al.* 1986). For example, at the broadest scale, rivers may have occupied their drainage basins of thousands of square kilometres for millions of years ('geologic time'). At the segment scale, there may be shifts in tributary junctions and development of new first-order channels occurring at spatial scales of hundreds of metres and temporal scales of thousands of years ('modern time'). At finer scales, changes in flow and sediment deposition within a day ('present time') may destroy or create new microhabitats at spatial scales far smaller than 1 m^2. Furthermore, the physical processes operating at these different scales often differ from small headwater streams (Box 5.2) to broad lowland rivers because of differences in flow and hydraulics (the mechanical properties of water). Ecologists must always keep these scale issues in mind when testing hypotheses about the associations of organisms and their environment (Chapters 4 and 7).

5.3.1 Physical features and channel flows

Running waters are often categorized as either **bedrock-controlled** where the geology of the bedrock largely influences physical features such as channel shape and flow or **streamflow-controlled** where flow through alluvial (waterborne) sediments affects the channel's physical features. Streamflow-controlled rivers are more common in lowland areas, and their beds and banks are made up of unconsolidated sediments. Their channel shape, stability and gradient all change in response to flow magnitude, sometimes in a stepped fashion. In contrast, bedrock-controlled channels typify upland streams and their channel features are dictated by the erodibility of the bedrock.

This general broad trend from bedrock-controlled to streamflow-controlled channels as we move down a river's course is accompanied by general longitudinal trends in erosion and deposition. **Erosional zones** are common in the highest elevation areas of most catchments. Bedrock-controlled upland streams in this zone are generally steep and provide sediment for downstream reaches. However, many upland streams are also temporary, only flowing after rainfall, and so erosion by water may be sporadic. Mid-catchment,

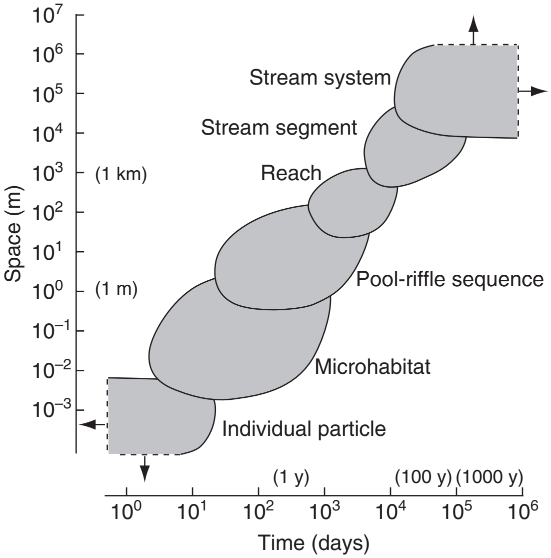

Figure 5.4 Approximate associations of spatial and temporal scale of the 'systems' in the hierarchical classification of Frissell *et al.* (1986). Individual 'particles' (e.g. leaf, pebble) are added as a potential subset within the microhabitats illustrated in Figure 5.3. (Source: Boulton and Brock 1999.)

Box 5.2 Physical habitats in small headwater streams

In terms of sediment transport and channel morphology, small headwater streams are so distinctive physically from the rest of the river system that they form an 'upstream heterogeneous zone', which is distinguished by having many large structural components in a narrow channel. The structural components include large rocks and boulders either fallen in from the banks or washed downstream, tree roots and woody debris, all of which are stochastically distributed and can constrain the morphology, hydraulics, and habitat composition of small headwater streams. This results in streams that are unable to move bed and bank material, and is ultimately responsible for these streams being more physically complex than downstream reaches. This is a fundamental driver of physical structure, dynamics, and possibly ecology in streams in the upstream heterogeneous zone. These relatively benign flow environments potentially uncouple the link between physical and biological patchiness, resulting in a faunal community composed of highly mobile generalists. However, testing of these ecological hypotheses lags behind the developments of geomorphic and hydraulic models.

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slopes are usually shallower but remain sufficiently steep for channels to convey water and sediment to lower reaches. By the time the river flows through the lower areas of catchments, gradients are very gentle and **depositional zones** now typically predominate, receiving runoff and associated sediments from the catchment as well as exchanging them with the floodplain.

Channel pattern is the 'bird's eye view' of the form of a stream or river. Channel patterns are arbitrarily classified as straight, meandering, anastomosing (= anabranching) or braided, and occur as a continuum of forms, often within a single river from source to end. Straight channels are much less winding than meandering ones; both are single threads. When the channel splits into two or more threads that later converge, it is braided when high stream power forces the threads to be quite straight before they converge, whereas in anastomosing streams, low stream power allows the separate threads to meander substantially before rejoining. Braided channel patterns typify rivers with steep slopes, faster flows and coarser sediments; anastomosing ones have finer sediments and are more common on broad floodplains. Individual threads may snake out over many square kilometres before converging, such as the Darling Anabranch, NSW.

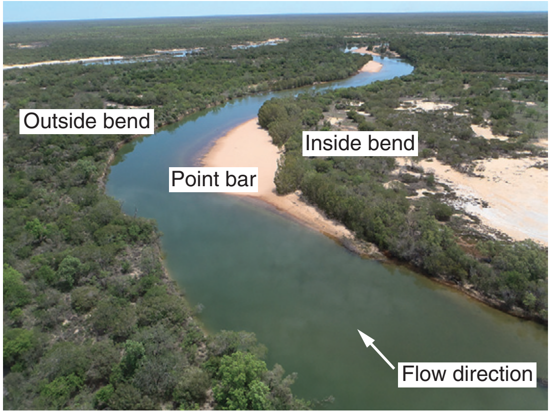

Figure 5.5 Most running waters erode the outer edge of bends and deposit sediments on the inner edges where point bars often form. (Source: Helen Dwyer.)

One useful measure for comparing the 'wiggliness' of river channels is sinuosity. This is assessed by dividing channel distance by the straight-line distance down the valley to yield the sinuosity index (SI). Rivers are said to 'meander' when SI exceeds 1.5 (Gordon *et al.* 2004). Meandering rivers have predictable regions of erosion and deposition, with flow-on effects to sediment particle size and distribution (Figure 5.5). The fastest velocities and deepest channels lie on the outer side of a bend, whereas inside a bend, water slows and may even back-eddy, depositing sediment. Bars often form on the inside of bends (Figure 5.5), and their sediments tend to be finer where velocities are lower. The deepest path along a river is the **thalweg**, and it usually carries most of the flow. A day's kayaking in a fast-flowing river soon illustrates the benefits of quickly recognizing the thalweg ahead.

The interactions of flow, channel form, sediment size and drainage patterns of running waters are studied in the discipline of **geomorphology**. The link between geomorphology and lotic ecology has been well known for decades, especially since one of the pioneers of lotic ecology, Noel Hynes (1975), wrote the oft-quoted: 'In every respect, the valley rules the stream.' To deal with the diversity of patterns of running waters, geomorphologists seek to classify them so that predictions and hypotheses can be generalized, if possible, more widely.

One widely used geomorphological classification in Australia is the 'River Styles' framework (Brierley and Fryirs 2000, Box 5.3). This classifies river reaches in terms of their channel geometry (size and shape), channel planform (i.e. 'bird's eye view') and arrangement of geomorphic units. Examples of geomorphic units include differing types of bars, sand sheets, pools, riffles, benches, levees, back-swamps and terraces. These units are used as building blocks to describe the physical form of fluvial systems, and can be used to describe reaches with differing physical forms. Using a geomorphic habitat-based approach for classifying river types is a useful way to explore the structure and connectivity of stream systems, especially in ecological research, management and restoration (Box 5.3).

5.4 HYDROLOGY AND STREAM FLOW

Traditionally, physical processes in rivers such as flow and erosion have been the domain of hydrologists and geomorphologists. Increasingly, ecologists are recognizing the central role of these physical processes in lotic ecology, greatly aided by excellent texts such as Gordon *et al.* (2004). The sources, volumes and even the timing of water inputs can strongly influence the creation and maintenance of physical features in running waters. For example, flow regimes in many dryland rivers are dominated by occasional immense floods that can dramatically change the physical structure of channels and floodplains. Before exploring these aspects of flow in detail, let's see how discharge and current velocity are measured in the field.

5.4.1 Measuring discharge

Discharge is the total volume of water moving past a point in a given time. Sometimes, discharge is loosely called 'flow' but this term is better reserved to describe the downstream movement of water. Discharge can be determined as the product of cross-sectional area (m^2) and average current velocity ($m\,s^{-1}$) so its units

Box 5.3 Using the River Styles framework to interpret the geomorphology of river systems

Rivers show a remarkable diversity of character and behaviour. Human activities have profoundly modified the patterns and rates of adjustment, altering how rivers look, how they behave and how they will adjust in future (Brierley and Fryirs 2008). The geomorphic structure and function of a river provides the physical template on which a range of ecosystem processes operate. The River Styles framework links the geomorphic character, behaviour, evolution, condition and recovery potential of river systems (www.riverstyles.com), and can be used to prioritize river conservation and rehabilitation initiatives. Interpretation of landscape forms and processes is undertaken by 'reading the landscape', a hierarchical, generic and open-ended approach to analysis (Fryirs and Brierley 2013). This allows for analysis of rivers across the spectrum of landscape, environmental and climatic conditions. The approach has been successfully applied in Australia and overseas, and is currently used to inform management policy and practice in New South Wales. Using this framework provides a coherent analysis of a river's physical template that forms the basis for river health and ecological condition assessment.

Kirstie Fryirs, Macquarie University

Table 5.1 Several common methods for measuring surface-water stream discharge.

Method	Procedure	Application
Volumetric	Measuring time taken to fill a container of known volume.	Springs or pipes where water can be concentrated and collected readily.
Velocity/ cross-sectional area	Measuring cross-sectional area of the stream (e.g. by stringing a tape across the channel, measuring water depths at frequent intervals, and determining cross-sectional area) and measuring velocity using floats, dyes or current meters. Discharge computed as the product of cross-sectional area and velocity.	Surveys for spot estimates of discharge, especially in shallow (<1 m) channels. Better for narrower (<30 m channels).
Dilution gauging	Introducing a chemical tracer (e.g. salt, dye) into the channel and monitoring changes in its concentration at some point downstream. These methods also reveal 'dead-water' zones where there is limited water exchange with the main stream. Tracers must be highly soluble, easily detected at low concentrations, inexpensive and nontoxic.	Ideal for rock-strewn, turbulent streams where the bed is highly irregular, foiling current meters.
Constructed gauging stations	Weirs, culverts and paved road crossings are ideal for permanent discharge gauging stations. If discharges and stream depths are measured simultaneously over a range of discharges, a stage-discharge relationship enables discharge to be estimated from the rating curve simply by measuring water level.	Suited for permanent gauging points on small streams and large rivers where repeated or continuous measurements are needed. Relies on a stable channel.
Rainfall-runoff models	Mathematical model to produce a surface runoff hydrograph. Requires knowledge of catchment surface area and infiltration excess and assumes uniform rainfall and runoff throughout the catchment.	Best suited to non-gauged systems. Used to model the effects of changed land use or climate on discharge.

are m^3s^{-1} (or, colloquially, 'cumecs'). Discharge of large rivers is also often expressed as megalitres (ML, 10^6 L) or gigalitres (GL, 10^9 L) per unit time (e.g. 25 ML per day).

There are several different ways for measuring discharge (Table 5.1). The most appropriate method to use depends on the aims of your study, how accurate you need to be, what equipment you have, and the shape and size of the channel. In the field, 'snapshot' estimates of discharge usually rely on measuring cross-sectional area of the wetted channel and then collecting enough measurements of current velocity (see Section 5.4.2) to obtain a reliable average. Multiplying the two gives an estimate of surface discharge at the location of the cross-section. Cross-sectional area is readily measured in most shallow streams with simple surveying methods (Table 5.1). However, in large or deep rivers, more sophisticated technology such as an Acoustic Doppler Current Profiler mounted on a boat and coupled with GPS-located velocity measurements might be needed. For example, Webster and Ford (2010) used acoustic profiles of the large Fitzroy River in northern Queensland to estimate temporal changes in discharge and suspended sediments of downstream inputs to near-shore areas of the Great Barrier Reef.

5.4.2 Measuring current velocity

Many methods to estimate discharge rely on being able to measure current velocity. Floats released into the channel can be timed to give a measure of velocity and are relatively cheap and simple to use. The best floats are those that are only slightly buoyant as they are less likely to be blown by the wind. Oranges are ideal (Hynes 1970), and you can eat them afterwards. Alternatively, a suitable twig snapped from fringing vegetation should also float, evoking memories of 'Pooh sticks' from the bear's pioneering work on stream hydrology and organic matter transport published by Milne (1928).

A suitable straight stretch with minimum turbulence is selected, and the float is released some distance upstream so that it can reach the speed of the water before entering the measurement area. Ideally, the stretch should be long enough to allow the float to travel for about 20 s. As surface velocity is greater than mean velocity (less friction from the bed), estimates should be multiplied by 0.9 in smooth water, 0.8 in turbulent water, and 0.67 in highly turbulent mountain streams. As a general rule, 0.85 is commonly used (Gore 2006). Dye can be used instead of a float, especially where water is very shallow. However, it is hard to identify the middle of the mass of dyed water, especially in turbulent streams.

Current velocity can also be measured using various sorts of meters. Propeller meters (Figure 5.6a) rely on the water passing a vane to spin a propeller. Cup meters use the same principle but water spins a vertical-axis cup rotor. The number of revolutions is related to the speed of the water. Cup meters are very sensitive in slow water but are buffeted by turbulence and readily fouled by detritus or aquatic plants.

Electromagnetic meters (Figure 5.6b) work on the principle that a conducting fluid moving through a magnetic field will induce a voltage. This voltage is detected by electrodes embedded in the sensor and is transmitted through the cable to the meter. The voltage amplitude, representing the speed of water flowing around the sensor, is electronically processed to give a direct measurement in specified units (e.g. $cm\ s^{-1}$). The meters do not work well in extremely fresh water, and the bulb must be kept polished and free of nicks so that water flows smoothly over it. These meters are useful in vegetated channels that would foul cup and propeller meters.

Acoustic Doppler meters emit sound impulses that bounce back from the bed to receivers, and can measure velocities over small areas ($<1\ cm^2$) and detect very low flows. One other advantage is that they measure the velocity some distance beneath the emitter and sensors so the probe itself does not interfere with the flow. However, measurements may be distorted by high turbidity and movement on the riverbed, such as plants waving in the current.

Where in the water column is best to take measurements? As mean velocity is of most interest for estimating discharge, current velocity is routinely measured at 2/10 and 8/10 of the maximum stream depth for

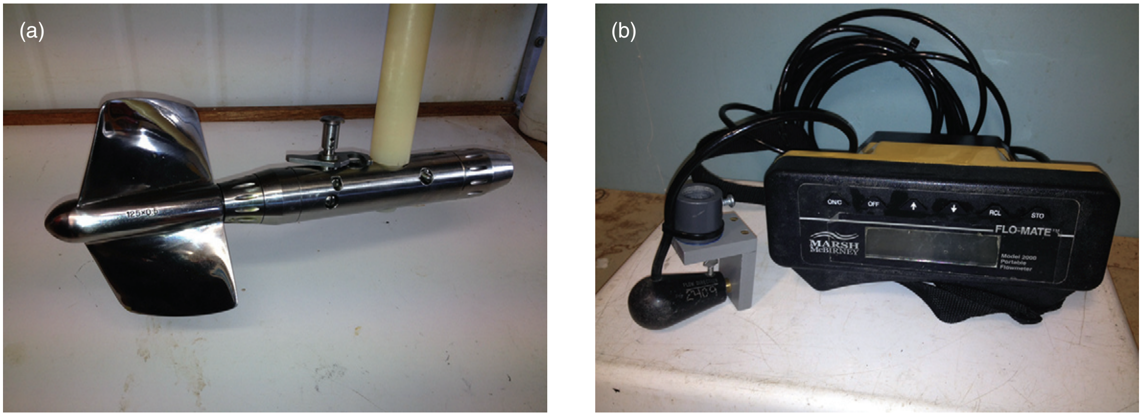

Figure 5.6 Current velocity can be measured using various meters: (a) a propeller design that counts revolutions of a spinning blade, (b) an electromagnetic meter that measures changes to the electromagnetic field around its bulb to estimate velocity. (Source: Darren Ryder.)

the selected location, and the values averaged. If only one measurement is to be taken, it should be at 4/10 the depth when measured upwards from the stream bed. A top-setting wading rod (Gordon *et al.* 2004) helps attain this depth and support the probe or propeller in turbulent or fast flow.

5.5 HYDROGRAPHS, CATCHMENT CHARACTERISTICS AND GROUNDWATER INTERACTIONS

A **hydrograph** ('water' + 'drawing') is a graph of discharge (water volume, or, less commonly, water depth or stage height) against time, and we saw an example early in this book (Figure 1.4). The time scale may be decades, years, months or days – sometimes even hours representing a single runoff event such as a flash flood.

Hydrographs convey immense amounts of useful information at a glance. At broad time scales of years to decades, they indicate whether a river is permanent (flows continually) or temporary (flow ceases periodically or only flows briefly after rain, Table 1.2). They also show whether the flow regime is stable, seasonal (e.g. peaking during the same period annually) or 'flashy' and given to unpredictable rises and falls. Other useful variables such as total annual discharge, median flow and aspects of the flood pulse such as frequency, average peak and flood duration can also be readily determined (Gordon *et al.* 2004), and in later chapters, we see how these relate to ecological processes.

At finer time scales of days to hours, the shape of a hydrograph during a storm event can reveal much about the characteristics of the catchment and how they affect the hydrological linkages of surface and subsurface runoff and infiltration that we first came across in Chapter 1 (Figures 1.7 and 1.8). When precipitation exceeds the infiltration capacity of the catchment, **overland flow** can occur (Figure 5.7). More commonly, the water infiltrates the ground and travels as **interflow** through permeable upper sediments above a relatively impermeable layer. Deeper flow pathways are often much slower, moving as **groundwater flow** (discussed in Section 8.3). When and where the ground in low-lying areas (e.g. floodplains) becomes saturated, interflow may be forced to the surface (Figure 5.7), forming permanent or temporary seeps.

We can now go back to interpreting the short-term hydrograph of a storm event, plotted over hours or days. Storm or flood hydrographs have a **rising limb**, a **crest** and a **falling limb**. The rising limb is usually concave and quite steep, and reflects the catchment's infiltration capacity (Gore 2006). The crest indicates the peak flow during the flood. The falling limb, sometimes called the recession curve, generally trails away more gently as the contribution of interflow into the channel subsides and the river returns to base flow fed by groundwater.

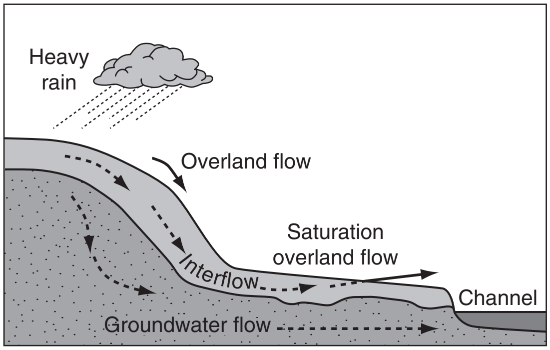

Figure 5.7 Heavy rain can cause overland flow when infiltration capacity is exceeded or when water is forced to the surface by saturation of low-lying ground. Other flow pathways towards the channel (far right) include interflow and the much slower and deeper groundwater flow. (Source: Boulton and Brock 1999.)

The shape of the storm hydrograph reveals much about the catchment's characteristics. For example, catchments with large storage capacities, broad channels or large absorptive surfaces will have hydrographs with lower crests than those from similar-sized basins but with less storage capacity (Figure 5.8). When catchment infiltration is reduced (e.g. as a result of urbanization and paved surfaces), the rising and falling limbs may be relatively steep compared to equivalent catchments with natural vegetation. These sorts of flashy hydrographs are also common in arid-zone streams where the desiccated catchment often becomes hydrophobic (water-repellent), reducing catchment storage and causing sweeping sheets of overland flow after heavy rain (Thomas 2011). This is also why flash floods occur in these regions, even when rainfall is quite low.

Another major determinant of the shape of the flood hydrograph is whereabouts along the river it has been measured. In the upper reaches, the peaks are usually

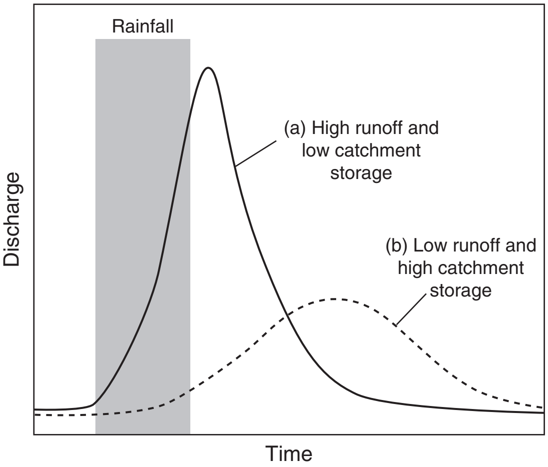

Figure 5.8 Two flood hydrographs showing hypothetical responses to a rainfall event (shaded) in a catchment with low storage (solid line) versus one with high water storage (dashed line). In the latter, the flow peak is reduced and delayed.

higher due to greater channel slopes and reduced storage. Further down the river course, the flood hydrograph has a reduced peak height because of the lower slope and increased storage. Other factors also affect hydrograph shape, including surface and subsurface geology, vegetation cover and type, catchment topography and sediment moisture content. Full details of these factors are reviewed in Gordon *et al.* (2004). A final point relates to the vertical linkage of surface water in the channel to the groundwater below. Most rivers continue to flow after rain ceases, deriving their water from interflow because the water table slopes down towards the channel (Figure 5.9a). These streams, termed **gaining** or **effluent streams**, typify running waters in temperate and sub-tropical Australia. In these areas, with increasing distance downstream, baseflow typically increases without the input from tributaries because of this groundwater contribution.

In contrast, where the water table lies lower than the permeable channel sediments, streams are said to be **losing** or **influent streams** (Figure 5.9b). These waterways are frequently intermittent, and many of them occur in arid and semi-arid parts of the continent. Along the course of a channel, due to variations in bed permeability, groundwater profile or changes in surface discharge, a stream can shift from effluent to influent and back again. Furthermore, the same section of stream can be gaining at one time of the year and losing at another, depending on surface flows and the height of the groundwater table. These localized upwelling and downwelling zones can alter the water

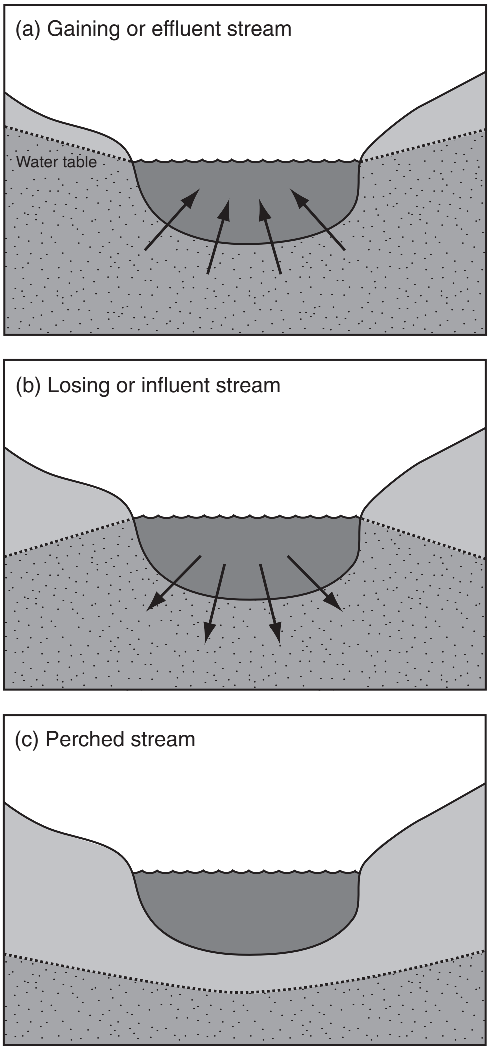

Figure 5.9 Cross-sections of (a) a gaining or effluent stream, (b) a losing or influent stream, and (c) a perched stream. Arrows show predominant direction of the vertical movement of water. (Source: Boulton and Brock 1999.)

chemistry and biota in both the surface stream and in the saturated sediments below the stream bed (Chapter 8). In addition to gaining and losing streams, **perched** or 'disconnected' systems can occur where the stream and water table are separated by an unsaturated zone (Figure 5.9c, Brunner *et al.* 2011). These are quite common, and may arise from causes similar to those of the perched standing waters described in Section 2.8.2.

The shapes of long-term and short-term hydrographs along with the type of hydrological connection of the channel to the groundwater have major implications for the chemistry and biota of running waters, explored further in Chapters 6 and 7. Many of these implications are associated with the *variability* of flow as much as with total discharge, catchment runoff or groundwater contributions. This variability, as we saw in lentic waters, underpins the diversity of biota and ecosystem processes in running waters across the different climatic regions of Australia (Chapter 1).

Figure 5.10 The Finke River, in central Australia, drains a geologically ancient and dry landscape. This river exists mainly as a channel of sand with infrequent pools of varying degrees of permanence, and surface water flows only after large, unpredictable rainfall events. (Source: Jenny Davis.)

5.6 FLOW VARIABILITY AND ITS IMPLICATIONS

In keeping with earlier comments on spatial scale, we should always specify the temporal scale when discussing flow variability. For example, in the lower Murray River where flow regimes have been altered by human activities (Chapter 9), annual flow variability has decreased but daily flow variability has increased. By world standards, most Australian rivers have low annual discharges and extremely variable annual flows. Variability of annual flow is conventionally expressed as a **coefficient of variation**, the standard deviation divided by the mean discharge, although this statistic is affected by the non-normal (skewed) distribution of flows. Not only are coefficients of annual flow variation for Australian running waters higher than the world average (Finlayson and McMahon 1988), they increase more sharply when plotted against catchment area because many large Australian rivers either rise in or flow through the arid interior (Figure 5.10).

In general, the flow characteristics of Australian rivers are more similar to those of southern Africa than to the rest of the world, especially the temperate regions of the Northern Hemisphere where many of the conceptual models of lotic ecology have been developed (Section 7.6). Even rivers in Australia's tropical zones experience variable runs of wet and dry years and cease flow more frequently than comparable rivers elsewhere. Floods are also more variable in Australian running waters. In rivers across the world, floods with a 100-year **recurrence interval** (Box 5.4) are about two to three times the volume of the mean annual flood. However, in Australia they average five times the size of the mean annual flood, and can range up to 30 times the size (Finlayson and McMahon 1988). The physical disturbances caused by this huge variability in discharge, flood magnitudes and the length and timing of cease-to-flow periods have significant chemical and ecological consequences (Chapters 6 and 7).

At the continental scale, there is also considerable variability in flow regimes across the country's diverse climatic zones. In a detailed analysis of flow regimes of Australian running waters, Kennard *et al.* (2010b) summarized these in 12 classes that differ widely in flow characteristics such as the seasonal pattern of discharge, degree of flow permanence, and variation in flood magnitude and frequency (Box 5.5). Such variability in flow regimes imposes huge economic costs when trying to obtain a reliable surface water supply for cities or irrigation needs. For example, water engineers suggest that the size of a dam should increase in proportion to the square of the coefficient of variation. This means that to obtain the same security of supply,

Box 5.4 The one-in-a-hundred-year flood

Following flooding caused by large rain storms, you might have heard media reports: 'This storm resulted in a one-in-a-hundred-year flood'. Obviously, this means that the river peaked at a stage (height) that happens only once every 100 years, right? Well, not exactly. Instead of saying 'one-in-a-hundred-year flood', a hydrologist would describe this event as a flood having a '100-year recurrence interval'. A recurrence interval is defined as the average number of years between floods of a certain size, sometimes also called the return period. A flood with a 100-year recurrence interval is one with a 1% chance of occurring in any given year (the annual exceedance probability), and could potentially occur once, several times or not at all in any 100-year period. The actual number of years between floods of any given size varies a lot because of Australia's high climatic variability. Finally, some words of caution: estimates of the likelihood of such rare events are seldom accurate, especially when the hydrologic record is short and variable such as for most Australian rivers.

Box 5.5 Flow variability in running waters

Flow variability shapes the biophysical attributes and functioning of all rivers. The structure and function of rivers and their riparian and aquatic species are largely dictated by patterns of intra- and inter-annual variation in river flows. The long-term physical characteristics of flow variability have strong ecological consequences at local to regional scales, and at time intervals ranging from days (ecological effects) to millennia (evolutionary effects). Critical components of flow variability include the magnitude of flows; timing of extreme flows; the frequency, predictability, timing and duration of floods, droughts and intermittent flows; daily, seasonal and annual flow variability; and rates of change in flow events (Kennard *et al.* 2010a, 2010b). Spatial variation in these hydrological characteristics is determined by variations in climate and mediated by catchment geology, topography, vegetation and groundwater connections. These factors interact at multiple spatial and temporal scales to influence physical habitat for aquatic and riparian biota, the availability of refuges, the distribution of food resources, and opportunities for movement, migration, reproduction and recruitment. They also influence critical physical and ecological processes such as transport of sediments and organic matter and rates of metabolism.

Mark Kennard, Griffith University

a dam in Australia needs to be twice the volume of the world average and nearly six times larger than the average for Europe (Finlayson and McMahon 1988). Impoundments on rivers come with other costs (Section 9.3), and wise water management must trade off between providing a reliable water supply and yet retaining the flow variability at multiple scales that underpins the ecology of most Australian running waters.

When considering flow regimes, we are often interested in the relationship between a given duration of flow (e.g. daily stream flows) and the percentage of time it is exceeded for a particular data set. This relationship is illustrated by a **flow-duration curve**, usually depicted on a log-log plot. One handy use is to assess the percentage of time a river might exceed a certain flow which is of ecological relevance, such as overflowing its banks onto the floodplain in a particular area. Another is to identify the percentage of time that the river has ceased to flow during the period of data collection. Both these bits of information are often used when planning the use of environmental water

(Section 9.5). Flow-duration curves are a convenient way of comparing the flow characteristics of multiple rivers or sites, and provide several useful indices such as Q_{50} (the median flow exceeded 50% of the time) and Q_{90} (a common 'low-flow index'). When comparing flow-duration curves, ensure the same period of record is used and remember that the curve does not indicate the sequence of flows or the time of the year when they occur (Gordon *et al.* 2004).

5.7 THE PHYSICAL PROCESS OF TRANSPORT

Flow in a channel may be either **laminar** where parallel 'layers' of water slide past each other at different speeds but in the same direction, or **turbulent** and mixing in a complex fashion. Turbulent flow is typical in surface streams and rivers, and exerts a shear force that can cause particles on the bed to move and roll. These moving particles are termed the **bedload**, whereas those entrained by eddies and travelling suspended in the water column are called **suspended load** (Figure 5.11). Suspended load includes particulate organic matter, living organisms, and **washload** comprising inorganic sediments such as clay and silt 'washed in' from catchment runoff. Only low velocities are needed to maintain washload in suspension and it may never settle out. For example, many inland Australian rivers such as the Murray-Darling system are naturally turbid, with high washloads (Hughes and Prosser 2012). High washloads typify running waters whose banks contain high proportions of silt and clay or whose catchments have been heavily cleared or recently burnt.

Flotation load consists of logs, sticks, leaves and organic debris floating on the surface (Figure 5.11, 5.12). The flotation load can pile up against bridges and jetties, increasing the chance of localized flooding. **Dissolved load** is simply material transported in solution. Its quantity is influenced by groundwater inputs, local geology, land use and weathering processes. In some Australian rivers, salt contributes substantially to the dissolved load, which can exceed sediment load by total weight (Stenson *et al.* 2011). During a storm, dissolved load declines initially due to dilution by rainwater but later increases as groundwater contributions enter the channel, introducing dissolved materials. In

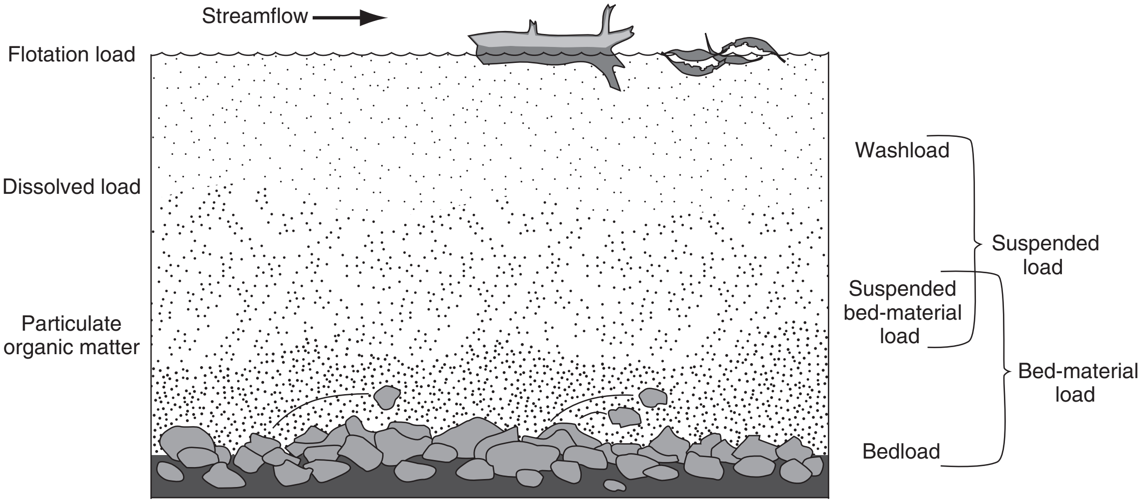

Figure 5.11 Categories of transported materials in a stream. Suspended load includes particulate organic matter, suspended bed material and washload. Particles moving on the streambed represent bedload, and most is shifted during floods. Together, these categories along with flotation and dissolved loads comprise the total load of a stream. (Source: Gordon *et al.* 2004. Redrawn with permission of John Wiley & Sons.)

Figure 5.12 Flotation load – a raft of organic matter moving downstream during a flood in the Bellinger River, NSW. (Source: Darren Ryder.)

many running waters, the largest mass of organic matter travels as dissolved load.

In many flowing waters in arid and tropical regions or in channels with actively eroding banks, sediments may comprise up to 90% of the total load. The movement of sediment (i.e. sediment flux) is calculated from discharge and sediment loads, although both of these are challenging to measure accurately, especially during floods. The reason this last point about floods is relevant is because most sediment transport occurs during high flows. Therefore, to get a realistic estimate of sediment flux, samples must be collected during floods as well as at base and low flows. Furthermore, sediments tend to travel in pulses and concentrations vary with depth and across the channel cross-section. Numerous samples are needed to obtain a reliable average.

The three main approaches to collecting suspended sediment samples from running waters are point samples, time- or depth-integrated samples and automated collection of water samples. For point samples where sediment concentrations are high, a small grab sample from near the middle of the stream usually suffices. However, at most flows, concentrations of suspended sediment are often low. This means hundreds of litres of water may have to be collected using a pump or vacuum bottle and the suspended sediment extracted by filtering or with a continuous-flow centrifuge. Time- or depth-integrated samples are collected in a special trap that slows part of the flow, causing particles to settle within the trap to provide an integrated sample over a defined period or across a series of depths. Designs of these samplers are explained in Gordon *et al.* (2004). Automated water samplers are costly but can collect instantaneous samples at almost any desired frequency from a given sampling point. They are ideal for getting fine-scale temporal resolution of sediment flux during, for example, a flood. By combining these data with a continuous record of discharge, researchers have been able to show that peaks in sediment flux often lag behind peak discharge during a flood.

Sediment flux and timing have major implications for water chemistry in running waters because macronutrients such as phosphorus (Section 3.9.1) are carried adsorbed onto sediments. When the sediments settle out, this affects redox conditions in the depositional zones, thus altering chemical processes within the bed-sediment (Chapter 6). Sediments, especially fine silt, also influence the distribution of aquatic biota (Chapters 7 and 10), and coastward-flowing running waters can extend this influence into estuaries and nearshore waters (Webster and Ford 2010). All these are reasons why sediment flux and its constituents are such useful variables to measure. However, we also need to know where the sediments come from, especially for managing problems associated with excessive erosion or sediment-bound contaminants.

5.7.1 The sources of sediment

Ultimately, all sediments are derived from erosion within the catchment. **Surface erosion** can make substantial contributions, especially in arid areas and catchments that have been cleared or that naturally have sparse vegetation. Across much of southern Australia, widespread land-clearance has contributed large amounts of sand to many rivers whose bed-sediments were previously gravels, pebbles and larger rocks. This 'sand-slug' dramatically alters the original channel shape, water depth and bed-sediment heterogeneity (Section 10.3). A second erosional process is **mass wasting**, which is the mass movement of materials by gravity, including landslides, soil creep and bank slumping (Figure 5.13, Prosser *et al.* 2001). When clay banks along lowland rivers wet and dry repeatedly, they tend to crack and slump, often bringing down large trees in the process. During the 'Millenium

Drought', there was major bank slumping along much of the lower Murray River, usually initiated as pool levels fell.

Determining the sources of sediment is crucial in catchment management. This is done by **sediment fingerprinting**, which relies on the collection of samples from all the potential sources and matching them with those in the sediment sample of interest. Potential sources include the catchment, upstream bed sediments, behind impoundments and from across the floodplain.

Figure 5.13 Mass wasting is evident along the eroding banks of this tributary of the McDonald River, northern NSW. (Source: Darren Ryder.)

Many different tracers have been used to 'fingerprint' sediments. Three of the most common are physical properties of the sediment such as colour, clay mineralogy and organic matter content (Hughes *et al.* 2012), major and trace elemental composition including carbon and nitrogen stable isotope ratios (Hancock and Revill 2013), and radionuclide characteristics (Olley *et al.* 2012). Whichever tracer is used, it should not be affected by sediment generation and delivery processes, and must remain measurable and representative. Identification of sediment sources using these techniques is now part of many management and restoration programs that require identifying areas of erosion risk to guide actions such as revegetation and sediment stabilization (Chapter 10). These programs often rely on outputs from models such as SedNet (Box 5.6) to derive budgets of basin-wide sources of sediments. It is also necessary to know how factors such as particle size and current velocity influence sediment transport once it enters the waterway.

5.7.2 Sediment particle size and distribution

Channel sediments in running waters comprise organic and inorganic particles that tend to decrease in size as

Box 5.6 SedNet – modelling sediment sources, transport and management in large river basins

Erosion control programs are more effective at reducing sediment loads in the long term if they target areas that have high erosion rates and are connected to waterbodies of concern. The SedNet model constructs a quantitative budget of sediment sources and sinks for each segment in a river network by mapping spatial patterns in hillslope, gully and riverbank erosion and deposition on floodplains and reservoirs. Field measurement, sediment tracing and river water quality monitoring can be used to constrain model parameters. Model outputs include maps of suspended sediment loads and the extent of bed material accumulation in river channels. For catchments draining to the Great Barrier Reef lagoon, SedNet estimated that >70% of the fine sediment exported comes from just 20% of the catchment area (McKergow *et al.* 2005). This information has been used with targeted land management to control sources and transport of sediments in many catchment management programs. Identifying dominant erosion processes is also crucial. In many river basins in eastern Australia, gully and riverbank erosion is a greater source of sediment than topsoil (Wilkinson *et al.* 2012).

Scott Wilkinson, CSIRO

Table 5.2 The modified Wentworth Scale for the description of particle size. Note that below 'coarse silt' are finer categories down to 'very fine silt' with a minimum size of 0.00024 mm ($\phi = 12$). These finer fractions may be relevant when assessing suspended loads or sediment chemistry.

Class	Size (mm)	ϕ
Large boulder	1024–2048	−10
Medium boulder	512–1024	−9
Small boulder	256–512	−8
Large cobble	128–256	−7
Small cobble	64–128	−6
Large pebble	32–64	−5
Small pebble	16–32	−4
Coarse gravel	8–16	−3
Medium gravel	4–8	−2
Fine gravel	2–4	−1
Very coarse sand	1–2	0
Coarse sand	0.5–1	1
Medium sand	0.25–0.5	2
Fine sand	0.125–0.25	3
Very fine sand	0.0625–0.125	4
Coarse silt	0.0312–0.0625	5

we move downstream. Lotic ecologists describe substratum particle sizes using the modified Wentworth Scale (Table 5.2) presented in a classic paper by Cummins (1962). The Wentworth Scale represents particle size in a geometric fashion that can be symbolized by phi (ϕ) where ϕ is the negative $\log_2$ of the mean particle diameter in millimetres. This has the advantage that the divisions of the Wentworth Scale are whole numbers that can be plotted and described readily (compare the two right-hand columns in Table 5.2). It also means that a phrase such as 'fine gravel' or 'small cobble' has quite an exact meaning in terms of particle size.

Particle size is a rather nebulous term because it can be defined in so many different ways. These include the width of the smallest square mesh through which the particle will pass, the diameter of a sphere with the same volume as the particle, and simply the longest dimension of the particle. These measures often reflect the method used. Large particles greater than about 50 mm are typically manually measured whereas grab samples of finer sediments are shaken through nests of square-meshed sieves whose mesh sizes match the thresholds between categories in Table 5.2. Proportions of the sample retained by each sieve are reported by weight or volume. Very small particles ($\phi > 4$) are determined by measuring the time taken for the particles to settle and using a hydrometer to periodically measure changes in the density of the sediment-water mixture.

As well as assessing actual particle size, it is also useful to examine their size distribution. In general, a plot of frequency distribution (e.g. percentages of the Wentworth size fractions) is used to illustrate the median size and variation in particle sizes. Poorly-sorted sediments (uneven particle sizes) occur in most upland stream beds although sections of depositional bars in streamflow-controlled channels may be quite homogenous in particle size (well sorted). Although particle size usually varies with depth below the stream bed, most lotic ecologists sampling benthic invertebrates or algae are usually interested in only the upper 10 cm or so. Sediment particle size, composition and stability are fundamental determinants of the habitats of most benthic organisms (Chapter 7). This partly reflects the association between particle size and current velocity in running waters, our next topic.

5.7.3 Current velocity, erosion and transport

In broad terms, faster currents are needed to move larger particles. However, this is not a simple linear relationship (Figure 5.14) because of the effects of factors such as particle shape, density, packing and biological activity such as algal growth on the stream bed. For example, plate-shaped particles on the bed of the channel are sometimes packed in such a way as to form an 'armoured' layer of sediments that otherwise would move at a lower current velocity.

Sediment movement in running waters involves initial erosion to entrain the particle, then transport of the particle according to the energy of the flow, and finally deposition or sedimentation. The **entrainment velocity** is the lowest current velocity at which a particle resting on the bed will move (i.e. erode), and can be quite variable as shown by the shaded band in Figure 5.14. Sand about 1 mm in diameter is the most easily eroded with a critical entrainment velocity of about 20 cm s^{-1}. Larger, heavier particles need faster currents

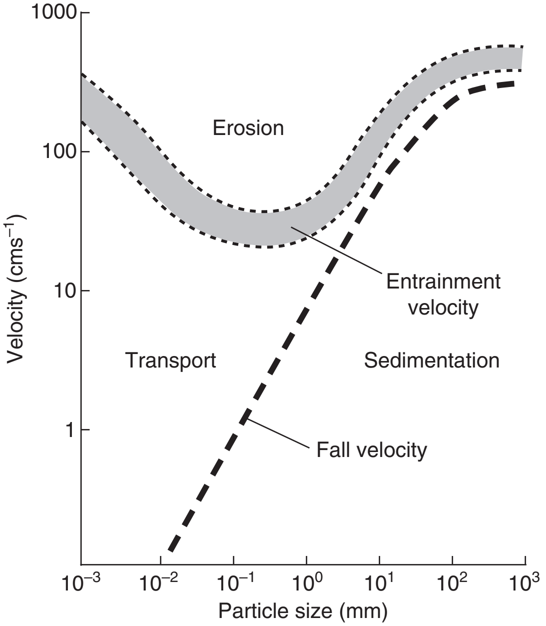

Figure 5.14 The limiting velocities required for erosion, transport and deposition of uniform particles differing only in size are represented by Hjulström curves. (Source: Hjulström 1939. Reproduced with permission of American Association of Petroleum Geologists.)

to move them. However, the finer particles of silts and clays are more cohesive and have anomalously high critical entrainment velocities.

Once in transport, particles will keep moving at a slower velocity than that needed to entrain them. The largest particle that can be carried at a given state of flow is termed flow **competence**. When the flow drops below that needed to move the particle, it settles out (termed 'fall velocity', Figure 5.14). Larger particles settle out before smaller ones, and this process is largely responsible for gradients in sediment particle size along gravel bars or down river channels.

The amount of sediments transported increases with discharge unless the sediment supply is depleted. In most running waters for most of the time, discharge is too low to move much of the larger sediment. However, floods can dramatically change this process, and the majority of channel formation and sediment transport occurs during these brief events. Interestingly, most bedload movement takes place during events of intermediate (bankfull) magnitude and frequency because the smaller flows have low competence and the larger floods are too infrequent. Extremely large floods, termed 'channel-forming events', may reroute channels and primarily define channel capacity (Page *et al.* 2005).

5.7.4 Sediment dynamics and channel form

Channel form refers to the shape of the channel – its depth, width, planform and cross-sectional and longitudinal profile. It arises from the interplay of flow regime with erosion, deposition and transport of sediments, influenced by factors such as topography, geology, catchment land use, climate and biota. As we have seen, sediments arise from erosion zones higher in the catchment and are then carried to depositional zones downstream. Along the way, combinations of flow, sediment dynamics and channel form produce patchy microhabitats nested within broader habitats (Figure 5.3) such as fast-flowing turbulent riffles and slow-flowing deep pools. In between these often lie runs (Figure 5.15), sections where the water flows faster than in pools but is not as turbulent as in riffles. With increasing distance downstream, the channel gradient becomes gentler, riffles are less common and broader floodplains develop.

Channel form and sediment dynamics in most running waters are influenced by geomorphic features of biological origin. The most obvious of these is **large woody debris** (Figure 5.16), often called 'snags'. Logs, sticks and root-masses in the channel create depositional areas for sediment and particulate organic matter such as leaf litter. Localized increases in velocity around the snags scour out pools or undercut banks, which then provide habitat for large fishes and other organisms. Experimental reintroduction of wood into an alluvial river in south-eastern Australia increased pool and riffle area and pool depth, added new pool–riffle sequences to the study reach, and substantially increased the spatial complexity of bed-material distribution (Brooks *et al.* 2004).

Channel form changes over time, usually in response to floods that shift large volumes of sediment or create new channels and cut off old ones. When catchments are cleared of their natural vegetation, changes in channel form are often accelerated, leading to severe management problems (Section 10.3). There are also

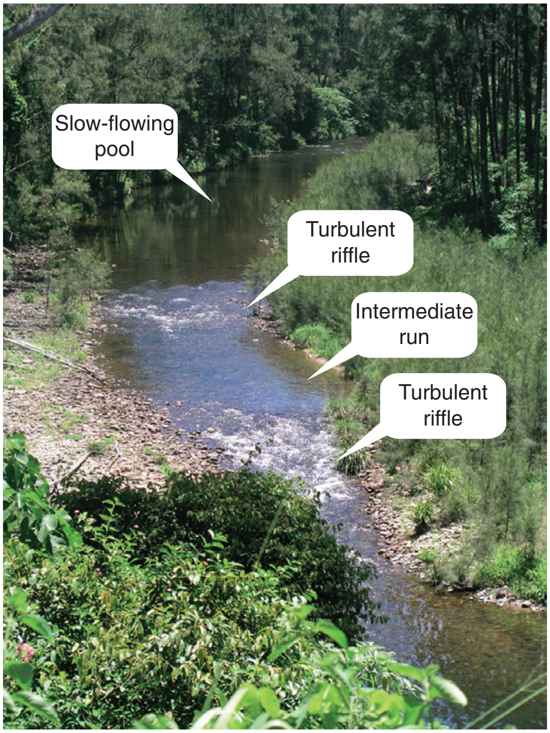

Figure 5.15 In upland streams, the spatial arrangement of habitats such as pools, riffles and runs is largely determined by the interplay of flow regime and sediment processes in the channel. (Source: Darren Ryder.)

Figure 5.16 Woody debris enhances structural diversity in this small tributary of the Wannon River, western Victoria. In the foreground, the fallen tree has collected other drifting debris and has slowed the current upstream and among the branches. In the distance, a log across the channel forms a small waterfall, creating a pool upstream and a faster-flowing run downstream. (Source: Edwin Chester.)

implications downstream. For example, heavy rains over largely cultivated catchments in Queensland in January 2005 led to massive plumes of suspended sediments and nutrients being carried from rivers into near-shore areas of the Great Barrier Reef. The nutrients caused an algal bloom that extended over 150 km offshore (Brodie *et al.* 2010). Sediment plumes also reduce light penetration with serious impacts on inshore reefs and seagrass beds (Box 5.7).

In upland streams, the differences in channel form are most apparent among pools, runs and riffles. In large rivers, the differences lie more at the level of segments and reaches where the channel carries varying amounts of water and sediments. Here, channel form can become more complex within reaches and segments with the development of backwaters, anabranches (side channels that rejoin the main channel) and billabongs. There is also the floodplain. This is still part of the river bed – it just happens to be inundated only occasionally. Nonetheless, it underpins many chemical and biological processes in lowland rivers, and so we examine its physical processes in more detail next.

5.7.5 Floodplain sedimentation and billabong formation

Floods are flows that overtop the banks (also called **overbank flows**). These high flows are erosive within the channel but when they spread out beyond the banks, friction slows the water and the sediments settle out. This process forms the floodplains typical of most Australian lowland rivers. Sometimes, the process involves ‘scour-and-fill’ when flows across the floodplain fluctuate enough to erode and then deposit sediments. Other times, there is a more gradual process of deposition with finer particles settling out further from the channel or in the lee of trees, rocks and other obstacles. Greatest sediment deposition occurs on broad, flat alluvial plains such as the Macquarie

Box 5.7 Sediment plumes on the Great Barrier Reef

During high flows, rivers draining out to the Great Barrier Reef carry extensive plumes of suspended sediments and other material, including particulate and dissolved nutrients, pesticides and the low salinity water itself. Levels of suspended sediments and contaminants have increased greatly following agricultural development (grazing and cropping) in the last 150 years, with sediment loads increasing four-fold. Plumes carry suspended sediments to the Great Barrier Reef but most of the coarser material is deposited near the river mouth. However, the finer fractions ($<10\,\mu$m) are transported hundreds of kilometres from the mouth. Within the plume, suspended sediments interact with organic matter generated from nutrients in the discharge to form organic-rich flocs (muddy 'marine snow') that are particularly detrimental to corals. After the fine sediments settle out, they are resuspended by the wind in coastal waters <10 m deep, producing turbid waters throughout the year. This reduces the penetration of light needed by benthic organisms such as corals and seagrasses (Bainbridge *et al.* 2012), and is one of the main factors in the degradation of inshore reefs and seagrass beds.

Jon Brodie, James Cook University

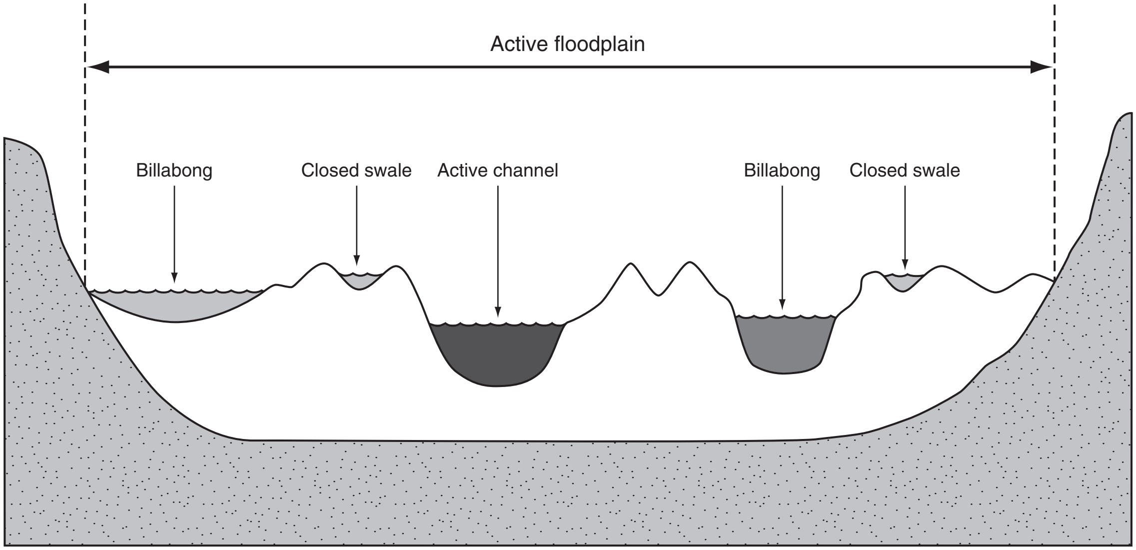

Figure 5.17 Cross-section of a typical active floodplain. Waterbodies at various elevations typically require different flood heights for filling. The darker the shading, the greater the water permanence.

Marshes in semi-arid NSW (Ralph and Hesse 2010). In all cases, the physical process of flooding and sedimentation in lowland river floodplains is essential to replenishing topsoil and nutrients, distributing propagules of plants and animals, and temporarily inundating the floodplain vegetation. Changes to flow regimes and disruption of natural floodplain formation and inundation have serious ecological implications and demand careful management (Chapters 9 and 10).

Over millions of years (i.e. geologic time), several levels of floodplain may form within the active channel (Figure 5.17). A 'modern' floodplain forms closest to

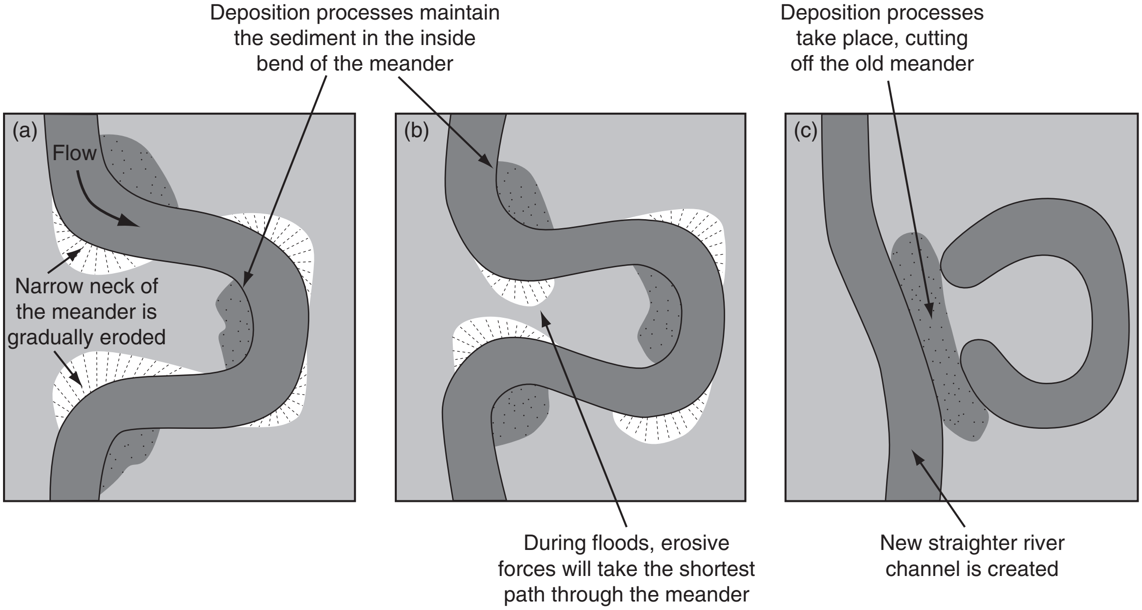

Figure 5.18 Formation of a billabong or ox-bow lake. Progressive erosion and deposition in a meandering river transform a meander (a) through increased erosion on the outer bends (b) into a straighter channel and a billabong (c).

the most hydrologically active channel. Further away lie 'abandoned' floodplains where the river channel deposited sediments over hundreds or thousands of years of flood events. These typically contain closed swales or sections of abandoned channel, often holding water after large floods or heavy rainfall. Usually, depressions at higher elevations or further from the active channel require larger floods with higher water levels to fill them. However, floodplain drainage patterns can be quite complex, and filling regimes can be difficult to predict.

Standing waters form on floodplains in several different ways. Natural deposition of levee banks across the mouths of small tributaries can close off the channel to form a waterbody. In other cases, scour pools near large pieces of wood on the floodplain create depressions that fill with water. However, the floodplain waterbody most familiar to many Australians and swagmen is the **billabong** or ox-bow lake. This forms when a meander of the main channel is cut off by erosion of the outer bends that eventually break through to form a straighter channel and a billabong (Figure 5.18). Not all billabongs are ox-bow lakes; deeper pools in the channels of inland rivers such as Cooper Creek are often called 'channel billabongs'.

Long-term changes in climate alter the dynamic patterns of deposition and erosion, changing the location and elevation of the floodplain as well as the distribution of active channels and floodplain wetlands. In the last 200 years in Australia, human activities have had similar effects although far more rapidly. Construction of levee banks and retaining walls along river channels prevent overbank flow, alienating the floodplain from the main river. Reduction of flow variability by river regulation (e.g. weirs and impoundments) has altered the hydrologic connectivity with floodplains and simplified channel complexity by removing in-channel features such as benches and terraces (Chapter 9). Flowing channels and their floodplains cannot be considered in isolation; the two are intimately linked in their physical, chemical and biological processes, and this theme is revisited in the next two chapters.

Box 5.8 Longitudinal changes in hydrology and physical features

Complex and dynamic flow and sediment pathways through catchments create physical habitats at multiple spatial and temporal scales. Hydrologic and geomorphic connections between headwater source areas and downstream river reaches are fundamental to understanding the abiotic environment of streams. Closely-coupled headwaters ensure that the hydrology of upland streams is highly responsive to storm events. Pulses of coarse sediment are supplied to the channel from steep slopes, producing a steep and dynamic upland stream morphology. Midway along the river system, transient groundwater and alluvial sediment stores buffer headwater inputs, weakening their direct influence on river channels. High stream powers, combined with hyporheic and floodplain flowpaths, extend water and sediment residence times, creating diverse biophysical conditions. Further downstream, large unconfined lowland rivers with finer bed sediments tend to have permanent flow supplied from headwaters and groundwater stores. Low sediment loads and stream energy produce slow rates of lowland channel and floodplain adjustment, with palaeo-features persisting as floodplain habitats for up to thousands of years. Low gradients can also produce complex distributary flow paths and terminal lake systems with seasonal or multi-year filling and drying dynamics.

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5.8 RIVER PROFILES AND LONGITUDINAL CHANGES IN PHYSICAL FEATURES

This chapter began by stating that unidirectional flow defines all running waters, and then discussed the effects of flow on physical features such as sediment dynamics and channel form. Most of these physical features show predictable trends associated with hydrology as we move down the channel from upland headwaters to the lowland river (Box 5.8). These trends are influenced by system-specific factors such as geographic and climatic features of the catchment, discharge and water regime, channel gradient and its longitudinal profile, and the supply of sediment and other material coming from the catchment.

In general, upland reaches of rivers have steeper gradients and coarser sediments than lowland sections (Figure 5.19). The water is often cooler because the stream is at a higher altitude and, in forested catchments, shaded by trees that may overhang the entire channel. Water temperature in lowland rivers tends to vary less than in upland streams (except in mountain streams and springs). The suspended components of the water column – turbidity, washload and dissolved load – all typically increase with distance downstream.

Channel cross-sections change from V-shaped, constrained valleys typical of bedrock-controlled upland streams to broader, unconstrained valleys with greater amounts of alluvium. Subsurface flow may be greatest in the middle reaches where there is much alluvium but the particles are not so fine that they inhibit interstitial flow. Sinuosity and floodplain formation tend to increase downstream with the decline in gradient (Figure 5.19). In ‘gaining’ streams, discharge also tends to increase with distance downstream. However, in the ‘losing’ streams common in inland Australia, discharge is often highest in the mid-reaches before it drains into distributary networks (Page *et al.* 2005).

The trends described here are broad generalizations, and represent an idealized permanent waterway flow. Although there are exceptions to these longitudinal trends, the patterns have been sufficiently universal to encourage early river ecologists to suggest the existence of sequential ‘zones’ down rivers. These zones represented combinations of physical conditions that correlate with biological assemblages although specifying the boundaries between the zones proved elusive (Hynes 1970). Subsequently, models emphasizing the continuous nature of changes along a river (e.g. the River Continuum Concept, Vannote *et al.* 1980) were proposed although these, too, drew criticism. The prevailing view now seems to be one that acknowledges the relevance of general longitudinal trends down rivers but emphasizes patchiness at multiple scales along the ‘river discontinuum’ (Poole 2002). These concepts are discussed in more detail in Section 7.6.

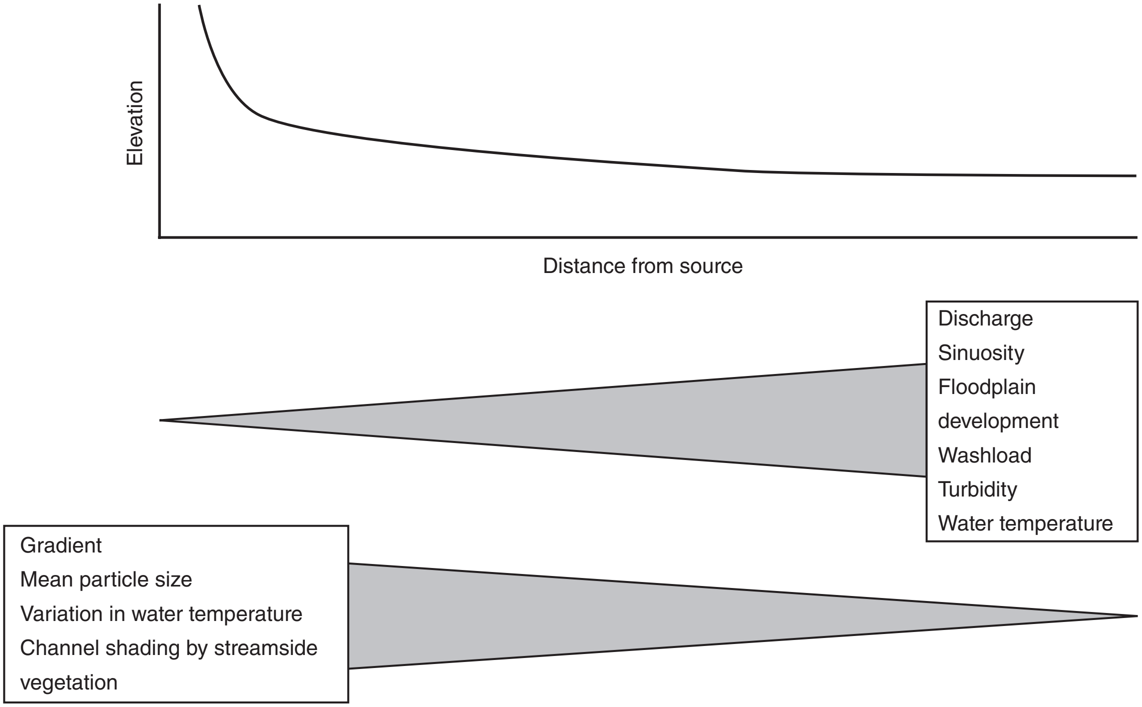

Figure 5.19 Longitudinal changes in physical features expected along a perennial temperate free-flowing river. These trends may not apply to dryland or wet-dry tropical rivers or those with cleared catchments or spanned by impoundments. (Source: Boulton and Brock 1999.)

5.9 SYNTHESIS

Unidirectional flow characterizes running waters and governs the physical processes of erosion and deposition that play such a large role in determining channel form, especially in streamflow-controlled rivers. As a result of this flow, river systems can be conceived as directionally nested networks whose components can be arranged in a hierarchy (e.g. Frissell *et al.* 1986) at different spatial scales. Associated with each level in the hierarchy are different temporal processes, confirming the association of space and time in fluvial landscapes. The interaction of flow and sediment dynamics produces spatial variability – **patchiness** – at these different scales. In the next two chapters, we see how this patchiness and the connectivity among different patches influence chemical and biological processes in running waters, especially downstream and out onto the floodplain.

There are several parallels in physical processes between standing and running waters. Although the role of water movement and its effects on bed particle size are more obvious in running waters, wave action and water movement in standing waters influence the sediments in the littoral zones (Chapter 2). Similarly, turbidity in running waters has the same effect on light penetration as it does in standing waters, and deep pools in slow-flowing rivers can thermally stratify. However, there are also marked contrasts in physical features between standing and running waters. These relate mainly to directional water movement and sediment transport, and are especially evident in the longitudinal trends in channel form and other factors as we move from headwaters to lowland rivers (Figure 5.19). The next chapter explores how these contrasts, mediated by the physical processes associated with flow, erosion and deposition, influence chemical processes in running waters.

CHAPTER 6

Chemical processes in running waters

6.1 THE COMPLEX WEB OF FACTORS

As we saw for standing waters (Chapter 3), the chemical composition of running waters is controlled by a complex web of physical and biological processes (Figure 6.1). These include catchment features such as geology, topography, land use and vegetation cover, and flow-associated features such as erosion and deposition rates. One particular factor affecting lotic water chemistry is the relative contribution from different water sources (e.g. perennial springs vs overland runoff) because these provide different suites of ions, nutrients and dissolved organic matter. Similarly, discharge characteristics and the stream load, especially the dissolved and suspended portions, will affect chemical processes. Finally, biological processes such as photosynthesis, decomposition and respiration are also significant, particularly for recycling elements and nutrients (Chapter 7).

In this chapter, we explore the effects of this complex web of factors on chemical processes in running waters. The role of unidirectional flow and its pervasive influence from headwaters to lowland reaches is particularly emphasized. While you read this chapter, think about how chemical processes differ between lentic and lotic environments (e.g. nutrient cycling versus nutrient spiralling). What might be the ecological implications of these differences?

6.2 DISSOLVED GASES

Earlier chapters described the importance of dissolved gases in aquatic ecosystem processes, especially photosynthesis and respiration, in lentic environments. Naturally, regardless of whether the water is standing or running, gases will obey the fundamental laws that govern processes such as dissolving in water or the effects of water temperature and salinity (Section 3.2). What we want to focus on here is how flow affects these processes in running waters and what the implications are.

In some sections (e.g. rocky riffles) of upland streams, most dissolved gases approach or exceed saturation because the turbulence enhances diffusion. For example, water cascading over a waterfall (Figure 6.2) or dam spillway forces atmospheric gases into solution under pressure, and percentage saturations can exceed atmospheric concentrations (i.e. supersaturation, Section 3.2.1). Biological and chemical processes producing or consuming dissolved gases in these situations have little effect on total concentrations because the equilibrium is rapidly re-established by turbulent flow. In other sections such as long pools or runs (Section 5.3), chemical and biological processes may have more influence on dissolved gas concentrations. Typically, concentrations change seasonally and daily owing to changes in temperature, photosynthetic activity and other factors. Longitudinally, total concentrations change with distance downstream as turbulent upland streams grade into lowland rivers. Finally, concentrations vary with wetting and drying in temporary streams and rivers as well (Section 3.10).

Compared to upland streams, atmospheric diffusion in large rivers plays less of a role in regulating dissolved gases, mainly because of the reduced turbulence and ratio of surface area to volume. There are some

Australian Freshwater Ecology: Processes and Management, Second Edition. Andrew J. Boulton, Margaret A. Brock, Belinda J. Robson, Darren S. Ryder, Jane M. Chambers, and Jenny A. Davis.

Companion Website: www.wiley.com/go/boulton/freshwater

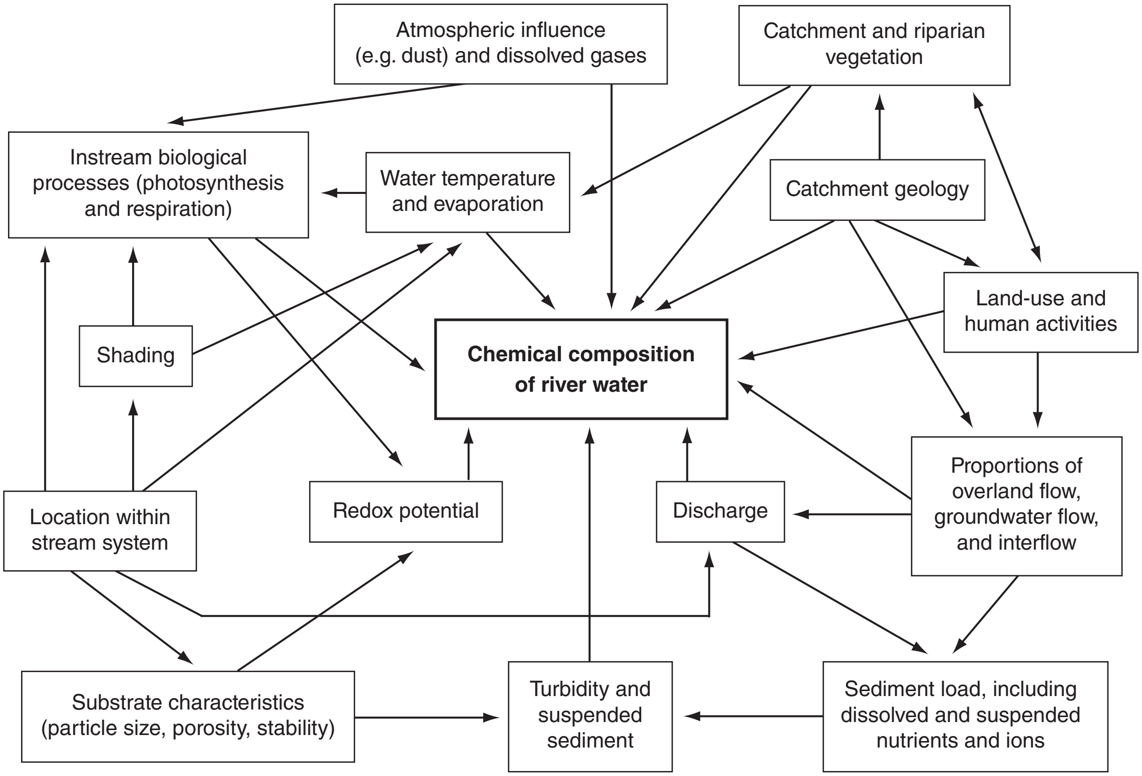

Figure 6.1 The web of factors potentially influencing the chemical composition of running waters. Unidirectional flow and the physical processes of erosion and deposition interact with most of these factors, either directly or indirectly. (Source: Boulton and Brock 1999.)

Figure 6.2 Turbulent water, such as here in Ebor Falls, northern NSW, results in most dissolved gases being close to or exceeding saturation immediately downstream. (Source: Darren Ryder.)

parallels with features that influence gas solubility in standing waters (e.g. biological activity, pH). For example, in rivers with dense beds of aquatic plants, dissolved oxygen concentrations often rise during the day from photosynthetic activity and decline at night owing to on-going respiration. This trend is the converse of the one seen in many shaded upland streams where oxygen concentrations are predominantly regulated by diel (24-hour) thermal changes, and are largely a function of the inverse relationship between oxygen solubility and water temperature (Figure 6.3).

Diel patterns in dissolved oxygen in running waters can be measured using the same methods described in Section 3.2.1. Sealed submersed chambers are often used (Grace and Imberger 2006), and provide useful insights into factors affecting stream metabolism, inferred from changes in dissolved oxygen (Box 6.1). Ryder and Vink (2007) used submersed chambers in the Murrumbidgee River, NSW, to show how flow regime influenced primary production and the distribution of dissolved gases. During flows dominated by clear-water releases from dams, dissolved oxygen and carbon dioxide concentrations increased downstream relative to equivalent flows from natural runoff. Clear water increased the depth of the euphotic zone, increasing rates of photosynthesis in the water column.

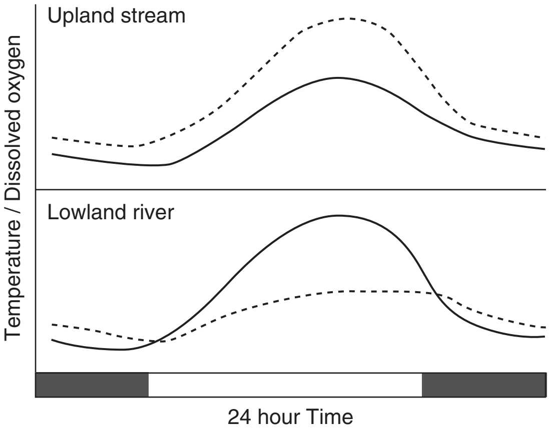

Figure 6.3 Diel changes in percentage saturation of dissolved oxygen (solid line) and water temperature (broken line) in a shaded, turbulent upland stream (top panel) and a lowland river with beds of aquatic plants (lower panel). Note the lower thermal variability typical in lowland rivers. The bar at the bottom represents night (shaded) and day (open). (Source: Boulton and Brock 1999.)

Typically, groundwater contributions to running waters (Section 5.5) are low in dissolved oxygen but high in dissolved carbon dioxide, depending on factors such as contact time with sediments and the rate of flow (Chapter 8). Consequently, depending on the relative contribution of groundwater to total discharge, there may be differences in water chemistry in the surface water. These differences can be used as tracers, in conjunction with assessments of hydrographs and concentrations of other dissolved chemicals, to identify groundwater inflows and outflows (McCallum *et al.* 2012).

As we have seen, the processes regulating the distribution of dissolved gases in running waters change with distance along the river. These longitudinal trends may be disrupted by impoundments and weirs built across rivers. Further, accumulated organic material in anoxic sediments behind the dam wall usually emits methane to the atmosphere. This occurs in the same way we saw in Section 3.2.4 for standing waters with anoxic environments. Similarly, methane from dam sediments finds its way to the atmosphere via direct bubbling or molecular diffusion. Measurements of methane fluxes from three reservoirs in south-eastern Australia have revealed that direct bubbling is the

Box 6.1 Measuring stream metabolism

Stream metabolism reflects the interplay of photosynthesis (producing oxygen) and respiration (consuming oxygen), providing the food resources and energy underpinning most aquatic food webs. Stream metabolism is typically measured by tracking changes in dissolved oxygen (DO) at intervals of 5–15 minutes over at least one day. The ecological variables of interest are the rates of photosynthesis (P) and respiration (R), estimated from:

$$\text{Change in DO} = P - R \pm E$$

where E is the physical re-equilibration of oxygen across the water-air interface, traditionally determined using empirical methods (e.g. tracer gas evasion). More recently, non-linear modelling has enabled estimation of all these variables directly from the profiles of DO over time. Introduction of fluorescence-based DO probes (Section 3.2.1) has greatly facilitated collection of reliable long-term (weeks to months) data sets that remove uncertainties arising from daily fluctuations in cloud cover (affecting photosynthesis) and discharge. Rates of P and R may then be compared under different conditions including altered nutrient concentrations, removal of bank-side vegetation and changed hydrology as well as to assess ecological condition of streams and the effectiveness of environmental flow releases.

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main pathway of methane flux to the atmosphere, with between 60 and 80% of total emissions emanating from just 10% of the surface area of each reservoir (Sherman and Ford 2011).

6.3 IONIC COMPOSITION OF AUSTRALIAN RIVERS

Given that the ionic composition of Australian standing waters does not match 'world average fresh water' (Table 3.1), it is no surprise that the chemical composition of most Australian rivers differs from that of 'world average river water'. As in standing waters, the cation Na^+ and the anions HCO_3^- or Cl^- dominate the ionic composition of Australian running waters (Table 6.1). Sources of ions are also shared between the two types of waters. Sea spray provides sodium, chloride and sulfate to many coastal systems, whereas most of the ions in lotic environments far from the coast have been washed or blown in from relictual marine deposits and other weathered rocks inland. Groundwater

Table 6.1 Chemical composition of some Australian running waters compared with unpolluted 'world average river water'. Salinity is in grams per litre (converted from parts per thousand where necessary) and ionic concentrations are in milliequivalent percentages of total cations or total anions (meq %) (Box 3.5). The dominant cation and anion in each waterbody is in bold type. (Source: 1 = Berner and Berner 1987; 2 = Williams and Buckney 1976; 3 = Glatz 1985; 4 = Bayly and Williams 1973; 5 = McNeil 1998; 6 = Williams 1975; 7 = Williams *et al.* 1970; 8 = Buckney and Tyler 1973; 9 = Blinn and Bailey 2001; 10 = Muir and Johnson 1978; 11 = Wright *et al.* 2011. * includes CO_3^{2-} in assessment.)

Location and river	Salinity (g L^{-1})	Na^+	K^+	Mg^{2+}	Ca^{2+}	Cl^-	SO_4^{2-}	HCO_3^-	Source
World average river water	<3.0	19	3	23	**55**	14	14	**72**	1
Camfield, NT	333.0	38	2	**41**	18	35	10	**54**	2
Willochra, SA	120.0	**72**	<1	19	9	**82**	17	<1	3
King Edward, WA	16.5	**54**	1	43	2	**57**	0	43	2
Dalyup, WA	9.57	**78**	1	18	2	**94**	5	1	2
Loddon, Vic.	3.52	**60**	<1	29	10	**93**	2	5	9
Wannon, Vic.	2.51	**68**	–	23	9	**81**	9	8*	4
Glenelg, Vic.	2.20	**70**	<1	21	8	**85**	3	12	9
Blackwood, WA	2.18	**62**	1	31	6	**90**	2	7	2
Wimmera, Vic.	0.95	**70**	<1	20	9	**77**	3	20	9
Brisbane, Qld	0.67	**34**	<1	33	33	**57**	0	43*	5
Condamine, Qld	0.54	36	<1	**43**	21	**50**	1	48*	5
Ku-ring-gai, NSW	0.40	**60**	4	5	31	**71**	10	19	11
Cudgegong, NSW	0.39	**38**	2	25	35	25	33	**42**	10
Darling, NSW	0.37	**50**	4	25	21	29	0	**74**	6
Sixth Creek, SA	0.35	37	–	**38**	25	37	8	**54***	4
Dawson, Qld	0.31	**53**	<1	17	30	45	2	**53***	5
Paroo, NSW	0.25	**64**	7	11	18	50	0	**53***	7
Weld, Tas.	0.21	4	7	**45**	44	11	1	**88***	8
Murray, NSW/Vic.	0.10	**51**	6	24	19	**49**	14	44	6
Cooper, SA	0.10	**36**	11	23	30	14	12	**74**	3
Murrumbidgee, NSW	0.09	22	10	**34**	**34**	21	19	**49**	7
Harvey, WA	0.08	**73**	2	20	5	**82**	6	11	2
Maracoopa, Tas.	0.08	8	1	10	**81**	10	2	**88***	8
Thomson, Qld	0.06	**53**	<1	16	30	24	18	**56***	5
Groom, Tas.	0.05	**61**	6	20	13	**79**	7	14*	8
LaTrobe, Vic.	0.05	**66**	8	13	13	**58**	4	38	9
Daintree, Qld	0.05	**51**	<1	22	14	**81**	0	18*	5

Box 6.2 Salinity profile of the Blackwood River: an alarming example of ecological change

Clearing land for agriculture in south-western WA over the past century has mobilized salt from the soil and groundwater, resulting in human-induced salinization. Only about 44% of flow in the rivers of this region remains fresh, and this has profoundly altered ecosystem structure. Many plant species are predicted to disappear and there will be continued reduction in the distributions of freshwater fishes and crayfishes. One prime example is the Blackwood River. This river has a 'reverse' salinity profile, with tributaries in the upper catchment being salinized by seasonal inputs of mobilized salts (about 1 million tonnes per year). The lower catchment is underlain by fresh groundwater and receives fresh water from tributaries draining remnant forests; this progressively dilutes the river downstream. Since the anthropogenic salinization of the Blackwood River, salt-tolerant fishes have moved hundreds of kilometres upstream from the estuary, replacing the regionally endemic freshwater fishes and crayfishes in the upper catchment. Freshwater species are now largely restricted to the area of fresh groundwater intrusion and forested tributaries, and lead a precarious existence.

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inputs of ions (Section 8.4) are also significant in some cases.

Continent-wide summaries such as Table 6.1 potentially mask regional differences in ionic composition. For example, in eastern Queensland, streams (often with short steep catchments in areas with high rainfall) are dominated by sodium whereas the more arid western Queensland streams are higher in calcium and bicarbonate (McNeil *et al.* 2005). The large rivers flowing from Queensland into central Australia have a highly variable ionic composition although sulfate is commonly elevated.

Another limitation of Table 6.1 is that it does not reveal the time of year when the sample was collected. Floods can have a huge effect on ionic composition, which is especially influenced by when the flood occurs and the conditions preceding the flood. In dryland rivers of inland Queensland, the ionic composition of floodwater is primarily influenced by catchment inputs, thus reflecting geology and land use (Sheldon and Fellows 2010). When flow ceases, groundwater contributions become more significant, along with evapoconcentration and precipitation of compounds. Spatial and temporal variability in the concentrations of individual ions peaks during the no-flow phase in response to local physical features of the channel and the variable rates of drying (Sheldon and Fellows 2010).

Finally, Table 6.1 also does not indicate where along the river the sample was collected. When tributaries draining areas with different land use, geology or sources of groundwater recharge join the network, there can be marked changes in ionic contributions. There is a general trend for ionic concentrations to rise with distance downstream but this is not universal, and 'reverse' profiles may occur (Box 6.2). We revisit this theme of longitudinal trends later (Section 6.7) but the main point to make here is that 'snapshots' in time and space are unlikely to reliably represent the ionic composition of any running water in Australia.

6.4 SOURCES OF IONS

The primary sources of ions in running waters are the **atmosphere**, the **groundwater** and the **catchment** – much as we saw for standing waters (Figure 3.9). The concentrations and proportions of these ions are largely governed by climate, local geology and proximity to the sea, as well as the proportional contributions of groundwater flow, interflow and overland flow. These hydrological contributions vary over time, affecting the ionic composition of the surface water. During very low flows, most of the ions typically originate from groundwater as baseflow, and in arid areas, will be evaporatively concentrated in the surface water as flow ceases and pools start to dry (Figure 6.4). In contrast, contributions from overland flow and atmospheric sources may predominate during high flows, altering the ionic composition of the surface water.

Figure 6.4 When flow ceases and waterholes, like this one on Kanyaka Creek, Flinders Ranges, SA, start to shrink, concentrations of ions increase through evaporation. (Source: Andrew Boulton.)

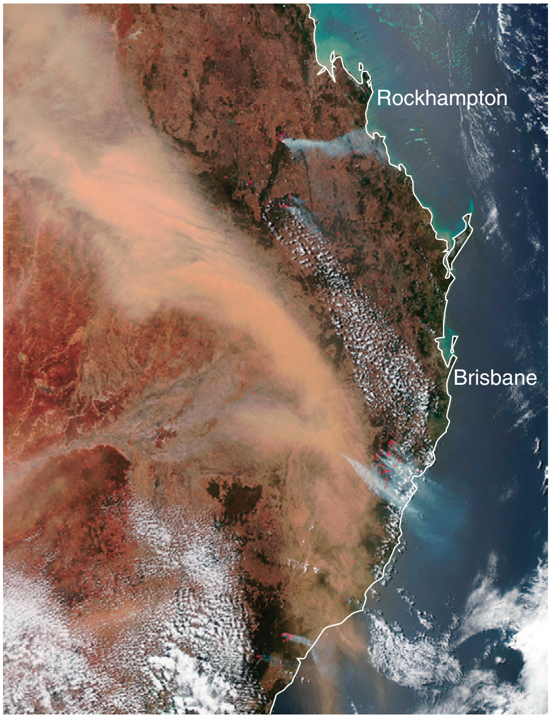


Figure 6.5 Dust storms can mobilize and deposit large amounts of nutrients and ions in standing and running waters. (Source: NASA, Image 23 October 2002. Reproduced with permission of NASA Visible Earth catalogue (http://visibleearth.nasa.gov/).)

The sources and chemical transformations of all the common ions in Australian running waters are virtually the same as for standing waters (Chapter 3), and do not warrant repetition here. However, we briefly touch on pH and sulfate in running waters to provide a basis for later discussion (Chapters 7 and 11). As in standing waters, hydrogen ions in running waters are largely derived from organic acids and from the dissociation of carbonic acid and bicarbonate. How pH responds to these inputs of hydrogen ions depends on the buffering capacity (**alkalinity**) of the water (Section 3.2.2). Poorly buffered streams draining granitic catchments generally have a low but highly variable pH because the naturally acidic rainfall (pH about 5.6) is not neutralized within the stream. Conversely, streams draining basaltic catchments often have a high pH, and are well buffered owing to the alkaline parent material.

Rivers draining exposed acid sulfate soils usually have low pH. Although acid sulfate soils in Australia are usually associated with coastal systems (Section 11.5), sulfidic sediments can occur in inland river floodplains (Hall *et al.* 2006) where high concentrations of sulfide minerals (mainly pyrite, FeS_2) sit below a shallow water table. Undisturbed, the sulfides in these soils are relatively harmless. However, problems occur when the water table is lowered, such as by human activities or during prolonged drought, and sulfides exposed to air are oxidized to sulfuric acid. As a result, waters and sediments become acidic ($pH < 4$), with severe impacts on aquatic biota, as discussed in Chapters 3 and 11. High concentrations of organic acids leached from detritus will also lower pH, and many alpine streams and those draining tea-tree swamps often have low pH because of the high concentrations of dissolved organic carbon.

The extended periods of drought in arid regions of Australia are often associated with **dust** storms that can transport large amounts of ions across the continent (Figure 6.5). Increases in nutrient concentrations from dust deposition in river systems have been described in the arid-zone reaches of endorheic river basins (Tainsh and Strong 2007). In some rivers (e.g. Murrumbidgee River, NSW, Ryder *et al.* 2007), atmospherically transported dust is hypothesized to be a major input of Ca^{2+}, Mg^{2+}, K^+ and Na^+. In inland Australia, wind-borne dust originating from adjacent agricultural land may be a significant pathway for ions into many rivers.

The relative contributions of the three major processes controlling river water chemistry (atmospheric precipitation, dissolution of rocks, and evaporation/crystallization) can be summarized by plotting the relative proportions of the principal anions and cations against the concentrations of total dissolved salts (Figure 6.6, Gibbs 1970). This plot, called a **Gibbs diagram**, is a very useful method for comparing the ionic composition of rivers from different regions or the changes within a river with distance downstream from its source.

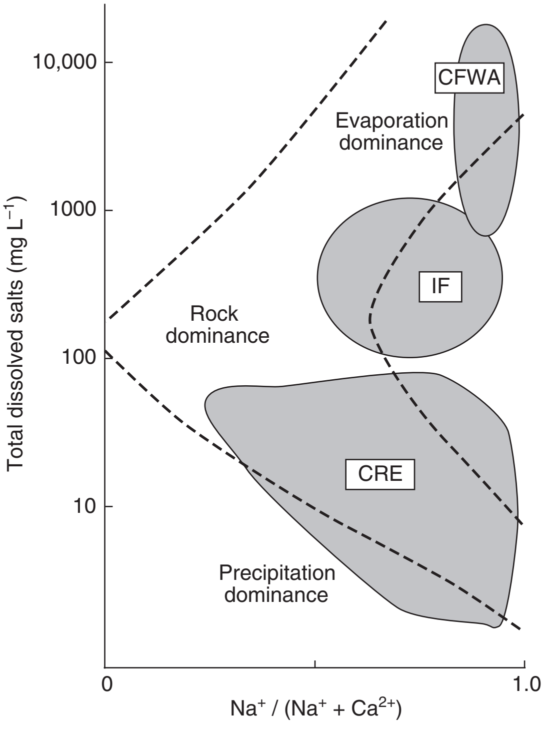


Figure 6.6 A Gibbs diagram of ionic composition of some Australian rivers. These sites are grouped into clusters of coastward-flowing rivers in south-western WA (CFWA), inland-flowing rivers (IF) and coastal rivers in the eastern states and Tasmania (CRE). The broken line is the envelope of rivers surveyed by Gibbs (1970). (Source: Hart and McKelvie 1986.)

The vertical axis of Figure 6.6 represents the concentration of total dissolved salts (i.e. salinity). The horizontal axis is the ratio of sodium to sodium plus calcium ions, and helps differentiate streams based on topographic relief, climate and the age and hardness of the rocks. To the bottom right of Figure 6.6 are waters that are lower in salts and whose chemical composition resembles rainwater with some domination by sodium and chloride ions. Running waters typifying this section of the Gibbs diagram would include tropical rivers sampled during the wet season when rainfall is high. To the upper right of Figure 6.6 are sites with high concentrations of dissolved salts, dominated by sodium and chloride. These would be lotic systems in more arid regions or areas cleared of perennial vegetation, where the combination of evaporation and crystallization of salts is the key process affecting water chemistry. Most coastward-flowing rivers in south-western WA lie in this zone (upper right), inland-flowing rivers have intermediate salinities, and sites from many eastern and Tasmanian coastal rivers are in the lower right of the plot.

Superimposing data from the Murrumbidgee catchment on a Gibbs diagram reveals a trend of decreasing salinity from headwater tributaries to floodplain reaches (Figure 6.7). Ionic composition of the water column was dominated by Na^+ with very low concentrations of calcium. Total concentrations of salts and Na^+ peaked in tributaries in the upper catchment, declining with distance downstream. From these data, it can be inferred that rainfall in the upper catchment has the potential to mobilize salts and deliver them to downstream reaches.

6.5 NUTRIENTS AND NUTRIENT SPIRALLING

The forms and concentrations of nutrients and trace elements (defined in Section 3.9) in running waters are the outcome of complex and dynamic interactions between the sources of water and catchment geology, land use and biological processes such as microbial activity. These forms exchange constantly between living (biotic) and non-living (abiotic) compartments, and we saw this in the cycles of phosphorus, nitrogen and carbon described in Section 3.9. In standing waters, much of the aquatic cycling of nutrients is confined to the waterbody. This process can be visualized as cycli-

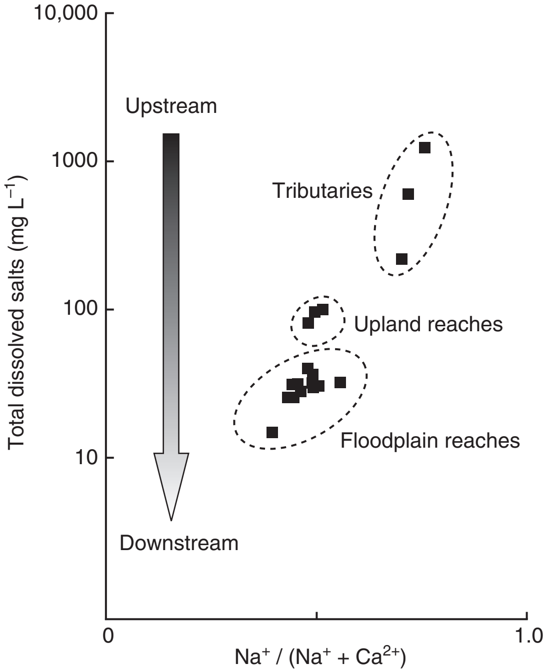


Figure 6.7 A Gibbs diagram showing the relationship between total dissolved salts and cation composition for the water column in tributaries and main-stem reaches of the Murrumbidgee River, NSW. (Source: Data from Ryder and Vink 2007.)

cal, representing the passage of a nutrient from starting in a dissolved phase, then getting incorporated into living tissue, and eventually being released by excretion or decomposition to re-enter the dissolved phase. Inputs of nutrients come from the catchment, immigrating biota and groundwater inflows. Outputs occur via seepage, emigrating biota and occasional surface outflow.

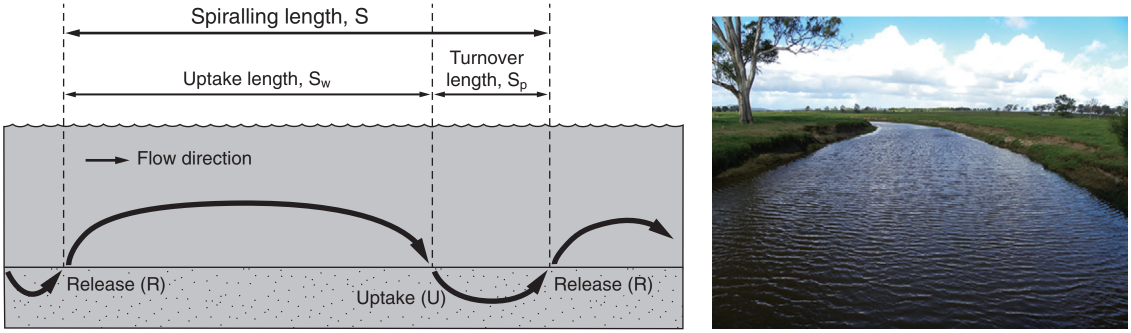
In running water systems, the nutrient cycle is superimposed on the longitudinal movement of water to produce spirals rather than circles. Recognition of this downstream displacement led to the **nutrient spiralling concept** (Newbold *et al.* 1981), a significant advance in our understanding of lotic ecosystems. This concept describes the processes of hydrological nutrient transport (governed by flow regime) and exchange (i.e. uptake or release of nutrients by chemical and biological processes in the water column or sediments) in determining the flux and availability of nutrients to downstream ecosystems.

To apply this concept, we need to quantify the distance travelled by a nutrient atom completing a spiral. This distance, the spiralling length S, is the sum of the distance moved in the water column (S_w) as an inorganic nutrient until taken up by the biota and the distance moved in the biota (S_p) until released back into the water in a dissolved inorganic form. Usually, S_w is longer than S_p because most biota (e.g. biofilms, benthic algae) are unlikely to move as far as an inorganic atom travelling in the flow. Unless flows are particularly slow, a short S_w implies greater demand for the nutrient and more frequent cycling of the nutrient over a given distance down the channel.

This leads on to the idea of the **efficiency** of nutrient cycling in a given reach, which has major implications for reach-scale productivity (Chapter 7) as well as the effects of the export of nutrients from running waters into downstream ecosystems such as estuaries or terminal wetlands. Where there is flow in channels with little habitat complexity (e.g. channelized streams) or during periods of substantial hydrological transport (e.g. floods), S_w will be longer than S_p, retention will be low and the reach is said to be 'leaky' (Figure 6.8a). Nutrients are swept quickly downstream, limiting access by local biota and potentially impairing productivity. When flows are lower and where the channel is complex (e.g. lots of woody debris, backwaters, leaf packs and subsurface hydrological exchange), S_w is shorter and biotic uptake can be higher, retaining nutrients within a given section of stream for longer (Figure 6.8b). These reaches are referred to as 'retentive', characterized by shorter spirals, slowing the loss of nutrients downstream.

The spiralling of nutrients often occurs between the sediments, associated biota (e.g. biofilms, microorganisms) and the water column, resulting in the exchange of nutrients between surface and subsurface compartments with distance downstream (Chapter 8). However, remember that nutrient cycling has an upper limit, constrained by the capacity of biota to assimilate nutrients. When this capacity is exceeded by factors such as increasing amounts of organic pollution (Section 11.3), there is an abrupt over-supply of nutrients and the river becomes eutrophic. Thus, the concept of nutrient spiralling is an elegant illustration of the interplay between physical, chemical and biological processes.

(a) ‘Leaky’ reach



(b) Retentive reach

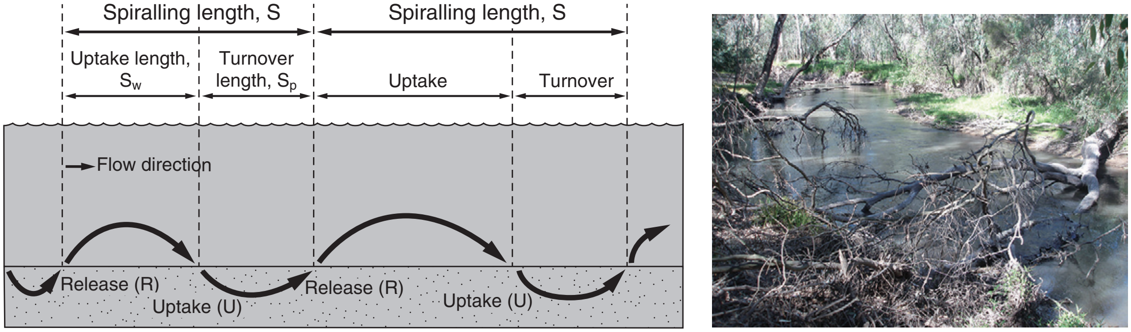


Figure 6.8 Nutrient spiralling in a non-retentive (‘leaky’) reach (a) and a retentive one (b). Spiral length (S) is the distance a nutrient atom travels as it completes one cycle from release (R) and then transport in the water column (S_w)until biological uptake (U) and then movement downstream (if any) by the biota (S_p) before release again as an available form. (Source: (a) Darren Ryder, (b) Andrew Boulton.)

6.5.1 Transport and retention of nutrients

In many rivers in temperate regions, most nutrients are transported by floods in particulate form, either adsorbed (chemically attached) to fine sediments such as silt and clay or as particulate organic matter. In contrast, in running waters of the arid zone and the wet-dry tropics, nutrient transport is often interrupted by extended periods of low or zero flows. Most of the rivers in these areas are turbid, and phosphorus primarily travels attached to suspended particles. Although not as readily bioavailable as orthophosphate, some of it is available to benthic algae and phytoplankton (Steward *et al.* 2012). During the wet season in tropical rivers of the NT, frequent floods prevent the colonization and growth of benthic algae. When flow ceases during the dry season, retained nutrients imported during earlier flows drive the rapid growth of benthic algae (Townsend and Padovan 2005). However, as we saw in Section 4.4, high turbidity limits the euphotic zone to the upper few centimetres, restricting biological uptake by aquatic plants except for emergent or floating ones.

An intriguing reversal of the downstream transport of nutrients is represented by fishes that migrate upstream, carrying nutrients with them. In many streams in the United States, spawning runs of fish such as salmon transfer immense quantities of nutrients upstream, through excretion and carcasses deposited on the streambed (Janetski *et al.* 2009). We have yet to learn about the extent of this process in Australian rivers, where patterns of native fish movement differ from those of salmonids (Chapter 7). Perhaps lateral movement by fishes onto the floodplain of some lowland rivers is a significant nutrient subsidy to these environments?

The **mass-balance** of nutrients in a reach or an ecosystem is an estimate of the total mass of nutrients present. The difference between the total imported and exported masses or loads determines whether a system is acting as a source or sink of nutrients (von Schiller *et al.* 2011). Rivers acting as nutrient sinks are likely to have a number of abiotic and biotic pathways to intercept and retain nutrients and organic matter. The rate of biotic processes such as autotrophic production and heterotrophic decomposition of organic matter can control in-stream nutrient uptake and form the biotic pathways of nutrient retention. In-stream habitat heterogeneity and channel complexity increase the frequency of abiotic interception of organic matter and nutrients, resulting in stream segments acting as nutrient sinks (Gooseff *et al.* 2007). For example, protruding bedrock outcrops or riffle crests (Figure 6.9) can influence the quantity of organic matter and nutrients retained within a reach, which affects the rate of heterotrophic decomposition and therefore the microbial uptake of dissolved nutrients from the surface water.

Different channel features and habitats promote different processes of nutrient retention. Beds of aquatic plants frequently accumulate fine particles that increase nutrient retention and act as a nutrient sink (Kleeberg *et al.* 2010). The plants themselves also are a source of nutrients during annual senescence and decomposition (Warfe *et al.* 2011). Fallen wood, branches, sticks and bark trap leaf litter (Figure 6.9b) and enhance nutrient retention. The removal of instream wood and bank-side (riparian) vegetation decreases in-stream habitat heterogeneity and channel complexity, potentially reducing the number of interception pathways and the overall nutrient retention within the stream (Box 6.3; Section 10.4).

6.6 CARBON AND ORGANIC MATTER

In running waters, much organic matter originates from outside the channel (**allochthonous**), entering as either leaf litter and other particulate organic

Figure 6.9 Nutrient retention in running waters is enhanced by channel features such as protruding rocks and riffles (a), seen here retaining leaf litter in the Never Never River, NSW, or by woody debris (b) such as in Sassafras Creek, Victoria. (Source: (a) Darren Ryder, (b) Jenny Davis.)

Box 6.3 Sources and sinks of nutrients in stream channels: interaction of biotic and abiotic retention

Nutrient retention is a crucial ecological process in streams. It occurs through abiotic processes such as physical entrapment by geomorphic features, and biotic processes including uptake by aquatic plants or microorganisms. Removing riparian vegetation can affect the geomorphic features present and the ability of reaches to retain organic matter, thereby influencing the mass balance and cycling of nutrients. In the Gwydir River, northern NSW, extensive beds of aquatic plants line stream reaches cleared of bank-side trees, whereas in uncleared reaches, flood debris accumulation points (i.e. log jams) are the dominant geomorphic feature (Stewart and Ryder 2012). There was no difference in the mass balance of nutrients between the two types of reaches, apparently because beds of rooted aquatic plants efficiently trapped organic matter. However, there were differences in the dominant sources of organic matter being used by microbial communities. Aquatic plants were the dominant source in reaches lacking riparian vegetation whereas algae were the prime source in uncleared reaches. This suggests that differences in geomorphic features can affect nutrient cycling processes, despite there being no difference in nutrient mass balance.

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matter, or as dissolved organic matter from upstream or groundwater. Alternatively, organic matter is produced by in-stream photosynthesis (**autochthonous**). Techniques such as stable isotope analysis (Section 4.4) can be used to infer the sources and pathways of carbon to aquatic food webs. One study combining stable isotope methods with DNA sequencing revealed that a significant component of carbon entering the food web in the lower Murray River came from sources originating outside the channel (Hardy *et al.* 2009).

Why does it matter where the carbon came from? The **quality** (i.e. biological availability) of organic matter is largely determined by its source. High-quality low-molecular weight organic matter tends to come from autochthonous sources, whereas low-quality high-molecular organic matter comes from allochthonous sources (Burns and Ryder 2001). Organic matter from different types of vegetation varies in its concentrations of available nutrients and structural carbohydrates. These chemicals control differences in quality among litter, influencing its susceptibility to mechanical abrasion and its palatability to invertebrates and microbes. Compounds such as tannins and polyphenols can repel decomposers or inhibit detritivory. For example, Petitt *et al.* (2012) examined the effects of leaf litter quality (leaf nutrients, lignin and cellulose content) on rates of in-stream breakdown of different plant species in tropical streams of the NT, and concluded that riparian litter quality influenced rates of in-stream organic matter processing, microbial community composition and aquatic food web dynamics.

6.6.1 Dissolved organic matter in rivers

Although coarse particulate organic matter (>1 mm) is more obvious to the casual observer, most organic matter in most running waters is **dissolved organic matter** (DOM). This dissolved fraction primarily enters via groundwater or, during storms, as interflow or runoff. It is derived mainly from the leaching of leaf litter and other allochthonous detritus in the catchment although some comes from extracellular release and leaching from biofilms, phytoplankton and larger aquatic plants.

The terms ‘dissolved organic matter’ and ‘dissolved organic carbon’ (DOC) are often used interchangeably, assuming that DOM is 45–50% organic carbon by mass (Findlay and Sinsabaugh 2003). Ways to measure DOC range from measuring the absolute concentration of carbon through to separating the components of DOC into fractions such as carbohydrates and proteins (Box 6.4). In Australian running waters, concentrations of DOC average 2–10 mg L^{-1} although concentrations over 30 mg L^{-1} may occur (Hadwen *et al.* 2010). Concentrations reflect the volumes and sources of water (McGinness and Arthur 2011) as well as flow

Box 6.4 How do we measure dissolved organic carbon (DOC)?

DOC occurs in all aquatic systems. It consists of many different carbon compounds that vary in their bioavailability. Various methods are used to distinguish different aspects of DOC. Instruments such as carbon analysers tell you the total DOC in a sample. Chromatography and size fractionation methods are used to separate DOC into broad components such as carbohydrate and protein content. These are rather time-consuming analytical procedures, and are generally employed for specific studies. Three-dimensional fluorescence spectroscopy is another procedure that shows changes in broad chemical composition of DOC. Optical DOC probes, a recent innovation, measure absorbance over multiple wavelengths and, by applying conversion factors, reflect DOC concentrations. Although not yet widely tested, probes have the advantage that they can log DOC concentrations remotely and at short time intervals. Bioavailability measures usually involve direct estimates of DOC, usually while measuring oxygen consumption. Exoenzymes are produced by bacteria in response to specific carbon sources, so changes in enzyme activity will reflect changes within the DOC. Measuring enzyme activity is relatively easy and provides an indirect way to examine changes in DOC composition.

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regime, and may vary substantially over time within a reach. For example, concentrations of DOC sampled for 10 consecutive days during a flood in the lower Namoi River, NSW, peaked during the flood to 44 mg L^{-1} before returning to pre-flood concentrations of 10 mg L^{-1} (Westhorpe *et al.* 2012). This temporal trend in DOC concentrations appeared to be a response to the mobilization of large quantities of allochthonous carbon by the flood.

Although the DOM pool is large, most of the material is highly **refractory** and unavailable for direct consumption by most organisms. A much smaller fraction of the DOC is **labile** and is bioavailable for direct uptake by microorganisms and herbivores as a critical source of chemical energy in running waters (Baldwin *et al.* 2013). Labile DOC includes simple sugars, leachate from freshly shed leaves, exudates from aquatic plants including algae, and other organic compounds with low molecular weight. In upland streams, benthic microbes are the primary consumers of DOC, whereas in larger rivers uptake by suspended bacteria may predominate (Section 7.4.9). In some lowland rivers in NSW, ambient DOC availability limits the abundance and productivity of suspended bacteria (Westhorpe *et al.* 2010). When labile DOC was experimentally added to river water, dissolved oxygen concentrations declined owing to increased bacterial respiration and growth. Labile DOC can also be removed by abiotic adsorption onto clays and some metal oxides. For example, in catchments predominantly under pasture in the Mt Lofty Ranges, SA, concentrations of DOC were shown to correlate negatively with the clay content of the upper soil horizons (Varcoe *et al.* 2010), implying abiotic uptake.

Sometimes, concentrations of DOC are high enough to turn the water a dark 'tea' colour. The water also tends to have low pH because the DOC is primarily in the form of organic acids. When this water is flushed into a river, a **blackwater flood** may occur. These events are a natural part of the ecology of many Australian running waters where carbon compounds leach from organic matter lying on the floodplain or unwetted stream banks (Hladyz *et al.* 2011a). Ecological implications arise not so much from the water colour as from the fact that when microorganisms consume the DOC, they use up dissolved oxygen far faster than it can be replenished. Consequently, blackwater floods have very low levels of dissolved oxygen and can kill fishes and other animals. Artificial flooding of the Barmah-Millewa Forest, a river red gum forest on the Murray River, flushed 'black water' into the river, killing fishes and crustaceans (Howitt *et al.* 2007). After drought, re-wetting of the southern reaches of the Murray River caused a blackwater flood that depleted populations of Murray crayfish *Euastacus armatus*, shrimps and native fishes but did not affect densities of the non-native common carp *Cyprinus carpio* (King *et al.* 2012).

Interestingly, the change in riparian-zone vegetation composition from native eucalypt to exotic plant species appears to have increased the likelihood of blackwater floods in many Australian lowland rivers (Esslemont *et al.* 2007). This change has altered the biogeochemistry of affected rivers toward faster and more complete processing of allochthonous carbon, freeing up greater concentrations of DOC. The interaction of vegetation composition and flow regimes of Australian running waters needs further investigation to minimize the adverse impacts of blackwater events and better manage the timing of environmental water delivery (Section 9.5).

6.6.2 Solute processes: dissolved substances in running waters

The blackwater floods we just discussed provide great examples of solute processes in running waters. A **solute** is simply any substance dissolved in the water. Solute processes are processes that affect the transfer of solutes such as nutrients and other ions among the physical compartments of the catchment, the water column, the surface stream bed and the interstitial water below (Figure 6.10). We have already come across this transfer process when we looked at nutrient spiralling earlier and of course the nutrient cycles we reviewed in Section 3.9 all involved solute processes in standing waters.

In running waters, solutes are transported downstream and are constantly exchanging with abiotic and biotic compartments (Figure 6.10). There are also lateral solute processes involving interactions with bank sediments, vegetation growing along the edges of the river, and across the floodplain of lowland rivers during high flows. Vertical hydrological exchange between the surface stream and interstitial water in the hyporheic zone (Section 8.2) carries solutes between these compartments and the deeper groundwater (Figure 6.10) where variations in redox conditions influence their transformations (Box 6.5). All of these hydrological linkages (recall the theme from Chapter 1 and Figure 1.7) underpin solute processes to varying degrees in all running waters, and are responsible for many of the longitudinal trends we see down river networks (Section 6.7).

Many Australian running waters are temporary and dry to pools that are disconnected at the surface (Figure 6.11). However, interstitial flows may still mediate solute processes along the channel. In isolated pools, properties of the sediments now become relevant to solute processes. At the fine scale of the individual sediment particle, its geological nature determines its ability to bind and adsorb solutes, and to release nutrients back into the water column following re-wetting. At broader scales, transformations of sediment characteristics by the previous history of wetting and drying may alter its porosity and permeability, such as when the clay bed of a stream bakes dry and becomes impermeable to water. This changes the movement of water and, obviously, solutes.

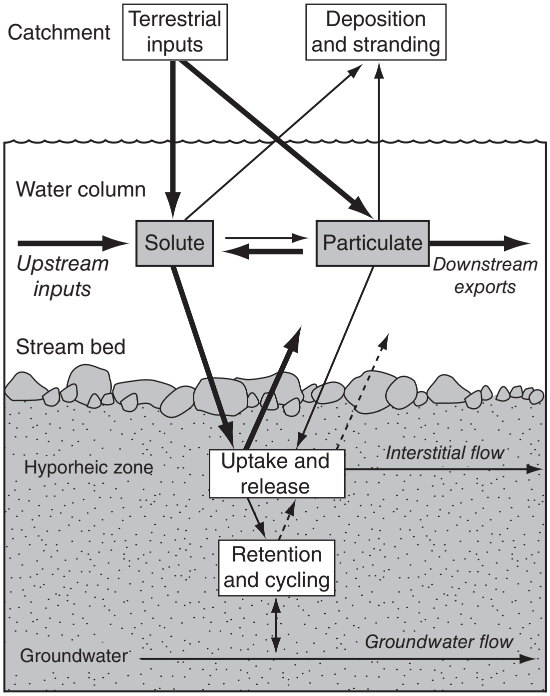

Figure 6.10 Major pathways of solute transfer in running waters. Arrow thickness represents the relative importance of these pathways although this varies among streams and over time. Broken lines represent pathways that may not be substantial. (Source: Boulton and Brock 1999.)

These fine-scale physical and chemical properties also govern the susceptibility of different types of sediments to contamination by various toxicants. For example, organic contaminants usually chemically adsorb to particulate organic matter, and this can influence their toxicity (Box 6.6). Changes in pH and the redox potential will affect the strength of attraction between the particles and the chemicals in the surrounding water (Hose *et al.* 2006), markedly altering

Box 6.5 Surface-subsurface nutrient spiralling in streams

Hydrological connections between rivers and shallow groundwater are dynamic and complex, creating biogeochemically distinct patches within alluvial aquifers, surface waters and the hyporheic zones (Chapter 8) that mediate fluxes of water, solutes, organic matter and organisms. This patchiness controls the diversity of many riverine habitats and ecological processes, and promotes ecological resilience in rivers through water storage, biogeochemical filtration, nutrient cycling, thermal buffering and biological production that occur in hyporheic zones. Particulate and dissolved organic matter enters or leaves the streambed sediments by various pathways, usually concurrently. These pathways include hydrological exchanges of surface and subsurface water and biological exchanges mediated by microbes in interstitial biofilms. The rich microbial communities in the hyporheic zone are largely heterotrophic and break down organic matter by catalysing redox reactions. Because strong redox gradients can occur across very small spatial scales (less than millimetres), organic matter can be remineralized and nutrients returned to their biologically available mineral forms ('regenerated') over very short distances along the stream. This results in 'biogeochemical hot-spots' on the stream bed that can fuel surface production and may strongly influence reach-scale nutrient cycles and metabolism.

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Figure 6.11 In this pool in the western MacDonnell Ranges, NT, solute processes during periods of surface water disconnection in intermittent rivers likely mimic those of standing waters. (Source: Belinda Robson.)

solute processes in different areas of the channel. Many solutes are chemical contaminants from human activities and their profiles and concentrations in the sediments can reveal much about land-use history and the spread of contaminants by various solute processes. For example, Mackay *et al.* (2011) used concentrations of cadmium and arsenic in wetland and floodplain sediments to assess long-term contamination of dryland river systems in north-western Queensland. Local factors such as the proximity of waters to contaminants from modern and historic mine wastes primarily influenced metal contamination of remnant pools.

6.7 LONGITUDINAL CHANGES IN CHEMICAL FEATURES

In Section 5.8, we saw how a number of physical features changed along a hypothetical permanently flowing river. The same holds generally true for many chemical features in similar types of permanent rivers, depending upon the geographic and climatic features of the catchment, flow regime and total discharge, and the longitudinal profile of the channel. Turbulence and the cooler water of shaded upland reaches of rivers promote the solubility of dissolved gases (Figure 6.12), and so dissolved oxygen saturations are higher. If the stream banks are heavily

Box 6.6 Sediment chemistry and contamination

Sediments act as a sink for contaminants in a catchment. Most contaminants bind strongly to sediment particles. Fortunately, this tends to immobilize them rendering them generally unavailable to biota. However, it also slows the breakdown of some organic contaminants, prolonging the risk they pose to aquatic ecosystems. Although the chemical makeup of sediments will differ, contaminants are generally associated with organic matter and with particles containing iron and manganese oxyhydroxides and sulfides. Contaminants bound to sediments are in equilibrium with the surrounding pore-water whose properties (e.g. pH, specific conductance) control exchange and the chemical speciation and fate of the contaminants. Contaminants released from sediments to pore-waters become available to biota, but even those remaining bound can sometimes be ingested. The change in the chemical environment of the organism's gut may liberate the contaminants from the sediment, leading to a toxic response. Contaminated sediments can be readily redistributed throughout aquatic systems, aided by bioturbation and physical resuspension forces such as floods. Although the Australian guidelines for sediment quality in marine and estuarine sediments are well developed, those for freshwater sediments need more work and will require a better understanding of contaminant–sediment–biota interactions.

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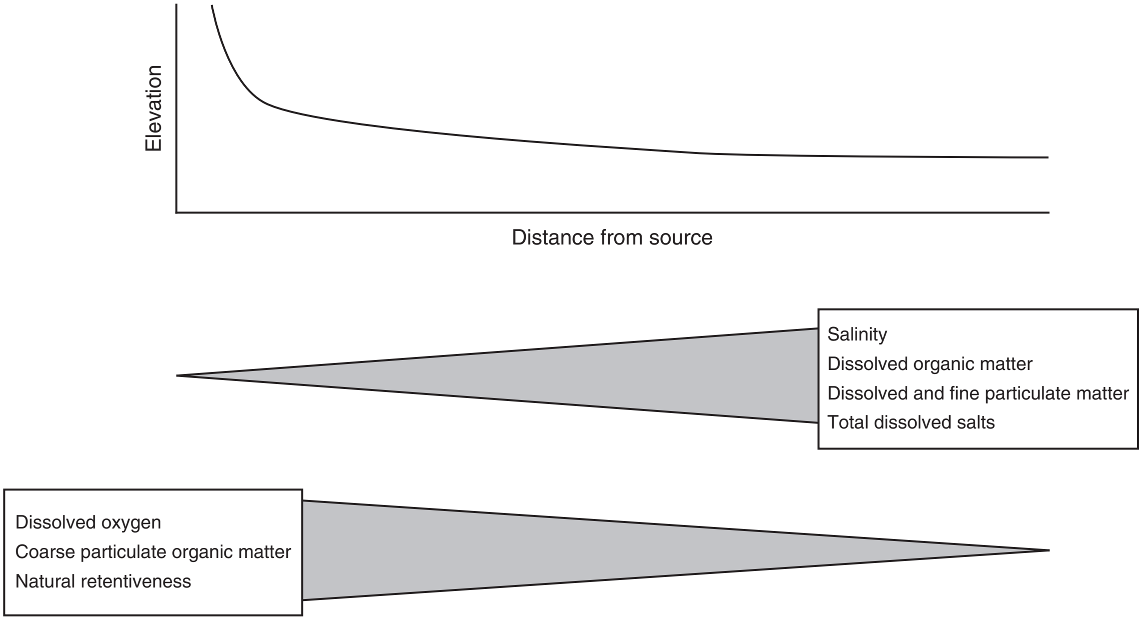

Figure 6.12 Longitudinal changes in chemical features expected along a hypothetical permanently flowing river. These generalizations may not apply to all rivers, especially those with variable flow regimes or that flow off tablelands.

vegetated, it is likely that large amounts of allochthonous coarse particulate organic matter such as leaf litter enter the streams. Greater bed complexity caused by logs, cobbles and other channel features enhance natural retentiveness of this particulate material (Figure 6.12), reducing nutrient spiralling length. The hyporheic zone is likely to be more porous in upland streams with cobble streambeds than in the broader channels and finer sediments typical of lowland rivers, also potentially contributing to retentiveness.

Conversely, the lower reaches of most rivers have usually accumulated salts and other solutes from their catchment as well as increased amounts of fine and dissolved organic matter (Figure 6.12) washed in from upstream and entering from the groundwater. In general, percentage saturation of dissolved oxygen is lower because of the warmer water and the reduced surface-area-to-volume ratio. Greater turbidity downstream will limit the depth of the euphotic zone, constraining primary production by phytoplankton that would otherwise raise dissolved oxygen concentrations during the day. The key point here is that many of the longitudinal trends in chemical features are influenced by concurrent changes in physical features along the river profile (Section 5.8).

It is crucial to emphasize that these generalizations about longitudinal changes in physical and chemical features described here and in Section 5.8 are not consistently true everywhere (for example, the case of the Blackwood River in Box 6.2), and that these pictorial models are simply tools to help us think about potential differences between upland streams and lowland rivers. Some Australian running waters will not fit these visual models because of differences in channel longitudinal profile (e.g. streams draining from tablelands before dropping down near-vertical gorges to lowland reaches) or because of highly variable flow regimes, sometimes involving complete or partial drying of surface water along the channel.

6.8 SYNTHESIS

Although the sources and fundamental chemical processes of gases, ions and organic matter in running waters are much the same as in standing waters (Chapter 3), there is the pervasive effect of *unidirectional flow*. Thus, the cycling of nutrients in a standing waterbody conceptually becomes a spiral in running waters when the cycle is superimposed upon the movement of water downstream. Channel complexity and rates of biological uptake influence retention of gases, ions and organic matter along the channel. Changes to the flow regime, such as increases in discharge, will alter rates of transport and the distance moved by different chemical compounds. When the effects of lateral and vertical hydrological exchanges are included, we start to see why there is such massive spatial and temporal variation in water chemistry within a single river network.

Nonetheless, there are some general trends in water chemistry evident down a permanently flowing river. Most of these correlate with trends in physical features such as channel form, elevation, shading and water temperature. Together, these physical and chemical features create the living conditions for the biota of running waters. Flow regulates most of these features across multiple scales as well as having a direct effect on the biota and biological processes of running waters, and this is the topic of the next chapter.

CHAPTER 7

Biological processes in running waters

7.1 FACTORS AFFECTING BIOLOGICAL PROCESSES AT VARIOUS SCALES

In running waters, the interplay of chemical and physical processes (Chapters 5 and 6) creates conditions at a range of scales that heavily influence biological processes. In many ways, the effects of this interplay on biological processes parallel those seen in standing waters (Chapter 4) and need little further discussion here. What is different is the effect of **unidirectional flow** (Figure 7.1). This chapter explores how the effects of flow on physical features and water chemistry in running waters influence lotic biota and biological processes. Flow also transports and disperses many aquatic plants and animals (**connectivity**), and is a powerful selective force on the morphology, behaviour and life history of most lotic organisms.

Lotic organisms can be viewed in the same trophic context (producers, consumers and decomposers) that we used for standing waters in Chapter 4. Ecologists have integrated this context into various models proposed to show how streams and rivers function as ecosystems. Early models attempted to predict changes in assemblages largely according to the longitudinal trends in physical and chemical features described in Chapters 5 and 6. Tests of these predictions revealed that many Australian and overseas running waters do not conform to these early models and new perspectives were needed. It now seems that the role of disturbances such as drying and flooding, superimposed on naturally variable flow regimes (Chapters 1 and 5) and projections of climate change (Chapter 12), must be explicitly included in any realistic model of Australian lotic ecosystems. These models might then be used to clarify how human activities that alter the flow, channel shape and water quality (Chapters 9–11) influence riverine plants, animals and ecosystem processes.

We start by comparing zones and habitats between running and standing waters, and then explore pathways of energy through the food web and review the main trophic groups of organisms. This leads into a brief outline of the major conceptual models that lotic ecologists use to understand the interplay of physical, chemical and biological processes in running waters and the roles of disturbance and patchiness at multiple scales. To finish, we discuss refuges, recolonization and biogeography.

7.2 ZONES AND HABITATS: PARALLELS AND CONTRASTS WITH STANDING WATERS

In parallel with standing waters, all running waters have an **open water zone** (Figure 7.2). In large lowland rivers, this can be substantial and its inhabitants are subject to the same physical and chemical constraints faced by organisms in the open water of standing waters. Similarly, all running waters have an **air-water interface**. Even in fast-flowing streams, this interface is used by water striders and whirligig beetles, for example, preying on insects trapped on the

Australian Freshwater Ecology: Processes and Management, Second Edition. Andrew J. Boulton, Margaret A. Brock,
Belinda J. Robson, Darren S. Ryder, Jane M. Chambers, and Jenny A. Davis.

Companion Website: www.wiley.com/go/boulton/freshwater

Figure 7.1 Unidirectional flow is the characteristic feature of running waters, influencing lotic organisms and biological processes across a range of spatial and temporal scales. (Source: Andrew Boulton.)

meniscus. Finally, all running waters have wetted edges along their banks, similar to the littoral zone in standing waters. However, the term ‘littoral zone’ is seldom used when we talk about streams. Instead, this zone is termed ‘**edge**’ to distinguish it from the open-water ‘**channel**’. Like standing waters, inundation of this lotic edge zone fluctuates (e.g. in response to changes in discharge) and provides diverse habitats for many aquatic and semi-aquatic organisms. Extending landwards from the water’s edge on both banks is the **riparian zone**; strips of land that are usually vegetated and that directly influence or are influenced by the river (Section 10.4). It has many functional parallels to the fringing zone in standing waters (Chapter 4).

Flow is responsible for many of the contrasts between the habitats of standing and running waters. The most obvious contrasts are within the channel where changes in water surface, current velocity and depth, especially in upland streams, create three broad habitats: turbulent, shallow and fast-flowing **riffles**, deeper and slower-flowing **pools**, and **runs** whose water surface is smooth but where flow is faster than in pools (Figure 7.2). Although these three physical environments are artificial categories along a gradient of depth and flow velocity, they can usually be distinguished in the field and often support different assemblages of aquatic plants and animals. However, assemblage composition may overlap because most organisms in Australian running waters occupy a wide variety of habitats. Many species found in running waters, especially in pools, are frequently the same as those living in nearby lentic environments.

Another example of this overlap across standing and running waters occurs in temporary streams and rivers. During the cyclical flow regime (e.g. flow-flow cessation-drying-dry-re-wetting-resumption of flow) of temporary streams, many surface-water habitats will change from running to standing to running again. Attached flora and fauna must be able to withstand the changes in physical and chemical conditions in these habitats as well as varying periods of desiccation. Other organisms move among the habitats, demonstrating a variety of traits to cope with such variable conditions.

So far, we have dealt with surface habitats. Shallow groundwater can interact with surface water in running waters to create the **hyporheic zone**, an area of hydrological exchange in the sediments below streams and rivers with porous beds (Figure 7.2). Where groundwater upwells into the surface stream, surface habitat conditions may be modified by the upwelling water. For example, cooler groundwater may provide a thermal refuge for fauna in upwelling zones in unshaded arid-zone streams. The hyporheic zone itself is a habitat for many specialized animals (Section 8.5) as well as a potential refuge from drying surface water (Section 7.7.1).

Also in parallel with standing waters, different methods are used for collecting biota from different habitats. For pools in rivers, the same techniques described in Section 4.3 are often used. However, flowing water can be used to assist sampling. For example, a pond-net held open on the bed downstream of a patch of sediment in a riffle that is then kicked or stirred up by hand (Figure 7.3a) to dislodge organisms is an effective qualitative technique for collecting benthic invertebrates. Similarly, a Surber sampler (Figure 7.3b) that encloses a known area of streambed can be used to collect fauna dislodged manually, and is a popular technique worldwide. However, the sampling efficiency of these flow-dependent methods varies with flow velocity, potentially increasing inter-sample variability (Giri *et al.* 2010).

Many invertebrates move by drifting downstream in the current, and are sampled using drift nets (Figure 7.3c) with purpose-built frames to minimize backwash. Collecting individual rocks from riffles and pools, and scrubbing them to remove attached organisms can be an effective sampling method, especially if rock

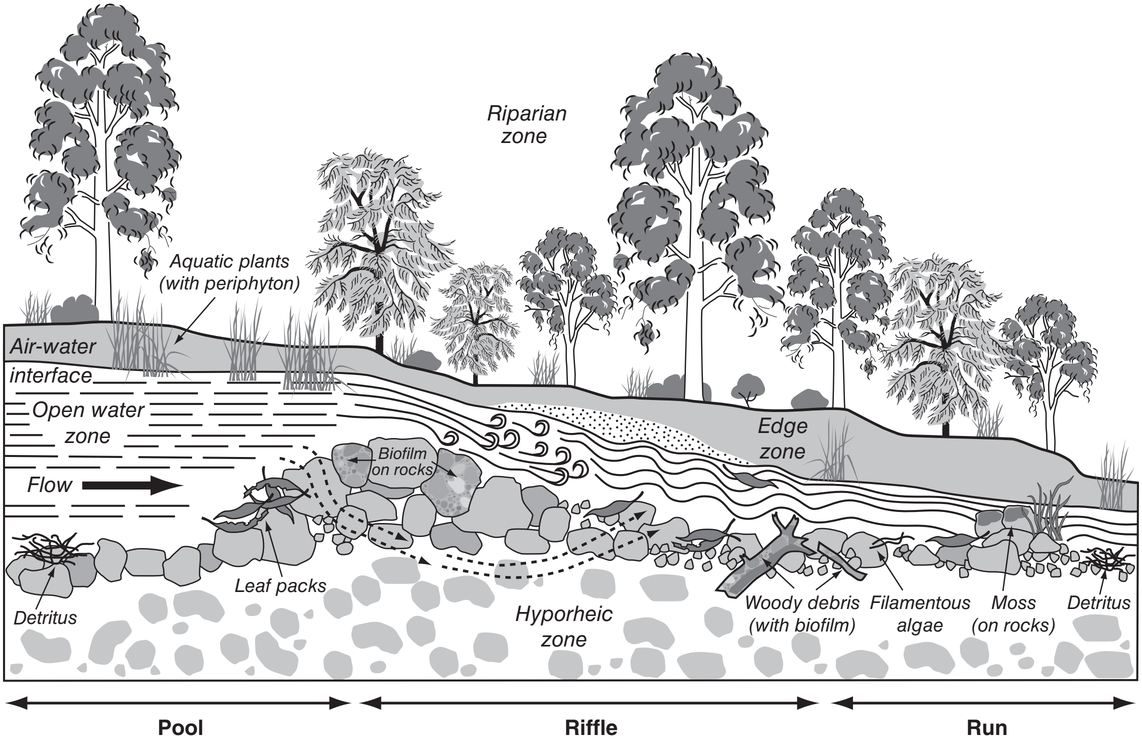

Figure 7.2 Steeper channels of many running waters have sequences of pools, riffles and runs with varying depths, turbulence and current velocities. Within these three major habitats, smaller microhabitats such as leaf packs and detritus, woody debris, moss, biofilms and filamentous algae provide food and shelter for diverse plants and animals. There are also broad zones along the channel (edge zone), the bank (riparian zone) and within the river-bed where groundwater exchanges with surface water (hyporheic zone) as well as the open-water zone and air-water interface. Further downstream where gradient declines, riffles become less common but backwaters and floodplains are more frequent, providing further habitats for many aquatic organisms. Dashed lines represent subsurface flow. (Source: Image drawn by Belinda Cale.)

surface area is measured to enable the estimation of the density of organisms. Finally, artificial substrates with consistent surface areas and other physical features (Figure 7.3d) can be used to collect benthic animals and plants across different habitats, including lentic ones. However, results must be interpreted cautiously because the catch may not represent all the organisms occurring on natural substrata in the area.

7.3 LIVING WITH FLOW

As we saw for habitats in standing waters (Section 4.3), boundaries between lotic habitats are also ‘blurred’ because mobile organisms move readily among the different areas. However, there are some plants and animals that are more common within the channel habitat than along the wetted edges of lowland rivers. Others are more frequent in riffles than pools. Organisms reliant on fast flows are called **rheophiles** (*rheos* = flow; *philia* = loving), often employing the current to feed and respire. Many have morphological features and behavioural tactics to live in strong currents. For example, some rheophilic invertebrates such as blephariceridmidge larvae (a type of fly) have small ‘suction cups’ on the underside of their body (Figure 7.4a) that allow them to hold onto smooth rocks, even in waterfalls. Blackfly larvae (Simuliidae) also occur in fast-flowing water, sometimes in huge numbers, where they attach themselves to a suitable substratum and

Figure 7.3 Habitats in flowing waters can be sampled using a pond-net (a), Surber sampler (b), drift net (c) or from artificial substrates (d). (Source: (a) Jenny Davis, (b) Judy Davies, (c) Belinda Robson, (d) Edwin Chester.)

filter-feed using their antennae to capture tiny particles swept along in the current. If a larva becomes dislodged, it is often able to escape being carried downstream because it has a small 'safety line' of silk that it uses to regain its position.

Larval water pennies (Coleoptera) graze biofilms on the upper surface of stream rocks. Their flattened form (Figure 7.4b and c) acts to minimize drag because current velocities very close to solid surfaces such as rocks are strongly reduced by friction. However, the exchange of respiratory gases in this low-flow boundary layer is limited to the extremely slow rate of molecular diffusion. Water pennies overcome this constraint by intermittently lifting the last abdominal tergite (a small dorsal plate at their hind end) and extruding actively pumping gills. This creates turbulence at the rear of the beetle larva's body (Figure 7.4c) that enhances respiration and waste transport, without increasing drag.

For further details about modifications for life in flow, see the reviews by Vogel (1994) and, for aquatic insects, Williams and Feltmate (1992) and Lancaster and Downes (2013). Many older books, including the first edition of this one, describe features such as flattened

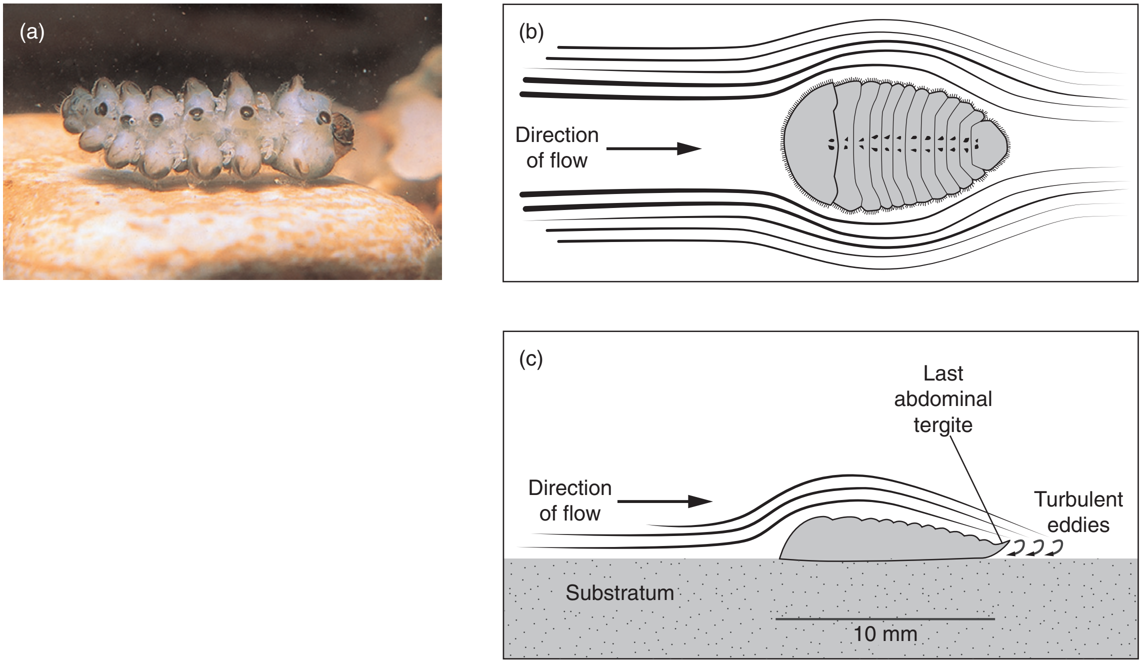

Figure 7.4 In fast flows, some invertebrates, such as this blephariceríd net-winged midge larva (a) that is temporarily turned half on its back, use suction cups (the dark rings visible down the middle of the underside) to cling to smooth rocks in swift flow. Other invertebrates, such as the larval water penny (Psephenidae: Coleoptera) are flattened (b, c) and lie in the slow laminar flow (illustrated by the even flow lines) of the boundary layer. Raising the last abdominal tergite (c) creates turbulent eddies that enhance oxygen uptake and water transport without increasing drag. (Source: (a) Gooderham and Tsyrlin 2000. Reproduced with permission of John Gooderham and Eddie Tsyrlin. Images (b) and (c) drawn by Belinda Cale.)

bodies and small body size as 'adaptations' to a rheophilic existence. Empirical evidence supporting these traits as evolved adaptations is sparse, and there are plenty of flat or small organisms in pools as well. There is much yet to be learned in this field of 'ecohydraulics' (Box 7.1), with applied relevance to flow management (Chapter 9) as well as the fundamental fascination of flow for most stream scientists and river fishers.

The finding that certain species of plants and animals cope with high flows better than other species has led some ecologists to use a **functional approach** to classify lotic organisms into 'flow exposure groups'. For example, three flow exposure groups ('obligate', 'facultative' and 'avoiders') were proposed as functional categories of stream invertebrates in Carey Brook, south-western WA, by Growns and Davis (1994) to predict associations with other ecological aspects such as substratum roughness. Functional approaches can be used to classify other traits too. In Section 4.5.1, for example, we saw how aquatic plants could be classified into functional groups based on growth forms and associated with where they germinate, grow and reproduce according to the presence or absence of water (Figure 4.7). These approaches are attractive because they allow us to compare assemblages that might differ greatly in taxonomic composition but may share functional parallels. Hypotheses can then be generated about how the abundance or distribution of functional groups in different aquatic ecosystems might respond to changes in particular factors such as flow or availability of different types of food.

Overseas, functional approaches based on biological traits such as flow exposure and feeding mode have

Box 7.1 Ecohydraulics: biophysical coupling of stream organisms

Ecohydraulics address questions about how ecological processes and the autecology of aquatic organisms are influenced by the forces of flowing water and by substratum topography. The size and arrangement of sediment particles on the stream bed produces three-dimensional flow patterns, so characterizing the small-scale flows experienced by individuals is difficult, often requiring sophisticated measurement technology and an understanding of fluid mechanics. For every species, there are maximum flow parameters (e.g. velocity, turbulence, shear stress) that limit where they can occur. Most species tolerate a wide range of flows below that threshold, especially mobile organisms that encounter many different flows as they move across the stream bed, and many alter their behaviour in response to ambient flows. For example, larval caddisflies in the family Hydropsychidae spin nets attached to substrata and feed on particles captured by these nets. Fine-meshed nets are vulnerable to damage in high flows, whereas coarse meshes are ineffective at capturing small particles in slow flows. These caddisflies can alter the net mesh size so it corresponds to the local flow, thereby ensuring efficient feeding with minimal costs of net repair, and the ability to feed in diverse flow environments.

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Box 7.2 Life histories and flow variability

Quantitative information on the life history of *Agapetus pontona* and *A. monticolus* caddisfly larvae (Glossosomatidae) from the Acheron River, Victoria, illustrates the complexities of coping with variable flow. Like all members of this family, these larvae graze on algae on the upper surface of stream rocks. Growth, secondary production (P), biomass (B) and P/B (the turnover ratio) were estimated at two sites on each of three streams within the Acheron catchment. Growth and turnover ratios of both species were highest in the stream that suffered the least amount of rock movement (a function of stream flow), probably because low levels of bed movement caused less disruption to the feeding of the larvae. Pupal mortality was also influenced by flow. Low and relatively constant discharges during late summer, when *A. pontona* pupated, provided predictable conditions leading to density-dependent pupal mortality. In contrast, *A. monticolus* pupated in spring when discharge was high and variable, resulting in stranding (and thus death) of pupae, and haphazard rather than density-dependent mortality. Ecological consequences of flow variability for both these species are evident in these differences in subtle but vital life-history attributes.

Richard Marchant, Museum of Victoria

been widely used to support predictive and modelling studies (e.g. Statzner *et al.* 2005). However, application of this biological trait approach in Australia (and many other parts of the world) remains hampered by a lack of basic knowledge of the functional ecology of most species. Another problem arises when the findings demonstrate that few species actually fit neatly into any of the categories. Many lotic organisms in Australia appear to be generalists that defy easy classification into single functional groups with respect to flow, feeding mode or other ecological attributes.

Many Australian running waters have highly variable flows (Section 5.6). This may partly explain why there are many widespread and generalist species in our streams and rivers; a form of 'bet-hedging' (Seger and Brockmann 1987) to cope with predictable variability. The variability of flow may also govern aspects of the life histories of many stream organisms, even in permanent upland streams in the temperate zone (Box 7.2). These life histories are often strongly influenced by available sources of energy.

7.4 SOURCES OF ENERGY IN RUNNING WATERS

As we saw in Chapter 4, aquatic food webs encompass the three trophic groups of **producers**, **consumers** and **decomposers**. To refresh your memory, most producers are green plants that use photosynthesis to convert energy from the sun into chemical energy. Consumers (herbivores, omnivores and carnivores) gain their energy by eating living producers or other consumers whereas decomposers gain their energy when consumers and producers die and decay to yield detritus. Thus, there are two broad pathways for energy and matter in aquatic ecosystems: a 'grazing' one of producer-consumer and a 'detrital' one of detritus–decomposer–consumer (Section 4.4). These pathways represent **food chains** that are supported by organic matter but in different forms.

Furthermore, as in standing waters, lotic ecosystems are described as **autotrophic** if photosynthesis (P) exceeds respiration (R) and **heterotrophic** if the reverse is true (i.e. $P < R$). In a naturally forested river ecosystem, shaded upland streams where the main energy source is **allochthonous** organic matter (mainly leaf litter from terrestrial sources, Section 3.9.3) would be considered heterotrophic and dominated by a detrital food chain. In less-shaded reaches, inputs from in-stream production of **autochthonous** organic matter are likely to exceed allochthonous inputs, so the system is potentially autotrophic and dominated by a grazing food chain. In many lowland rivers where turbidity is so high that lack of light limits in-stream photosynthesis, the system is probably heterotrophic again. Thus, we might predict longitudinal trends in energy sources along naturally forested rivers as the channel widens, with potential implications for the ecology of the three trophic groups at different points along the river. These predictions are explored in more detail later (Section 7.6) but first we need to know more about the ecology of producers, consumers and decomposers in Australian running waters.

7.4.1 Producers

Photosynthesis in running waters depends on the same factors as in lentic environments (Section 4.5). However, **flow** conditions and **substratum type** are also significant determinants. Flow conditions are relevant because high flows can dislodge plants and wash them downstream. Therefore, the types of producers observed in a fast-flowing stream will be determined by which ones can remain in place. This, in turn, usually depends on substratum type, which has to be either stable enough to form a reliable attachment site or fine enough to allow anchoring roots to penetrate.

As many headwater streams draining naturally forested catchments are well shaded, light tends to limit the abundance of in-stream producers. Furthermore, the beds of most upland streams comprise large boulders or outcrops of bedrock. In these streams, epilithic algae and bryophytes (mosses and liverworts) tolerant of low light are the most abundant producers. They lack true roots, and instead use holdfasts, rhizoids or polysaccharide secretions to remain attached. Both these groups of producers are small, streamlined and persist in the fast currents and changeable depths typical of upland streams.

Further downstream where there is more light, filamentous and single-celled benthic algae grow where stable substrata such as stones or wood are present (Box 7.3). Where finer sediments such as gravel, sand and silt occur, particularly along the margins of pools, rooted aquatic plants can establish. Many Australian rivers dwindle to a trickle or lose all surface water during the dry season, and so these rooted plants often need to be amphibious (Section 4.5). Some also have hardy structures such as rhizomes or tubers that withstand drying and resprout upon rewetting. Aquatic plant diversity is usually highest in the middle and lower reaches where shading diminishes (Figure 7.5a) and sediments are deeper, finer and more suitable for plants to attach. However, turbidity can limit the euphotic zone to a few centimetres in these reaches, restricting most aquatic plant growth to the edges or, in slow rivers, the air-water interface (Figure 7.5b).

The complex spatial patterns of inundation typical of most floodplains (Section 5.7.5) generate similarly complex spatial patterns of producers. Islands dominated by riparian trees such as the river red gum *Eucalyptus camaldulensis* lie within flowing channels whose edges support a diverse array of reeds, rushes, sedges and, higher up the bank, trees. Out on the floodplain, billabongs typically contain submerged, emergent and floating plants as well as algae growing on plants and wood. Despite the complexity of the riparian vegetation and its carbon inputs, algal productivity dominates many of these systems, especially those with highly turbid waters (Burford *et al.* 2008, Box 7.4).

Box 7.3 Algae in rivers

Slippery in all senses, algal communities in rivers are remarkably variable in time and space. Patterns depend upon light, nutrients, substratum texture, herbivory and flow variability. Algal communities often appear haphazardly structured by these variables. The influence of water velocity is confounded by interaction with nutrient availability. In nutrient-enriched streams, highest biomass occurs in pools and runs with low flow velocity; however, the reverse occurs in unenriched streams. Algal 'blooms' tend to be associated with eutrophic waters. Streams flowing through farms and cities are often choked in summer with filamentous green algae (mostly *Cladophora* species). Sometimes, slippery pads of cyanobacteria (Oscillatoriaceae) coat rocks, surrounded by disintegrating sheaths of brown diatoms such as *Aulacoseira* species. Where land use is less intensive, the algal flora is more diverse. Taxa include the widespread green alga *Spirogyra*, which develops large floating or attached tangles and the red alga *Audouinella*, which is usually mucilaginous and forms bushy tufts on rocks in swift-flowing streams. On sand and mud, charophytes may form a coarse carpet. All these groups of producers provide habitat and food for many lotic organisms.

Lucy Nairn, Federation University Australia

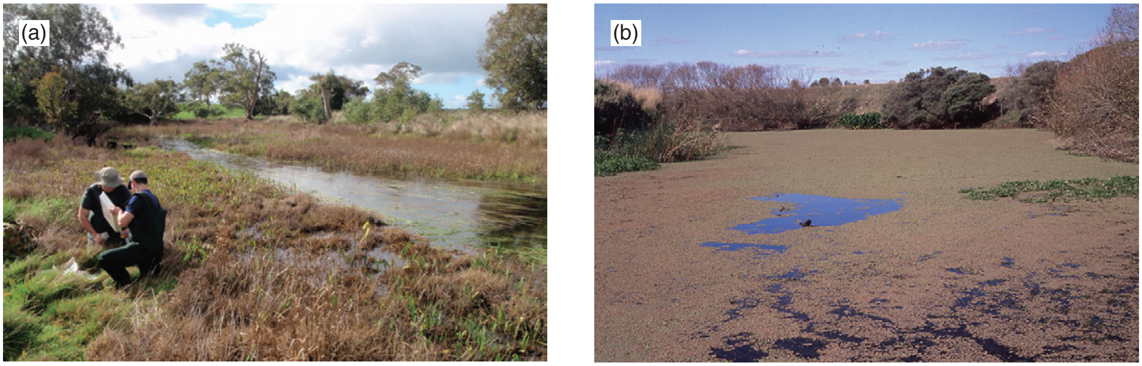

Figure 7.5 Examples of lotic producers. Mount Emu Creek (a), Victoria, has extensive beds of submerged and emergent plants. These aquatic plants dominate the biomass of producers, and epiphytic algae on the stems and leaves of the plants provide food for aquatic invertebrate grazers such as snails. Another unshaded Victorian stream, Merri River (b), is dominated by floating plants during summer and autumn, mainly the native fern *Azolla filiculoides*. (Source: (a) Edwin Chester, (b) Belinda Robson.)

However, there can be substantial variation among rivers and over time, and autotrophic production is not universal in all lowland rivers or floodplain wetlands.

7.4.2 The distribution of different life-forms of producers

The distribution of many lotic producers is largely governed by flow and substratum. The **bryophytes** include liverworts and mosses (Figure 7.6a), and frequently carpet bedrock or boulders that resist movement during floods (because, of course, 'rolling stones gather no moss'). Many bryophytes provide shelter from the current for invertebrates, a substratum for the growth of microalgae and the accumulation of fine detritus, and a food source for some detritivores and herbivores. They usually support high densities and species richness of invertebrates (Robson and Chester 1999). Bryophytes also tolerate shading, so they can be found in

Box 7.4 Algal production in turbid rivers: autotrophic production and the 'bathtub ring'

Many inland and wet-dry tropical rivers have long periods of little or no surface flow, creating shallow disconnected waterholes that are ideal environments for algal production. However, production may be limited by colloidal clay material washed in during periods of high flow. These particles remain suspended in the water column for long periods, making these waterholes turbid and reducing light availability for algal growth. Therefore, species capable of active movement or that can regulate their buoyancy gain a competitive advantage because they can access higher light intensities at the surface. Benthic algae can also form a band, or 'bathtub ring', where light availability is highest around the edge of waterholes (Bunn *et al.* 2003). Using stable isotope analysis, Jardine *et al.* (2013) showed that these algae can be an important food source for higher trophic levels. The relative importance of light versus nutrients in controlling primary production varies between river systems. For example, in Flinders River, Queensland, nitrogen rather than light availability limits algal production (Faggotter *et al.* 2013) whereas the converse is true in the highly turbid Cooper Creek in Queensland.

Michele Burford, Griffith University

densely forested streams as well as in less-shaded river sections.

Like bryophytes, patches of **filamentous algae** (Figure 7.6b,c) provide food and shelter for various aquatic invertebrates. Single-celled benthic microalgae (dominated by diatoms, Figure 3.15) grow as epiphytes on filamentous algae and also form benthic biofilms (Figure 7.6d) that are grazed by invertebrate herbivores. Stream algae are a major food source for herbivores such as snails and some larval caddisflies and nymphal mayflies. Lack of light rather than nutrient limitation usually constrains algal biomass in shaded upland streams. In unshaded clear-water rivers, algae generally grow on stones (termed epilithic), fine silt and sediments (epipelic), woody debris (epixylic) and on aquatic plants (epiphytic). In turbid rivers, benthic algal production can be restricted to a narrow band round the water's edge (e.g. the 'bathtub ring' in dryland river waterholes, Box 7.4). In the lower reaches of many Australian rivers, woody debris provides the largest area of hard and stable substratum, enabling epixylic algal growth to contribute substantially to autochthonous production (Ryder 2004, Ryder *et al.* 2006).

Slow-flowing rivers share the same functional groups of **aquatic plants** as standing waters (Figure 4.7): microscopic and macroscopic plants that may be attached, suspended or floating. The submerged macroscopic plants have reduced root systems, little woody tissue, large air spaces among the tissues and a thin cuticle on their leaves and stems. Common genera include *Myriophyllum*, *Potamogeton, Triglochin* (Figure 7.7a) and *Vallisneria*. In faster waters that are sufficiently well lit, submerged plants with strong root systems flourish where there is reduced competition and herbivory. Other genera survive the variable flows that typify many Australian rivers because they can tolerate drying and are amphibious, as we saw in Section 4.5. One interesting feature in some species is the possession of two types of leaves: thin streamlined ones below the water surface that resist high flows and thicker leaves above water that resist desiccation and support the flowers.

In addition to emergent plants, the banks of most intact rivers in Australia support **riparian trees**, most commonly she-oaks (Casuarinaceae) and eucalypts (Myrtaceae). Which riparian eucalypts are observed depends on location. For example, in the south-west, flooded gum *Eucalyptus rudis* is present whereas in much of the semi-arid south-east, river red gum *E. camaldulensis* is widespread together with black box *E. largiflorens*. In cooler areas of the south-east, many riparian zones are dominated by swamp gum (various species), mountain ash (*E. regnans*) or manna gum (*E. viminalis*). In northern and central parts, red gums and coolibah (several species) are typical riparian and floodplain species. Across Australia, other common genera of native riparian trees include paperbarks (*Melaleuca*), tea-trees (*Leptospermum*), wattles (*Acacia*) and, in northern subtropical and tropical

Figure 7.6 Some examples of producers in running waters: (a) bryophytes in Dans Rivulet, Tasmania; (b) filamentous algae growing on cobbles in Susannah Brook, WA, and (c) on sand in the Harvey River, WA; and (d) algal biofilm on a stream stone. In (d), the rows of growth are a response to flow conditions across the stone and the glossy appearance is caused by polysaccharide mucus that reduces friction. (Source: (a) Danielle Warfe; (b), (c) and (d) Belinda Robson.)

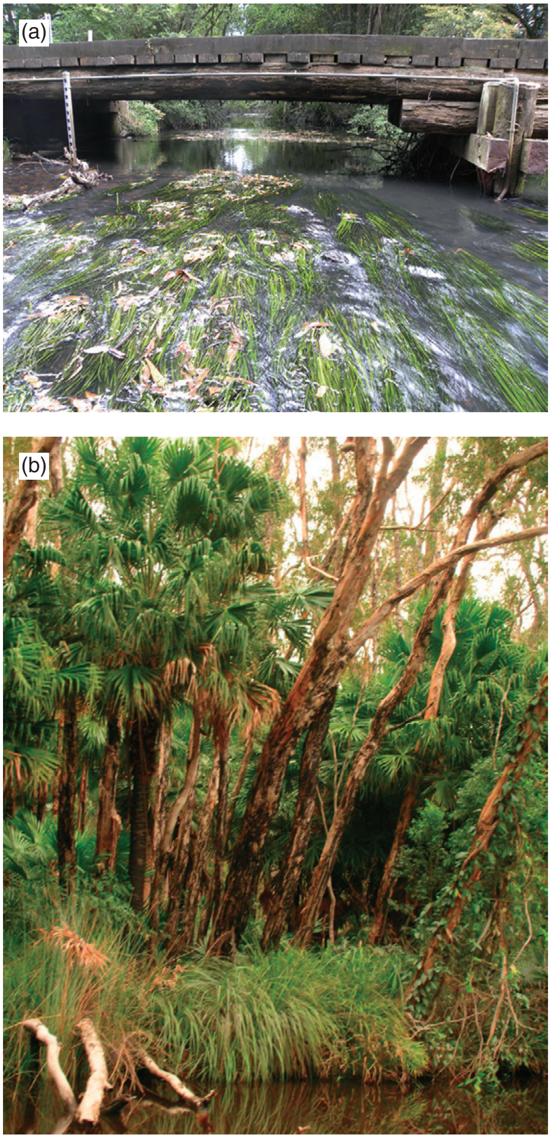

Figure 7.7 Examples of aquatic plants in rivers: (a) water ribbons (*Triglochin procerum*) in the Thone River, NSW, and (b) riparian palms and eucalypts with a grassy understorey on the banks of the Noosa River, Queensland. (Source: (a) Darren Ryder, (b) Belinda Robson.)

areas, *Pandanus* and palms (Figure 7.7b). Some species (e.g. red gum and black box) retain seeds in the canopy (Jensen *et al.* 2008) whereas the seeds of other species accumulate in the seed bank of the soil below, and primarily germinate after flooding. Recruitment is inhibited by river regulation that prevents flooding (Chapter 9), and seedlings are usually vulnerable to grazing and trampling by livestock in riparian zones (Section 10.4).

7.4.3 Open-water producers in large rivers

Slow-flowing rivers in Australia provide suitable conditions for many **phytoplankton**. As in standing waters, light, temperature, nutrients and herbivory limit growth and vary over space and time. Other relevant factors include flow regime and the proximity and flushing dynamics of nearby standing waters (e.g. backwaters and billabongs) that act as sources of colonists. In some inland floodplain rivers in Australia, longitudinal trends in phytoplankton assemblage structure are associated with channel shape, water quality and organic matter deposition (Box 7.5).

Even at low flows, phytoplankton productivity in most lowland rivers is limited by turbidity and flushing. However, if nutrient concentrations are high and the depth of the euphotic zone increases as particles settle out, blooms of phytoplankton may occur. The capacity of many cyanobacteria to fix nitrogen and tolerate high turbidity gives them a competitive advantage, especially where rivers are enriched in phosphorus from agricultural runoff. In the summer of 1991, Australia hosted 'the world's longest cyanobacterial bloom' that stretched for over 1000 km along the Darling River. This bloom was triggered by a combination of low flows and limited flushing, nutrient enrichment (Section 11.3) and high summer temperatures. Drinking water had to be transported to towns along the river and a 'state of emergency' was declared, showing the seriousness of eutrophication issues in lowland rivers.

7.4.4 Classifying consumers in running waters

As in standing waters (Chapter 4), invertebrates in running waters are the major link between producers and vertebrate consumers such as fishes, amphibians,

Box 7.5 Factors affecting phytoplankton along an Australian lowland river

In floodplain rivers, phytoplankton community structure may vary longitudinally within a single channel. Kobayashi *et al.* (2011) investigated spatial patterns in plankton, water quality and other ecological variables along 124 km of the lower Macquarie River, NSW, during several flow pulses. Two distinct ecological zones occurred along the channel: an upstream zone with relatively high densities of diatoms and high dissolved oxygen and turbidity, and a downstream zone with relatively high densities of cyanobacteria and high levels of dissolved organic matter. The downstream zone had diminished discharge and flooding, and shallower and wider channels than the upstream zone. These hydrogeomorphological conditions seemed conducive to greater in-channel deposition and retention of organic and inorganic matter, potentially benefiting different components of phytoplankton along this river. Further work is needed on finer-scale investigation of relationships between hydrogeomorphological attributes, phytoplankton dynamics and other ecological processes, and their spatio-temporal connectivity in floodplain rivers. This will help us understand how altered ecosystem connectivity from regulation and water extraction has exacerbated the ecological stress on inland floodplain rivers.

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reptiles, birds, platypuses, water rats and other mammals. Taxonomically, the same keys used to identify freshwater invertebrates in Australian standing waters can be used for most invertebrates from running waters (e.g. Gooderham and Tsyrlin 2002, www.mdfrc.org.au/bugguide/index.htm). In fact, many of the same species found in standing waters in arid and semi-arid areas also occur in nearby rivers that cease flowing and dry to pools for long periods (Williams 1980).

Freshwater Australian fishes can be identified using national field guides by Allen *et al.* (2002) and Gomon and Thompson (2009: www.fishesofAustralia.net.au/home/content/173) or regional guides such as Pusey *et al.* (2004) for the north-east, Lintermans (2007) for the south-east, and Wager and Unmack (2000) for inland Australia. Adult Australian frogs can be identified using Tyler and Knight (2011) or http://frogs.org.au/frogs, and there are taxonomic keys to tadpoles of the south-east by Anstis (2007). Wilson and Swan (2013) is useful for identifying Australian aquatic and riparian reptiles. There is also a species list and annotated key to Australasian freshwater turtles (Georges and Thomson 2010).

To help illustrate parallels and contrasts with standing waters discussed in Chapter 4, the same broad division into invertebrate and vertebrate consumers is used next. However, don't forget that these two groups of consumers frequently interact in many streams and rivers; our classification is just for convenience but is often used.

7.4.5 Invertebrate herbivores

As we saw for phytoplankton, **herbivorous zooplankton** are rare in upland streams but quite abundant in lowland rivers, providing a food source for other zooplankton, invertebrates, fishes and waterbirds, and acting as intermediaries in decomposition and nutrient cycling. Sometimes a distinction is made between the plankton of lakes (called limnoplankton) and that of rivers (potamoplankton) because they often differ in species composition. However, alterations of flow regime can favour one group over another. For example, in the hydrologically stable weir pools of the regulated Murray River, species of limnoplankton proliferate whereas the less-regulated Darling River supports a more typical potamoplankton. Communities of potamoplankton change in species composition in response to seasonal changes in water temperature and nutrient status as well as variations in the source of water. In the Murray-Darling system, most flows from the turbid Darling River reach the lower Murray in autumn carrying a distinctive plankton dominated by rotifers (Figure 7.8a) and protozoans. This contrasts with flows from the Murray River that peak in winter and spring, and are dominated by microcrustaceans, mainly from impoundments (Box 7.6).

Compared with phytoplanktonic algae such as green algae and diatoms, cyanobacteria are a poor food resource for herbivorous plankton (Wilson *et al.* 2006). The planktonic food chains that are so well developed

Figure 7.8 Some examples of lotic herbivorous invertebrates: (a) herbivorous rotifer *Brachionus*; (b) introduced European pond snail (*Physa acuta*); (c) microcaddisfly larvae (Hydroptilidae), hanging underneath the stem of an aquatic plant. (Source: (a) Joan Powling; (b) and (c) Gooderham and Tsyrlin 2002. Reproduced with permission of John Gooderham and Eddie Tsyrlin.)

Box 7.6 What drives zooplankton composition in Australia's lowland rivers?

The zooplankton assemblages of the lower Murray are determined principally by the flow contributions from the upper Murray River (and its various tributaries) and from the Darling River. Flows from the upper Murray originate in the Australian Alps in NSW whereas flows into the Darling enter from southern Queensland. The temperate and heavily impounded upper Murray contributes seasonal flows, largely released from upstream reservoirs and floodplain wetlands dominated by microcrustaceans. In contrast, the Darling River has a rotifer-dominated plankton consisting of tropical and thermally tolerant cosmopolitan species. Other factors affect composition too. During low flows, selective predation by small and juvenile fishes influences rotifer densities. During high flows, microcrustaceans and other plankton emerge from eggs stored in floodplain sediments of the lower Murray. When flows are especially high (e.g. the 2010–2011 floods), much of this plankton is washed into the main river channel, fuelling the riverine food web. This diversity of sources is reflected in the diverse zooplankton assemblages of the lower Murray, with over 200 species identified within its waters so far.

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in lentic environments (Chapter 4) may be less evident in large rivers owing to the high turbidity that limits phytoplankton production and the continual downstream displacement of the plankton by flow. Consequently, in rivers, invertebrate herbivory is unlikely to control phytoplankton productivity as it can in some standing waters (Chapter 4).

In streams and along the wetted edges of rivers, biofilms are grazed by aquatic stages of benthic insects such as various mayflies, beetles and caddisflies (Gooderham and Tsyrlin 2002) as well as most species of freshwater snails (Figure 7.8b). Although most grazing invertebrates have scraping mouthparts to abrade biofilms, some groups have specialized mouthparts for piercing plant cells (e.g. larval microcaddisflies in the Hydroptilidae, Figure 7.8c). Grazing invertebrates can regulate benthic algal density on stones in many streams for at least part of the year, leading to trophic cascades in many stony mid-upland rivers although they may be less able to control algal growth on gravel or sand (Power 1992). Experiments by Robson (1996) in Mountain River, Tasmania, showed that grazing larval caddisflies and chironomids controlled algal densities on bedrock but not in cobble-bed riffles because predatory trout (Salmonidae) do not forage on bedrock in fast flows, but can consume these grazers in cobble riffles.

Interestingly, the type of substratum can affect the **quality** of food for herbivores. For example, in the Ovens River, Victoria, the snail *Physa acuta* (Figure 7.8b) grew larger on cobble biofilm than on leaf biofilm, apparently because the C : N ratios were lower and more nutritious in the cobble biofilm (Hladyz *et al.* 2011b). Although invertebrate herbivory of living aquatic plant tissue is considered unusual in streams, stable isotope analyses and feeding trials revealed that three species of freshwater plants were preferred over leaf litter by several insect herbivores in the Macquarie River, Tasmania (Watson and Barmuta 2011). Further, the few species of aquatic herbivorous invertebrates that are able to eat living plant tissue can have a massive impact on the distribution of some aquatic plants, and several (usually various species of weevils) are used as biological controls on outbreaks of introduced aquatic plants in Australia such as *Cabomba caroliniana* (Cabrera-Walsh *et al.* 2011).

Most benthic invertebrates in Australian streams and rivers are generalist omnivores rather than solely herbivores. Analyses of gut contents and stable isotope data (Box 4.2) of many species indicate an ability to feed on algae and other plant material when it is available or, more likely, consuming it while feeding on detritus or other invertebrates. This generalist and **opportunistic** feeding mode is to be expected given the variability in flow regime and food resource availability in most Australian running waters. However, it confounds attempts at rigid allocation of freshwater invertebrates to specific feeding categories. For example, freshwater crayfishes are generally considered as omnivorous, consuming allochthonous detritus and the invertebrates found amongst it. In a study of four co-occurring freshwater crayfish species in Victoria, Johnston *et al.* (2011) found that although all four species were omnivores, two showed flexible patterns of consumption and assimilation that varied among sites whereas the other two did not, one being more carnivorous and the other more herbivorous.

Figure 7.9 Time to pray. The plate-like labium of this aeshnid dragonfly nymph unfolds forward to twice its length and the toothed mandibles at the end seize the prey. (Source: Gooderham and Tsyrlin 2002. Reproduced with permission of John Gooderham and Eddie Tsyrlin.)

7.4.6 Invertebrate carnivores

Lotic invertebrate carnivores are widespread and diverse, ranging from relatively large animals with imposing mandibles (e.g. nymphal dragonflies (Figure 7.9) and megalopterans) to smaller-bodied taxa such as flatworms, dytiscid beetles (as adults and larvae), various hemipteran water bugs, predatory caddisflies and dipteran larvae (Gooderham and Tsyrlin 2002). As in standing waters, prey-capture techniques range from ‘sit-and-wait’ ambush carnivores (e.g. dragonfly nymphs) through to active roving, either on the stream bed (e.g. some hydrobiosid caddisflies), in the water column (e.g. dytiscid beetles) or at the water’s surface (e.g. whirligig beetles, gerrid water striders). In addition, omnivorous species of net-spinning caddisfly consume animal prey swept into their nets by stream currents.

Surprisingly little research has been done on interactions between invertebrate carnivores and their prey in Australian streams and rivers. Experiments by McKie and Pearson (2006) in a tropical Queensland stream revealed predator-specific responses by two species of chironomid midge larvae to a roving predacious midge and a polycentropodid (caddisfly) ambush predator. Impacts included reduced survivorship of prey as well

Box 7.7 Diverse trophic groups in freshwater fishes

The dietary habits of present-day fishes are largely shaped by evolutionary and biogeographic processes. Fishes occupy virtually every aquatic habitat on Earth, consume a wide diversity of food from both aquatic and terrestrial ecosystems, and include some impressive adaptive radiations (e.g. African rift-lake cichlids). Despite the wide array of feeding modes evident among fishes, herbivory is rare compared to omnivory or carnivory. Australia's long-term biogeographic isolation has produced evolutionary challenges and opportunities for freshwater fishes. Our native freshwater fish fauna is unusual for its overwhelming proportion of marine-derived species and the corresponding absence of some freshwater families such as cichlids and cyprinids. While most of our freshwater fishes are mainly carnivorous or omnivorous, several marine-derived families such as the terapontid grunters have diversified to exploit trophic resources such as filamentous algae, terrestrial fruit and submerged plants. This dietary radiation is associated with corresponding changes in dentition and intestine length to meet the digestive challenges of plant-based diets (Davis *et al.* 2013a). Further research is needed to integrate data from the phylogenies, functional morphology and ecology to test hypotheses about the evolutionary biology of our freshwater fishes.

Aaron Davis, James Cook University

as indirect effects on larval development culminating in smaller females with smaller oocytes (immature egg cells). These findings imply that invertebrate carnivores may be a powerful selective force on some of their prey in tropical streams in the absence of physical disturbance by flooding (McKie and Pearson 2006).

The abundance and distribution of prey would be expected to influence the local densities of their predators. At two sites along a Victorian sand-bed stream, densities of a predatory ecnomid caddisfly were limited by the availability of prey-rich detritus patches (Lancaster *et al.* 2009) but dominant prey items in the ecnomid guts varied between the sites. However, until we know more about the ecology of invertebrate predators in Australian streams, it is premature to generalize about their effect on prey densities or their roles in food webs in streams with different flow regimes or energy sources.

7.4.7 Vertebrate herbivores

The main herbivorous vertebrates in Australian running waters are tadpoles and some fishes. There are also several species of freshwater turtles in rivers in the wet-dry tropics that are predominantly herbivorous (Armstrong and Booth 2005) and many species of waterbirds (Section 4.6.5) feed on plants in floodplain wetlands. Of the **fishes**, the freshwater grunters (Terapontidae) are trophically the most diverse with several herbivorous species feeding on filamentous algae and other submerged plants (Box 7.7, Davis *et al.* 2011). Although our rivers have relatively few native herbivorous fishes (examples include freshwater mullet *Trachystoma petardi* and bony herring *Nematalosa erebi*), many species such as silver perch *Bidyanus bidyanus* occasionally have plant material in their guts (Harris 2013). In contrast, and perhaps contributing to their success as invaders in many Australian rivers, some introduced fishes (e.g. tilapia) can eat attached plants, apparently exploiting these under-used food resources.

Even though strict herbivory is rare in Australian native fishes, stable isotope analyses of food webs in waterholes of a river in the wet-dry tropics indicated that 42–97% of standing fish biomass was derived from periphyton as opposed to phytoplankton and terrestrial plant detritus (Jardine *et al.* 2012a). This producer–consumer food chain contrasts with results from similar analyses from a temperate lowland stream in the south-east where allochthonous detritus (especially from eucalypts) appeared to be the main dependable energy source for fishes and benthic macroinvertebrates (Reid *et al.* 2008). Further stable isotope analyses of food webs in different rivers and at different times of the year will reveal the varying importance of herbivory versus other feeding modes, perhaps illustrating trends associated with various factors such as flow regime, fish assemblage structure, energy sources, substratum type and human activities.

The **tadpoles** of many frog species live in a wide array of habitat s from temporary and permanent upland streams to backwaters and margins of lowland rivers (Wassens and Maher 2011). Most of these tadpoles graze on epilithic biofilms rich in algae or feed on faeces and detritus wedged among rocks and litter on the streambed. Some tadpoles are streamlined and able to negotiate riffles to colonize pools upstream. In Australia, frogs in the Hylidae lay their eggs in water and there are several species in the genus *Litoria* typically associated with running waters (Richards 2002). In the Myobatrachidae or southern frogs, there are also some lotic species. Both families have species whose tadpoles have discs around the mouth with which they cling to rocks in fast-flowing creeks, grazing on algae.

Although tadpoles can reach high densities in some riverine habitats, especially in the pools of drying streams, little is known of their precise diet or the effects of their grazing on producers in running waters in Australia. This is despite the large amount of work done on the effects on introduced fishes on tadpoles (Section 12.8). However, several conservation programs are assessing the diets of tadpoles of various native species with a view to their efficient rearing and reintroduction back into the wild (e.g. *Litoria moorei*, Matson *et al.* 2010).

7.4.8 Vertebrate carnivores

Fishes dominate the open water nekton of most permanent and some intermittent Australian rivers. Most are planktivorous as larvae. As adults, many native species feed on benthic or terrestrial invertebrates and are significant top-level predators in riverine food webs. There are also ectoparasitic fishes such as lampreys. Fish species living in rivers with variable flows are likely to be omnivorous (Pusey *et al.* 2010) and prey consumption typically follows the seasonal availability of prey. Furthermore, as mouth gape increases with increasing body size, the larvae and growing fish within the same species may feed on different prey of different sizes (King 2005). This variability in diet makes it challenging to assign most of our native fishes to particular dietary 'trophic guilds' with any certainty.

Fishes can also be classified by their modes of feeding, and three of these are common: suction, ram and manipulation (Stoffels 2013). Suction feeders, as the name implies, can rapidly increase the volume of their mouth and suck food and water into the buccal cavity. As the prey moves and the fish stays still, suction feeders (e.g. bony herring, Macquarie perch *Macquaria australasica* – Figure 7.10a) typically eat slow-moving prey. Conversely, ram feeders (e.g. barramundi *Lates calcarifer*, mountain galaxias *Galaxias olidus* – Figure 7.10b) move while their prey either remains still or moves only slowly. Ram feeders are therefore able to feed on evasive and active prey such as shrimps and other fishes. Finally, manipulation predators either physically remove their prey from the substratum or take bites from a larger prey without ingesting it whole. They often have specialized mouthparts and behavioural traits. For example, archerfishes *Toxotes* spp. in northern Australia can spit jets of water at prey in flight or clinging to overhanging branches and then judge the fall of the prey into the water to intercept it

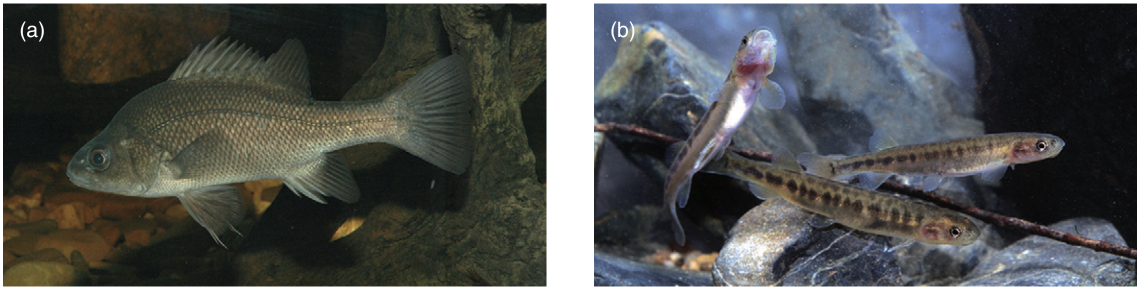

Figure 7.10 Macquarie perch *Macquaria australasica* (a) are suction feeders whereas mountain galaxias *Galaxias olidus* (b) are ram feeders. (Source: Tarmo A. Raadik.)

before other predators (Rossel *et al.* 2002). Most native fish species feed opportunistically using a combination of feeding modes, and their diet changes seasonally and with increasing body size.

Adult **frogs**, common in the riparian zones and floodplain wetlands of most Australian rivers, are predators of semi-aquatic and terrestrial invertebrates. They probably play a key role in transferring carbon and energy between aquatic and terrestrial ecosystems (i.e. aquatic-terrestrial subsidies, Section 4.6.9). Although most tadpoles are primarily herbivorous, some are opportunistic carnivores. Sadly, this may sometimes be to their detriment. In parts of tropical Australia, high mortality of tadpoles of native frog species now occurs just after spawning by the toxic invasive cane toad *Rhinella marina* (previously *Bufo marinus*); experiments have shown that most native tadpoles die soon after consuming cane toad eggs (Crossland and Shine 2010).

Reptiles associated with Australian running waters are most diverse in the tropics. As well as turtles, lizards and file snakes, there are the freshwater crocodile *Crocodylus johnstoni* (Figure 7.11a) and the estuarine or saltwater crocodile *C. porosus* (Figure 7.11b). Smaller freshwater crocodiles (<60 cm snout-vent length) mainly eat insects, spiders, crustaceans and small frogs whereas larger ones prey on a higher proportion of fish (Webb *et al.* 1982, Tucker *et al.* 1996). They tend to feed opportunistically at the water's edge and are especially active during the warmer wet season. As is the case for many predators in the wet-dry tropics, ingestion of even a single cane toad can be fatal to a freshwater crocodile (Letnic *et al.* 2008) but in some areas (e.g. Lake Argyle on the Ord River, WA), densities of freshwater crocodiles do not appear yet to have been affected by cane toad invasion (Somaweera and Shine 2012).

Crocodylus porosus grows much larger than *C. johnstoni* and eats a wider range of larger prey, including humans. Typically, adults are 'sit-and-wait' ambush predators at the water's edge. However, they may also actively stalk prey in the water, knock prey from small trees using their tail or scavenge carrion (Doody 2009). When doing field-work in the wet-dry tropics, always assume crocodiles could be present, and take precautions. They are not restricted to salt water and can travel considerable distances inland and up rivers.

In the south-east, there are two subspecies of water dragon – the eastern water dragon *Physignathus lesueurii lesueurii* and the Gippsland water dragon *P. l. howittii*. Both bask on rocks or wood, and drop into the water if disturbed. They usually eat riparian invertebrates such as spiders and crickets but large individuals can take small mice (Wilson and Swan 2013). In more arid areas, goannas of the genus *Varanus* show similar behaviour, and may be significant predators of stranded aquatic animals when streams are drying out.

Water skinks *Eulamprus* spp. are another common reptilian carnivore in south-eastern Australian streams, but they, unlike water dragons, feed on aquatic animals such as tadpoles and invertebrates as well as riparian invertebrates. Several species of snakes, such as

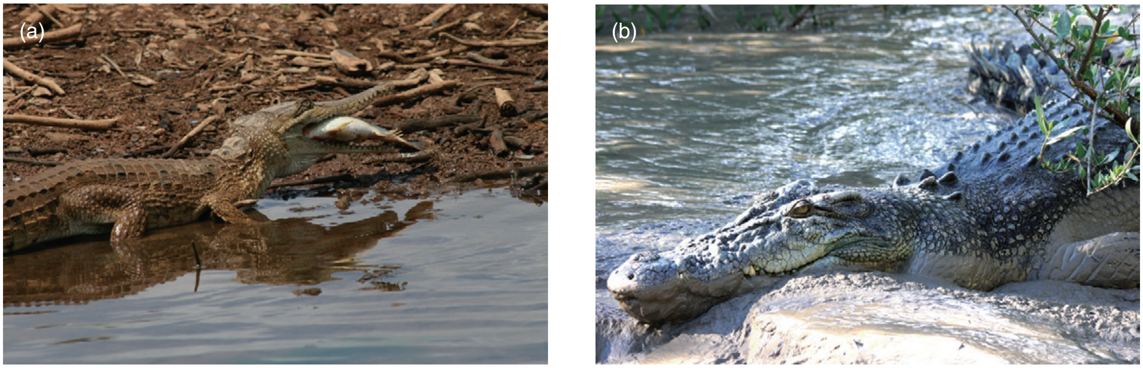

Figure 7.11 Two species of crocodile are common in some northern Australian streams and rivers: (a) the freshwater crocodile *Crocodylus johnstoni* and (b) the estuarine or saltwater crocodile *C. porosus*. (Source: Brad Pusey.)

tiger snakes *Notechis* spp., copperheads *Austrelaps* spp. and red-bellied black snakes *Pseudechis porphyriacus*, are also commonly found swimming in rivers or basking and foraging in the riparian zone. When pools start drying in temporary streams, snakes have been seen feeding on trapped tadpoles. Finally, species in two families of freshwater turtles (Chelidae and Carettochelyidae, Figure 7.12) occur in rivers and streams. Many are omnivorous (Box 7.8), taking advantage of available food resources in a variable environment. Turtles are a successful and widespread group across a diverse array of our inland waters.

Perhaps our most iconic vertebrate aquatic carnivore is the **platypus** *Ornithorhynchus anatinus* (Figure 7.13), found in rivers and streams of eastern Australia as well as various lentic waters including farm dams. This carnivore feeds exclusively on live prey including yabbies, shrimps, fishes and worms (Grant 2007). Platypuses forage on the streambed, using specialized sensory organs to detect electromagnetic

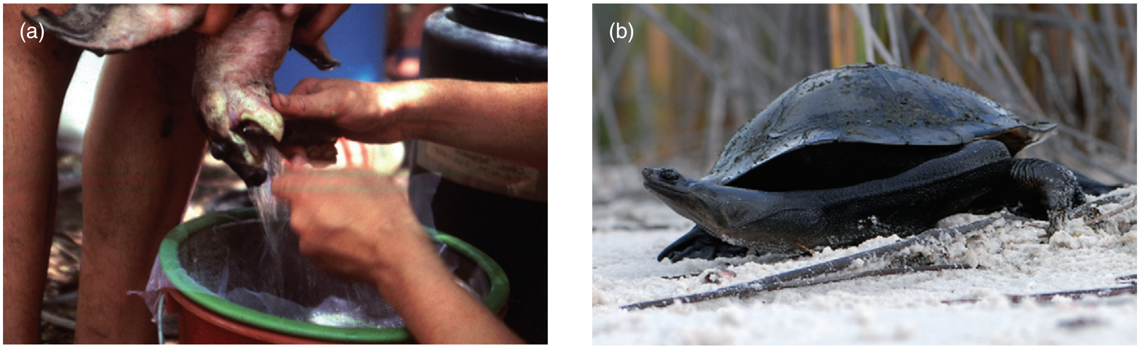

Figure 7.12 To assess stomach contents of freshwater turtles, and only after obtaining an Animal Ethics permit, a small tube is fed down the simple tubular oesophagus into the stomach (a) and the contents are flushed out with a gentle stream of water to be sifted through by scientists interested in such matters. The broad-shelled turtle *Chelodina expansa* (b) uses its exceptionally long neck to strike out and, gaping widely, ambush fast-moving prey. (Source: Arthur Georges.)

Box 7.8 Diets of freshwater turtles

Freshwater turtles typically eat a wide array of aquatic organisms: freshwater sponges, algae, aquatic plants, aquatic insect larvae, crayfishes, small fishes and molluscs as well as insects, flowers, fruit and leaves that fall upon the water and carrion when it becomes available. We know this because it is possible to extract their stomach contents without harming the turtles by gently flushing their stomachs with water (Figure 7.12a). Different species have quite different habits. The larger river turtles *Carettochelys insculpta* and species of Australian snapping turtles *Elseya* are principally herbivores, whereas the smaller river turtles in the genera *Emydura* and *Myuchelys* are typically omnivorous. The eastern long-necked turtle *Chelodina longicollis* is an obligate carnivore that forages for slow-moving prey, whereas its relatives with snake-like necks, such as the broad-shelled turtle *Chelodina expansa* (Figure 7.12b) and the northern snake-necked turtle *Chelodina rugosa*, are strike-and-gape ambush predators that can capture even fast-moving prey such as small fishes. Interestingly, none can eat out of water. The high abundance of Australia's freshwater turtles in some waterbodies implies they play a major role in food-web dynamics and community structure of our inland waters.

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impulses from their prey. The capacity of water to transmit electromagnetic impulses and vibrations makes it a very different medium to air for predators to hunt in. Platypuses store fresh and partially eaten invertebrates in cheek pouches that apparently partly compensate for the animals' small stomachs. Examination of cheek pouches of animals from streams in Kangaroo Valley, NSW, yielded aquatic benthic invertebrates from 55 families (McLachlan-Troup *et al.* 2010). Invertebrates in their diet were most similar to those from stream edges and pools rather than faster-flowing riffles, implying that foraging activity is greater or more successful in these deeper-water habitats. However, other analytical methods (Box 7.9) indicate that soft-bodied dipteran larvae are also eaten in large numbers. Although diet does not seem to limit the distribution of the platypus, warming associated with climate change (Section 12.9) may curtail its range (Box 7.9).

Figure 7.13 The webbed feet and 'duck-bill' are clearly visible on this male platypus, which is being held in a towel to protect the handler from the venomous spurs on the hind legs. (Source: Melissa Klamt.)

The **water rat** *Hydromys chrysogaster* is widely distributed in Australian waterways, preying and scavenging on crayfishes, freshwater mussels, frogs and fishes. Water rats tend to forage close to the shoreline but can dive up to two metres in search of food. The animals often have a favourite food platform on a log or rock on the bank, revealed by the tell-tale evidence of fragments of broken mussel shell or yabbie legs. Interestingly, water rats appear to be one of the very few native predators in Australia able to prey on cane toads; either they are immune to the toxin or have learned how to handle the prey without coming in contact with the poisonous skin-glands (M. Serena cited in Sullivan 2007).

7.4.9 Decomposers

Organic matter from autochthonous and allochthonous sources has been arbitrarily categorized into

Box 7.9 Dietary ecology of platypus

Often described as secretive and elusive, the platypus *Ornithorhynchus anatinus* spends most of its time foraging along the stream bed. Invertebrates encountered are stored in the cheek pouches for processing by horny grinding pads (analogous to teeth) upon surfacing. Although past investigations have used cheek-pouch contents to infer that Trichoptera, Ephemeroptera and Coleoptera are the main constituents of the diet, recent analysis using stable isotopes (Section 4.4) has revealed that dipteran larvae (e.g. bloodworms) are also common dietary items. Dipterans are seldom seen in cheek-pouch samples because their soft bodies are quickly destroyed. Climate change is likely to have an impact on the platypus because of this species' reliance on aquatic invertebrates and permanent freshwater environments. Modelling based on scenarios of future predicted emissions indicates decreases of >30% in thermally suitable platypus habitat by 2070 (Klamt *et al.* 2011). This potential habitat loss, combined with indirect impacts such as a predicted increase in fox predation under a drying climate, highlights the importance of providing refuges for this iconic species and learning more about its role in our running waters.

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three size classes (Section 3.9.3): **coarse** particulate organic matter (CPOM, >1 mm), **fine** particulate organic matter (FPOM, 0.045 – 1 mm) and **dissolved** organic matter (DOM, <0.045 mm). In most running waters, DOM is the dominant fraction (Section 6.6.1) and is decomposed by heterotrophic microbial assemblages, especially those within the matrix of biofilms coating submerged surfaces. However, as only a small fraction of this DOM is bioavailable carbon of high quality, changes in bulk concentrations of the dissolved organic carbon typically have little effect on stream metabolism (Imberger *et al.* 2008).

We saw in Section 4.6.1 how carbon flux through many aquatic microbial food webs is much greater than previously realized (the 'microbial loop'), and that bacterial uptake of dissolved organic carbon (DOC) is a significant pathway for energy transfer into higher trophic levels. The DOC passing through a stream food web provides abundant food for heterotrophic bacteria. However, bacterial uptake of dissolved organic carbon (DOC) may not be a significant pathway for energy transfer into higher trophic levels. Bacterial respiration consumes much of this carbon and energy, reducing that available to the higher trophic groups (Box 7.10). Research is also needed on the extent to which autochthonous production from phytoplankton and biofilms in running waters supplements the carbon supply coming from the microbial loop.

Microbial cycling of DOC occurs either in biofilms (Figure 7.14a) attached to leaves, rocks and logs or in the water column (Figure 7.14.b) of large rivers, floodplains and backwaters. Microbes growing in biofilms have an advantage over their water-column counterparts (i.e. bacterioplankton) because they are exposed to more nutrients in water flowing through the biofilm matrix as well as nutrients recycled within the matrix. In fast-flowing streams, bacteria in the water column have a short residence time and contribute little to the processing of dissolved and fine particulate organic matter. However, suspended within the water column of large rivers are aggregations of organic matter that range in size up to several hundred micrometres in diameter. These aggregates come from diverse sources, and consist of any materials that are free in the water column such as faecal pellets and aggregated FPOM. The formation of these pelagic aggregates creates substrata for colonization by microorganisms and generates biofilms that mineralize nutrients, in turn providing food in the water column for higher trophic levels (Wotton 2005).

During decomposition of organic matter, microbes release a host of extracellular enzymes (proteins that catalyse specific hydrolytic reactions) that chemically cleave larger organic materials into more labile forms small enough to pass across the microbes' cell membranes. Because enzymes can only be released at the expense of cellular resources, the release of enzymes by microbial communities is tightly regulated to adopt the most efficient strategy to obtain the necessary materials. The array of enzymes released reflects the resource requirements of microbial cells as well as the

Box 7.10 Viruses disconnect carbon and energy from the microbial loop

Only microbes can access the dissolved organic carbon (DOC) in freshwater. Heterotrophic bacteria use this DOC as a source of both carbon and energy. The 'microbial loop' concept presumes that the bacteria are a link between DOC and higher trophic groups. However, quantitative evidence for any natural link is lacking, and the reason could be viral infection and rupturing (lysis) of the bacteria. Pollard and Ducklow (2011) showed that viruses can release bacterial carbon back into the water as DOC. Thus, viral lysis of bacteria recycles DOC as food for new bacteria that re-oxidize the DOC, respiring more of the original DOC as CO_2. On each pass of this bacterial–viral loop, more and more DOC is respired as CO_2, depriving higher trophic levels of carbon and energy from the DOC. Evidence of this process is also provided by the low bacterial growth efficiencies (<25%) in freshwaters. Furthermore, ^{14}C-labelled glucose additions to mesocosms showed that bacteria respired 90% of the labelled carbon, and stable carbon isotope ratios demonstrated that higher trophic groups do not obtain their carbon from bacteria.

Peter Pollard, Griffith University

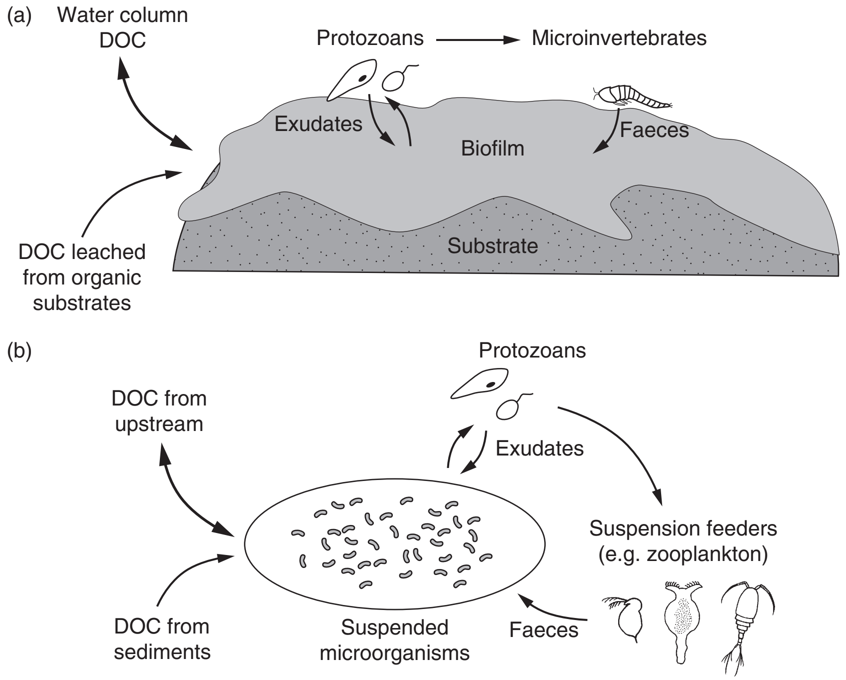

Figure 7.14 Benthic (a) and suspended (b) microbial food webs. The complex matrix includes bacteria, fungi and diatoms. (Source: Image drawn by Belinda Cale.)

quality of the organic matter (Harbott and Grace 2005).

One outcome of this enzymatic decomposition is that organic matter that has been colonized and '**conditioned**' by these organisms is rendered more attractive and nutritious to many detritivores. Experiments in an Australian tropical stream showed that the three most common species of leaf-eating detritivores preferred to feed on leaves that had been microbially colonized, and even leaves that had previously been ignored became more palatable with conditioning (Bastian *et al.* 2007). Conditioning also involves decomposition by aquatic fungi (Section 4.6.1), and in some south-eastern streams, growth and degradation of organic matter by fungi can exceed that by bacteria (Bärlocher *et al.* 2012).

The conditioned leaf litter and woody debris are consumed by a variety of detritivorous invertebrates. Some have large powerful mandibles that allow them to chew wood or leaves, and are termed **shredders**. They either mine into twigs and soft wood (Figure 7.15a) or cut out segments of leaves, eating all but the hardest parts. Other detritivores eat the finer fractions of organic matter that arise from the feeding activities of shredders, physical abrasion of leaf litter from flow, and the production of microbially coated faecal pellets. These animals are classified into either **collector-filterers** or **collector-gatherers**. Many collector-filterers take advantage of flow to carry fine organic matter particles into specialized mouthparts, appendages and even antennae (as in blackflies) or into small-mesh nets made of silk extruded from special glands. Collector-gatherers, such as worms and many chironomid midge larvae, are commonly found feeding on or within deposits of fine organic matter, and may reach very high densities in the benthic zones of streams and rivers. Others (e.g. some mayfly nymphs, Figure 7.15b) have brush-like mouthparts to sweep up fine detritus from the surfaces of wood, stones and other substrata.

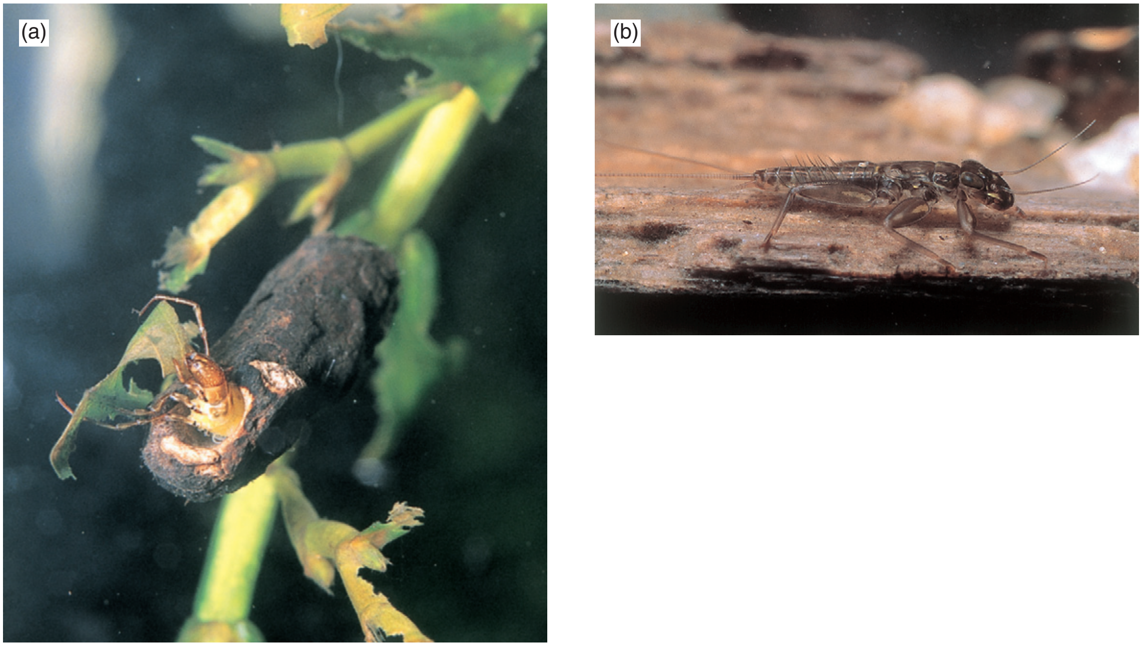

Figure 7.15 Invertebrate detritivores in Australian streams and rivers include shredders such as (a) this leptocerid caddisfly larva living in a stick that it has hollowed out with its powerful mandibles and (b) collector-gatherers like this mayfly nymph that uses brush-like mouthparts to sweep up fine detritus from the substratum. (Source: Gooderham and Tsyrlin 2002. Reproduced with permission of John Gooderham and Eddie Tsyrlin.)

Several native fishes are detritivorous, although sometimes for only part of the year. For example, in many dryland rivers, the ubiquitous bony herring *Nematalosa erebi* eats detritus and filamentous algae during the dry 'bust' periods when the rivers are flowing only slowly or are reduced to pools, but switches to non-filamentous benthic algae in 'boom' periods of flooding (Sternberg *et al.* 2008). The invasive common carp (Section 12.8) is also capable of extended periods of detritivory but supplements its diet with other food sources when available (Koehn 2004). Some native fishes such as lampreys are detritivores when juveniles (called 'ammocoetes') but metamorphose into parasitic carnivorous adults after about three years. However, detritus is a relatively poor-quality food in terms of energy and protein content. As consumers typically require high-protein diets for optimal growth, fishes that are solely detritivorous are rare. Most adult Australian fishes are omnivorous (Crook and Gillanders 2013).

7.4.10 Functional feeding groups

Earlier in this chapter, we discussed functional classifications. One of the most prevalent functional classifications in lotic ecology is the grouping of consumers and decomposers according to their mouthparts and diet into **functional feeding groups** (Table 7.1). This classification, first described by Cummins and Klug (1979) for invertebrates in North American running waters, has been used in studies of lotic invertebrates in many parts of the world. It has the advantage of providing a common 'currency' for comparisons of community structure independent of taxonomy. However, it requires a good knowledge of the feeding ecology of the invertebrates at different stages of their growth and in a wide variety of habitats.

The approach has proved challenging to apply to Australian lotic invertebrates. Firstly, we have relatively limited knowledge of the feeding ecology

Table 7.1 Functional feeding groups of invertebrates in running waters (based on Cummins and Klug 1979). CPOM = coarse particulate organic matter, FPOM = fine POM. The examples are not exhaustive, and many species are opportunistic feeders, occupying several feeding groups.

Feeding group	Food resource	Feeding mode	Australian examples
Shredder	Leaf litter (CPOM), living aquatic plants	Chewing	Larval caddisflies especially Leptoceridae and Calamoceratidae, some crustaceans (e.g. yabbies)
Shredder/gouger	Wood (often partly decomposed)	Mining	Larvae of some leptocerid caddisflies and chironomid midges
Collector-filterer	Suspended FPOM	Filter-feed using specialized mouthparts, antennae, nets or secretions	Larvae of some net-spinning caddisflies (Hydropsychidae), blackflies (Simuliidae) and chironomid midges
Collector-gatherer	Deposited FPOM or biofilms on rocks and other hard substrata	Brushing biofilms, burrowing in soft sediments	Nymphs of many mayflies and stoneflies, larvae of some caddisflies and true flies, some crustaceans, oligochaete worms
Scraper (sometimes collector-scraper or grazer)	Primarily periphyton and algal biofilms	Scraping and browsing	Snails, some nymphal mayflies, larvae of some caddisflies, beetles (e.g. larval water pennies, Psephenidae) and chironomid midges
Piercer	Aquatic plant cells	Piercing	Larval microcaddisflies (Hydroptilidae)
Predator	Animal prey	Biting, piercing and engulfing	Flatworms, nymphs of dragonflies and damselflies, larvae of megalopterans and some caddisflies, beetles and true flies, adults of true bugs

of many species, especially smaller and rarer ones. Secondly, many of the species that have been studied (especially insects) are generalist feeders, opportunistically eating whatever they come across (Lake 1995, Gooderham and Tsyrlin 2002). Thirdly, individuals within a single species may change feeding groups as they grow; for example, starting as collector-gatherers as small instars and becoming predators in their final stages before pupation. This means a complete analysis of functional feeding group representation at a site at a given time would require knowledge of the proportions of different size classes as well as species composition.

Nonetheless, the functional feeding group approach has been helpful in generating and testing hypotheses about the fate of autochthonous and allochthonous organic matter in lotic ecosystems. In combination with the three size classes of organic matter described earlier, the feeding groups can be integrated into the conceptual model of the two pathways of energy and material introduced in Section 4.4. Pathways and processes in this model can then be explored using, for example, stable isotope analyses (e.g. Reid *et al.* 2008, Leigh *et al.* 2010).

7.5 THE FATE OF A DEAD EUCALYPT LEAF THAT FALLS INTO A STREAM ...

When allochthonous particulate organic matter such as a dead eucalypt leaf falls into a stream, it may be carried along for a distance until, waterlogged, it sinks in a pool or is trapped by a rock or log jam. Within 1–2 days, dissolved organic matter leaches out, and this may aggregate or flocculate to form fine particulate organic matter (Figure 7.16). Meanwhile, the leaf has formed a substrate for fungal and microbial colonization, and becomes 'conditioned', improving its attractiveness for detritivores such as shredders (Table 7.1). Diatoms may also colonize the leaf, providing food for herbivorous scrapers. The leaf begins to break down because of water currents, abrasion and the feeding activities of shredders (Figure 7.16).

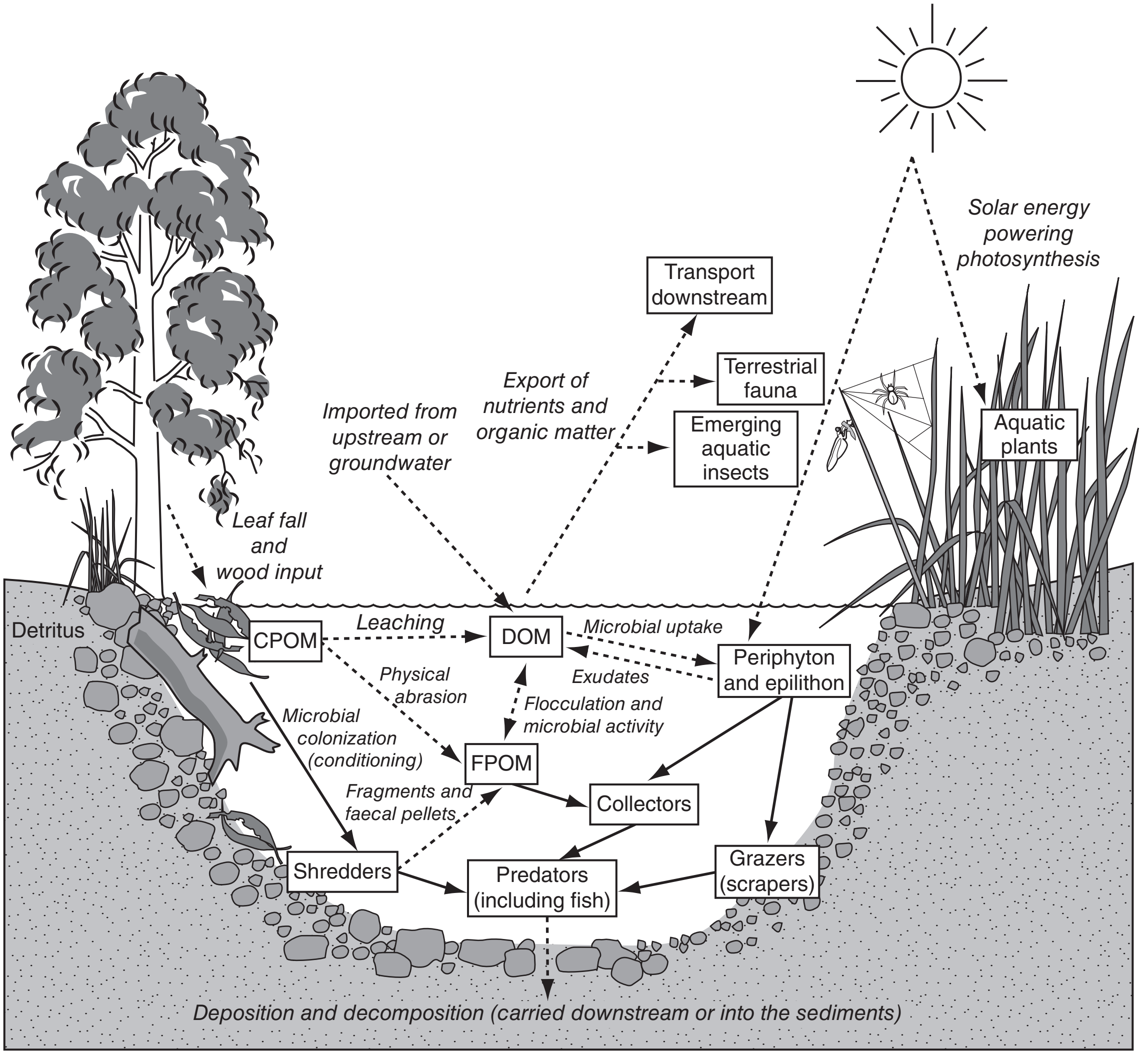

Figure 7.16 Conceptual model integrating functional feeding groups and organic matter size classes (CPOM = coarse particulate organic matter; FPOM = fine particulate organic matter; DOM = dissolved organic matter) with the two broad pathways of energy and materials in running waters. As we saw in standing waters, all decomposers and consumers excrete nutrients and, when they die, decompose to become detritus (pathways not shown). Solid lines represent energy transfer by feeding; broken lines are pathways of organic matter or processes of transformation. (Source: Image drawn by Belinda Cale.)

Finer fragments of organic matter and faecal pellets from the shredders and other consumers waft down to collectors that are either filter-feeding on or gathering the fine detritus. Predators roam the leaf packs or swim nearby, feeding on unlucky herbivores, decomposers and smaller predators before ultimately being eaten themselves or, after death, being broken down to recycle their nutrients.

At the same time, depending upon shading, season and location along the stream, in-stream photosynthesis occurs (Figure 7.16). Aquatic plants are available for shredders, exude leachates that become part of the pool of dissolved organic matter, and provide a surface for biofilms that in turn can be eaten by scrapers and collectors. Although few aquatic invertebrates eat living aquatic plants (but see Watson and Barmuta 2011), their litter is often more attractive than unconditioned dead eucalypt leaves for shredders. Whether dead or alive, this autochthonous material is a food resource for shredders, and a pathway for autochthonous production of carbon and energy (Figure 7.16).

These two energy pathways – autotrophic and heterotrophic – operate in parallel in nearly all streams and rivers. At a particular site, either or neither may dominate. Along its length from headwater streams down to the lowest reaches, the ecosystem may vary between being heterotrophic or autotrophic, depending on the degree of shading and litter inputs from riparian vegetation. Other factors also play a role as we have seen: substratum, flow regime, nutrient availability and biological interactions.

Conceptual models like this one are a powerful way to help us predict likely changes to the energy sources of stream and river reaches when human activities alter factors such as riparian conditions, substratum composition, flow regime and/or inputs of organic matter and nutrients. For example, if the riparian zone is cleared in a nutrient-rich headwater stream, we might predict an increase in autotrophic production and, subsequently, the abundance of herbivores. In Chapters 9–11, we discuss the effects of these human activities in more detail. When we do, keep Figure 7.16 in mind to help you envisage and even predict the probable mechanisms underlying the ecosystem responses. However, as lotic ecosystems are obviously not this simple, it is worth looking at how conceptual models of running-water ecosystems have evolved over the last few decades.

7.6 CONCEPTUAL MODELS OF RUNNING-WATER ECOSYSTEMS

Aquatic ecologists have long recognized the pervasive gradients in physical, chemical and biological features that occur along running waters. Early on, this led to various classifications of 'zones' along the river course from upland streams to lowland rivers, often based on the assemblage composition of various biota (especially fishes). However, at about the time that the classification of functional feeding groups was becoming accepted, lotic ecologists were also starting to conceptualize running-water ecosystems in terms of potential longitudinal gradients in ecological processes such as organic matter dynamics, nutrient transformations and interactions with the catchment. The first of these models to gain widespread popularity was the '**river continuum concept**' (RCC) proposed by Vannote *et al.* (1980). This concept suggested there was a predictable longitudinal sequence where, as a river broadens downstream and stream order (Section 5.2) increases, there are correlated changes in the ratio of P and R, the relative importance of various food sources, and correspondingly, functional feeding group representation (Figure 7.17).

However, the longitudinal trends predicted by the RCC were not always evident. For example, researchers in New Zealand pointed out that many of their streams rise well above the treeline and their forests are largely evergreen so there is no distinct autumnal pulse of litter; instead, small amounts of litter are produced continually and it is very woody (Winterbourn *et al.* 1981). Shredders are scarce and collectors feed largely on stone surface layers that derive their carbon from dissolved organic matter leached from the soil. In Australia, there was also scepticism about the widespread applicability of the RCC (Lake *et al.* 1986). For example, the model's predictions were poor in rivers in arid zones and grasslands where riparian shading is sparse. Furthermore, in most of our rivers, flow regime and reach-scale spatial variability appear to have greater effects on community structure and organic matter processing.

Despite its limitations, the RCC has persisted as one of the most influential ideas in stream ecosystem theory. It led ecologists to explore system-level research questions and encouraged further attempts at conceptualizing linkages between catchment inputs and in-stream processes in running waters. It also provided the foundation for the concept of managing the river

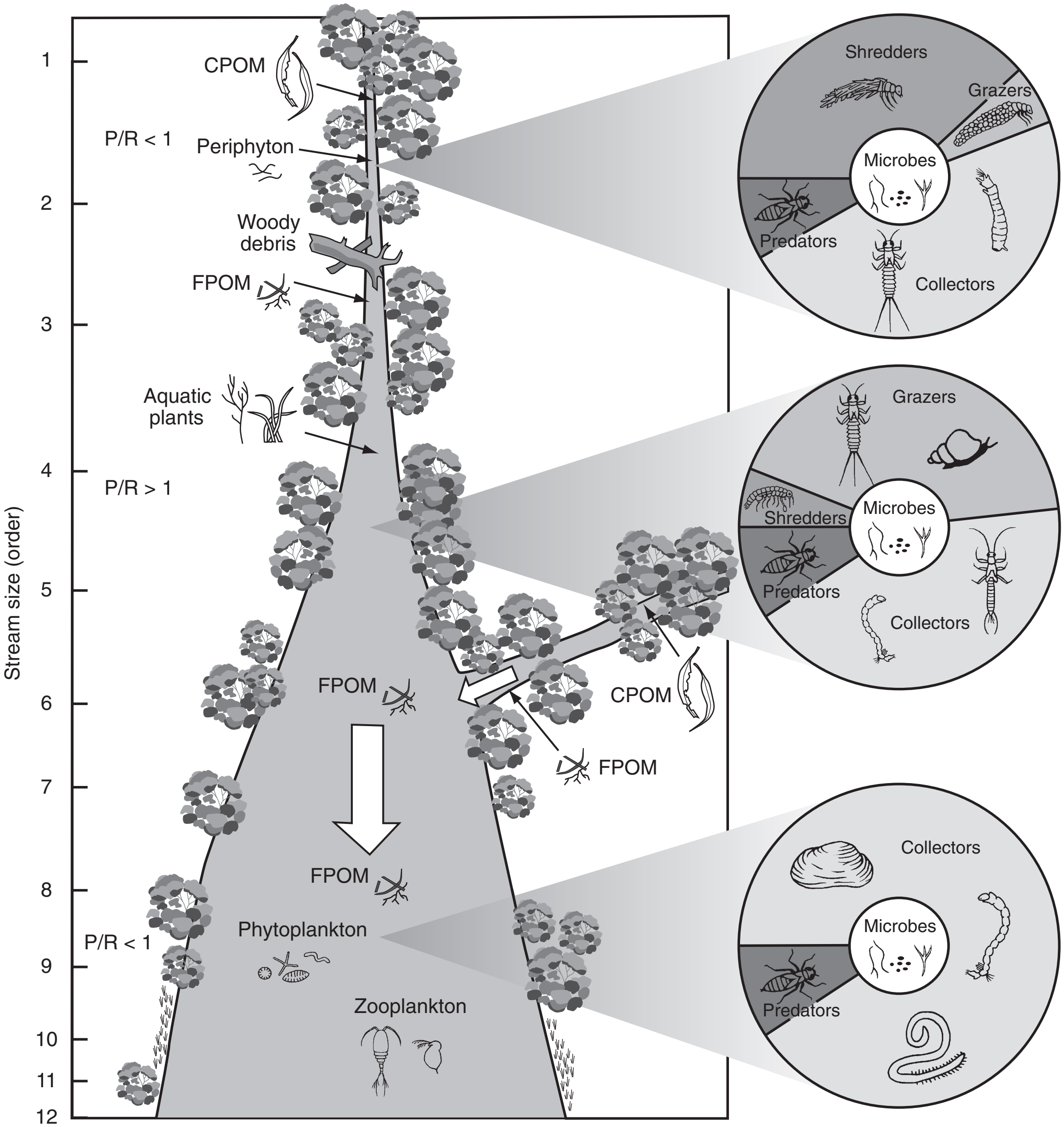

Figure 7.17 The RCC predicts longitudinal changes in the ratio of photosynthesis to respiration (P/R), food sources and proportions of functional feeding group representation with changes in stream size (order). In forested upland streams, P/R < 1 and shredders reduce CPOM to FPOM, making it available to collectors that become proportionally more abundant downstream. As the stream widens and shading declines, in-stream primary productivity increases and P/R > 1. Proportions of shredders fall whereas herbivorous scrapers are more abundant. Even further down the river, silt is likely to contribute to turbidity, limiting light penetration and causing P/R < 1. Collectors now predominate and shredders are virtually absent. Along the continuum, the proportion of predators remains relatively consistent. (Source: Modified from Vannote *et al.* 1980 and reproduced with permission. © 2008 Canadian Science Publishing or its licensors. Image drawn by Belinda Cale.)

Table 7.2 Some of the models proposed by ecologists to conceptualize ecosystem processes in running waters.

Model	Broad theme	Seminal reference
River continuum concept (RCC)	There is a predictable longitudinal sequence in P : R, organic matter input and functional feeding group representation along a continuum of physical and chemical conditions	Vannote *et al.* 1980
Serial discontinuity concept (SDC)	Barriers such as dams along a river will disrupt longitudinal trends predicted by the RCC, shifting or resetting the effects by some 'discontinuity distance' from the barrier	Ward and Stanford 1983
Flood pulse concept (FPC)	The primary source of productivity in lowland rivers comes from nutrients and material derived from regular floods that promote lateral exchanges between channel and floodplain	Junk *et al.* 1989
Hyporheic corridor concept (HCC)	Along alluvial rivers, there is predictable zonation of groundwater communities and aquifer-river interactions from the headwaters to the river mouth	Stanford and Ward 1993
Riverine productivity model (RPM)	Local inputs of autochthonous and allochthonous production are relevant because they are potentially more bioavailable than material metabolized and transported over long distances. Essentially a corollary to the RCC	Thorp and Delong 1994
Riverine ecosystem synthesis (RES)	Predictions of some of the models described above can be combined with a patch dynamics approach (Townsend 1989) where hydrogeomorphic differences create unique 'functional process zones' that may recur along the river	Thorp *et al.* 2006

and its catchment together, replacing former perceptions of rivers being merely conduits that drain water from higher in the landscape.

Over the next few decades, various models, 'concepts' and 'syntheses' followed (Table 7.2), initially expanding the RCC to include lateral and vertical linkages as well as attempting to synthesize processes occurring at multiple spatial and temporal scales. A key paper by Ward (1989) was especially useful in alerting river ecologists to the relevance of the 'fourth dimension' of time in addition to the three spatial dimensions of longitudinal, lateral and vertical linkages in running waters. This is because static models cannot capture crucial seasonal or annual patterns in river ecosystem processes. Subsequent papers have built on the theme that ecologists should consider streams in terms of networks, trees and nodes (as geomorphologists have for decades, Chapter 5) rather than simply linear systems because this will enhance understanding and appreciation of the relevance of stream junctions and subtle terrestrial-aquatic linkages (Fisher *et al.* 2004). This three-dimensional perspective, extending to the hydrologically connected catchment and groundwaters, is now widely accepted.

However, few of the concepts proposed last century adequately captured the key role of disturbances such as flooding and drying in altering or 're-setting' linkages and ecosystem processes (but see, for example, the 'telescoping ecosystem model' proposed by Fisher *et al.* in 1998). Instead, the variable and often unpredictable flow regime typical of many of our rivers appears to over-ride many of the expectations of these conceptual models. This has necessitated modifications and extensions of some of the models. For example, Walker *et al.* (1995) and Puckridge *et al.* (1998) extended the flood pulse concept to dryland rivers in an attempt to better encompass the ecologically relevant aspects of the variable flow regime. Rivers in the wet-dry tropics also have particular aspects of their flow regime and ecology that defy successful application of any of these conceptual models (Box 7.11).

The prevailing view is now one that incorporates the significance of unidirectional flow and differences

Box 7.11 Applying contemporary conceptual models to running waters in Australia's wet-dry tropics

None of the popular conceptual models describing river ecosystems wholly matches those in our wet-dry tropics. Seasonal drying causes most rivers in this region to hydrologically disconnect during the dry season, precluding the longitudinal requirement of the RCC (Table 7.2) in dictating energy sources. The FPC, developed in rivers like the Amazon, poorly represents the short (days to weeks) floods across many northern Australian floodplains. The RPM and RES, highlighting the importance of localized energy sources, miss the importance of the extensive movements of fishes in transferring energy across the landscape. In permanent rivers, local sources contribute little to fish biomass, whereas when rivers become disconnected, these sources become far more important. During brief floods, fishes move onto the floodplain to capitalize on the boom in algal growth. Consumers rapidly adapt to resource-rich conditions and actively transfer energy throughout the river system before sitting out the resource-poor dry season. Consequently, food webs in most wet-dry tropical rivers are linked by fish movements during the wet season, homogenizing assemblages before dry-season disconnection causes local extinctions and subsequent changes to the food-web structure.

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between upland and lowland rivers but also borrows heavily from the discipline of landscape ecology by explicitly acknowledging that all lotic environments are structurally heterogeneous or '**patchy**' across multiple scales that can be nested within the spatial hierarchy described in Section 5.3. Patches along this 'river discontinuum' (Poole 2002) are commonly inhabited by plants and animals capable of either resisting natural disturbances such as floods or recovering soon afterwards by being highly resilient. Disturbance plays a central role in the ecology of running waters and must be included in conceptual models that seek to capture the implications of patchiness (Townsend 1989) and chance events at multiple scales.

7.7 THE ROLE OF DISTURBANCE

In all ecosystems, disturbances create physical patches of different sizes, promoting a landscape mosaic that provides a range of habitats for a variety of species. In streams, extremes of flow such as floods or drying produce patches that suit different species. As well, these disturbances typically initiate sequential changes in assemblage structure so that this spatial patchiness varies over time too. The disturbance need not seem a great one; a leaf rolling across the stream bed may wedge against a rock, changing flow patterns and causing the finer sediments nearby to become redistributed, thus creating a habitat that suits a different suite of species from the one occupying the area beforehand.

Disturbances have been broadly classified into three types: **pulse**, **press** and **ramp** (Figure 7.18). Pulse disturbances are short-term events that peak sharply in intensity, contrasting with press disturbances that are long-term events whose intensity, once applied, remains constant (Bender *et al.* 1984). Ramp disturbances are also long-term events but they change in intensity over time (Lake 2000). In natural running waters, pulse events include floods, press events may result from nutrient and sediment inputs after fires in the catchment, and ramp disturbances are best exemplified by drought (Lake 2011). Human activities also create these three types of disturbances (e.g. pulse – spills of rapidly diluted toxins; press – channelization; ramp – cumulative urbanization). However, it is uncommon for a single agent to be the source of a disturbance, and multiple stressors usually provide a suite of these types of disturbance at the same time (Chapters 9–12).

Classifying disturbances in these different ways enables us to generalize about their effects on lotic systems. For example, different types of disturbance have different impacts and ecological responses, affecting processes such as aquatic-terrestrial **subsidies** between the catchment and the channel (Box 7.12). Understanding and measuring the effects of disturbances on aquatic ecosystems is also a crucial part of aquatic monitoring (Downes *et al.* 2002) and underpins

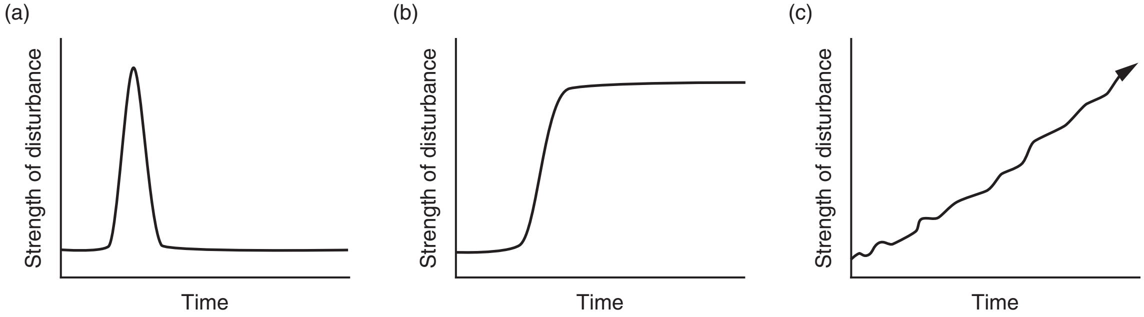

Figure 7.18 The three types of disturbance: pulse (a), press (b) and ramp (c). The arrow in (c) is to indicate that further change is possible. Responses to these disturbances can also be pulsed, press or ramped, sometimes lagging behind the disturbance. (Source: Adapted from Lake 2000. Reproduced with permission of North American Benthological Society.)

Box 7.12 Disturbances and subsidies in running waters

Floods occur as pulses; excessive water is rapidly delivered. In upland streams, organisms in the channel may be depleted by the short-lived scouring force. In lowland rivers, floods have less effect on channel biota but the floodplain is inundated, often for long periods. This usually stimulates recruitment and production. Floods in upland streams briefly strengthen the subsidy from the catchment to the stream, with nutrients, organic matter and biota swept into the channel. However, these inputs are only partly used before being washed downstream. In lowland rivers, the subsidy is initially from the channel to the floodplain, carrying water, nutrients and sediments that stimulate floodplain production. During flood recession, organic matter, nutrients and biota flow into the channel, reversing the subsidy's direction. In controlling flow regimes of floodplain rivers, humans have overlooked the importance of these subsidies and greatly reduced production by natural floodplain and channel biota. Ramp disturbances like drought reduce channel and floodplain habitat and biota, and impair terrestrial-aquatic subsidies in both directions. We have much to learn about aquatic-terrestrial subsidies in our running waters, especially how they are affected by different types of disturbances.

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successful management to mitigate the impacts of multiple stressors and the combined effects of pulse, press and ramp disturbances. To do this, we need to know more about how aquatic organisms either resist disturbance or recolonize afterwards.

7.7.1 Post-disturbance recolonization processes

In running waters, plants and animals that are attached to the substratum or that can move only slowly have various morphological and physiological mechanisms to resist disturbance, especially drying. For example, stranded filamentous green algae form a special crust that protects them during drying (Robson 2000). Once rewetted, they recommence growth within hours. Abrasion by severe floods usually removes most algal biomass but where fragments remain attached, vegetative growth soon resumes. The differential ability of attached species to survive floods or drought largely determines the composition of the assemblage immediately post-disturbance and, in turn, subsequent changes in energy sources and species composition (Robson *et al.* 2008a).

Various rotifers, protozoans and microcrustaceans have desiccation-resistant stages, which are deposited on riverbeds and floodplains when water recedes. When inland lowland rivers flood, the sediment 'egg bank' is an initial source of colonists from the floodplain (Box 4.8, Jenkins and Boulton 2003). However, recolonization from this source after drying in upland streams where the substratum is generally stony seems uncommon. Instead, stream macroinvertebrates typically recolonize from various refuges such as beneath leaf litter and stones, within damp sediments and in saturated spaces either within the hyporheic zone or as 'pholeteros' (= 'one who lurks in a hole', Lake 1977) in the burrow water of crayfishes (Table 7.3,

Table 7.3 Drought refuges used by selected taxa of stream invertebrates. Not all species within each taxon will use all of the refuges listed. Diving beetles includes both adults and larvae. (Source: Adapted from Robson *et al.* 2011. Reproduced with permission of CSIRO Publishing.)

Taxa	Dry sediment (aestivation)	Damp sediment (aestivation)	Remnant perennial pools	Terrestrial environment via mobile adult life stage	Dry sediment (desiccation-resistant eggs)	Saturated sediments (hyporheos) or crayfish burrows (pholeteros)
Leeches (Hirudinea)	X		X			
Scuds (Amphipoda)		X	X			X
Crayfishes (Parastacidae)		X	X			X
Shrimps (Decapoda)			X			
Diving beetles (Dytiscidae)		X	X	X		
Larval water pennies (Psephenidae)		X				
Non-biting larval midges (Chironomidae)			X		X	X
Blackfly larvae (Simuliidae)					X	
Mayfly nymphs (Ephemeroptera)			X	X	X	X
Damselfly nymphs (Zygoptera)			X	X	X	
Dragonfly nymphs (Epiproctophora)		X	X	X	X	
Stonefly nymphs (Plecoptera)			X	X	X	X
Caddisfly larvae (Trichoptera)		X	X	X		
Aquatic snails (Gastropoda)	X		X			

Figure 7.19 Potential drought refuges for animals and algae in a temporary stream in the Grampians, Victoria. See text and Table 7.3 for more details. (Source: Belinda Robson.)

Figure 7.19) or from eggs laid by terrestial adults. The most popular refuge in both upland streams and lowland rivers is permanent pools or waterholes that persist during the dry period (reviews in Sheldon *et al.* 2010, Chester and Robson 2011).

After disturbances, lotic invertebrates recolonize by aerial flight and oviposition (egg-laying), downstream drift from upstream refuges, upstream migration by swimming or crawling, and vertical migration from refuges in the stream bed. For **aerial flight** to be an effective refuge, the aquatic stage must either already have left the water or be ready to emerge when the disturbance is most likely to occur. Therefore, this strategy is best as a refuge from predictable disturbances such as seasonal drying. Most stream insect species select specific sites for **oviposition** (e.g. stones protruding out of the water, Reich *et al.* 2011) but this can limit population size if suitable sites are limited (Lancaster *et al.* 2010). Aerial flight is the main method of dispersal for most winged aquatic insects, and therefore it has been assumed that recolonization would occur readily among catchments. While this is true for some insects, population genetic studies reveal that flight dispersal actually covers surprisingly short distances in most aquatic insect species that are either weak fliers or short-lived (Hughes 2007).

Recolonization via **drift** takes advantage of downstream flow in rivers, and has been separated into accidental drift, catastrophic drift and behavioural drift. Accidental drift occurs constantly, mainly through accidental dislodgement from the substratum. Many individuals that drift this way are soon eaten by

Box 7.13 New perspectives on stream insect dispersal

In streams, the ubiquity of behavioural drift has convinced many researchers that dispersal is frequent, that animals travel reasonable distances downstream, and that individuals are therefore able to colonize every location offering suitable habitat. Recent work suggests this view is wrong. It takes careful experiments to test whether drifters actually contribute to benthic densities. In streams in Australia (Downes and Lancaster 2010) and Scotland (Lancaster *et al.* 2011), drifters are sometimes not going anywhere – either not leaving the site or exiting the drift within a few tens of metres. Additionally, some species hatch from egg masses laid in quite specific locations chosen by the female parents. Studies in Australia and overseas indicate that choices made by ovipositing females determine initial larval densities, and these choices can override the effects of any subsequent drift dispersal, mortality or supposed 'habitat preferences' of larvae. Two of these studies were on an animal considered the champion drifter in the world – the mayfly *Baetis*. If we have it this badly wrong for a species that we convinced ourselves is a master disperser, how wrong are we about other species?

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drift-feeding fishes and few survive to colonize downstream. Catastrophic drift results from disturbances such as bed-moving floods or when toxins are washed into streams. As this type of drift is associated with widespread mortality of invertebrates, it also contributes little to downstream recolonization. Behavioural drift is the main component of daily drift, and peaks at dawn and dusk, probably to minimize predation by drift-feeding fishes. Successful recolonization by drift varies widely among species, and may play a smaller role than previously thought (Box 7.13).

Upstream migration by crawling or swimming has been little-studied in Australian streams, but one study of dispersal by net-spinning caddisflies suggests that crawling may equal or exceed the importance of dispersal by drift for some species (Downes and Lancaster 2010). This pathway might be especially significant when flow declines in temporary streams during drought. Although the hyporheic zone has long been suggested as a potential refuge from natural disturbance (Williams and Hynes 1974), so far there is little empirical evidence for substantial **vertical migration** from this refuge after floods or drought in south-eastern streams (Boulton *et al.* 2004). Samples from saturated sediments of dry stream beds in Australia have yielded small mayfly nymphs (mainly Leptophlebiidae), amphipods, isopods and elongate chironomid and coleopteran larvae (Table 7.3, Boulton 2001) but whether any of these particular species are in surface waters when flow resumes has not been confirmed.

Post-disturbance recolonization by fully aquatic vertebrates such as fishes is limited to movements within channels or across inundated floodplains. After drying, some species of fishes start recolonizing new areas almost as soon as hydrological connectivity is established (reviewed in Koehn and Crook 2013). Although large waterfalls, weirs and dams prevent most native fish species moving upstream, some species are able to swim along surprisingly shallow channels (even inundated wheel ruts) to reach potentially suitable habitat. Many widespread species have behavioural traits that favour recolonization. For example, our most widespread native fish, the spangled perch *Leiopotherapon unicolor*, displays a strong urge to disperse with rising floods, allowing it to swiftly colonize newly wetted areas and maintain large, intermittently connected populations across the arid inland (Bostock *et al.* 2006). Many other inland native fishes also exploit the 'boom-bust' cycle of dryland rivers, and disperse across the floodplain when it is inundated in 'boom' times. During the 'bust' periods, these fishes seek refuge in perennial waterholes (Sternberg *et al.* 2008). Similarly, native fish species in the large rivers of the wet-dry tropics also disperse during the predictable seasonal floods, taking advantage of the pulse of productivity on the inundated floodplains (Jardine *et al.* 2012a).

So far, we have focused on recolonization by aquatic organisms. However, the abundance of floodplains and temporary streams and rivers across Australia provides potential habitats for colonization by semi-aquatic and terrestrial species of plants and animals when the water recedes. Unfortunately, the ecology of dry and drying stream beds remains poorly studied yet there may be substantial aquatic-terrestrial subsidies of nutrients and energy during the drying phase. For example, fishes trapped in drying pools are eaten by terrestrial predators such as goannas, quolls, scavenging birds, foxes and snakes, resulting in a transfer of energy from aquatic to terrestrial ecosystems (Steward *et al.* 2012). A diverse array of semi-aquatic and terrestrial insects, spiders and other invertebrates swiftly exploit the newly created habitat provided by the dry streambed or floodplain, devouring stranded aquatic organisms and colonizing leaf litter and other detritus. Opportunistic plants germinate, helped by residual moisture in the sediments, and when there are long periods between wetting events, the dry river bed may eventually appear completely terrestrial. That is, until the next aquatic disturbance …

7.7.2 Recolonization, dispersal and biogeography in Australian running waters

The diverse life histories of aquatic organisms allow a variety of modes of recolonization and dispersal. Taxa such as decapod crustaceans and fishes cannot fly, and are restricted to hydrological pathways of dispersal and recolonization via drift or active swimming or both (although some crayfishes can leave the water to crawl). Aquatic insects with a terrestrial adult stage may be strong or weak fliers, or may not fly at all (e.g. some adult beetles). This affects how far they can disperse. Weak fliers such as most stoneflies may be affected by the prevailing wind direction at the time they emerge, governing not only the dispersal distance but also its direction. Parasitic taxa such as gordiid worms, larval freshwater mussels and nymphal water mites rely on the dispersal capacity of their host. The variability in water regime of Australia's inland waters, combined with the diverse life histories and dispersal modes of aquatic organisms, result in the patterns of distribution that we see today.

Directly tracking the movements of most aquatic organisms, especially those that are small or cryptic, is extremely difficult. Fortunately, studies of the **molecular genetics** of their populations can be used to identify different models of dispersal (Box 7.14, Hughes *et al.* 2009). For example, widespread gene flow typifies strong fliers such as some large caddisflies that can disperse widely and populations of these taxa have more similar genetic composition and diversity across large areas (Figure 7.20a). In contrast, weakly dispersing taxa usually have many small isolated populations within a catchment, and the lack of genetic exchange promotes increased genetic differences among them (Figure 7.20b). Other genetic patterns imply dispersal by water (Figure 7.20c) or over short distances of land

Box 7.14 Using DNA to infer the dispersal capacity of riverine fauna

When animals move between parts of a stream, they take their genes with them. If they reproduce in the place to which they move, those genes should be represented in future generations. Failure to disperse to other streams will result in genes being isolated in particular streams, along with their carriers. By using genes, or parts of genes (e.g. mitochondrial DNA sequences, microsatellites or single nucleotide polymorphisms) as markers, it is possible to distinguish between dispersal models. For example, if a species fits the Stream Hierarchy model (SHM), an analysis of molecular variance will identify most genetic variance among catchments and least among streams within catchments. Furthermore, if genetic distance among pairs of sites is graphed against stream-distance between sites, there should be a positive relationship that can be tested statistically (Isolation by distance or IBD). Genetic analysis of a small fish, the gudgeon *Mogurnda mogurnda*, in the Daly River, Northern Territory, detected higher variance among catchments than among sites within catchments, and a statistically significant IBD effect, indicating that the mode of dispersal of this species fitted the SHM (Cook *et al.* 2011).

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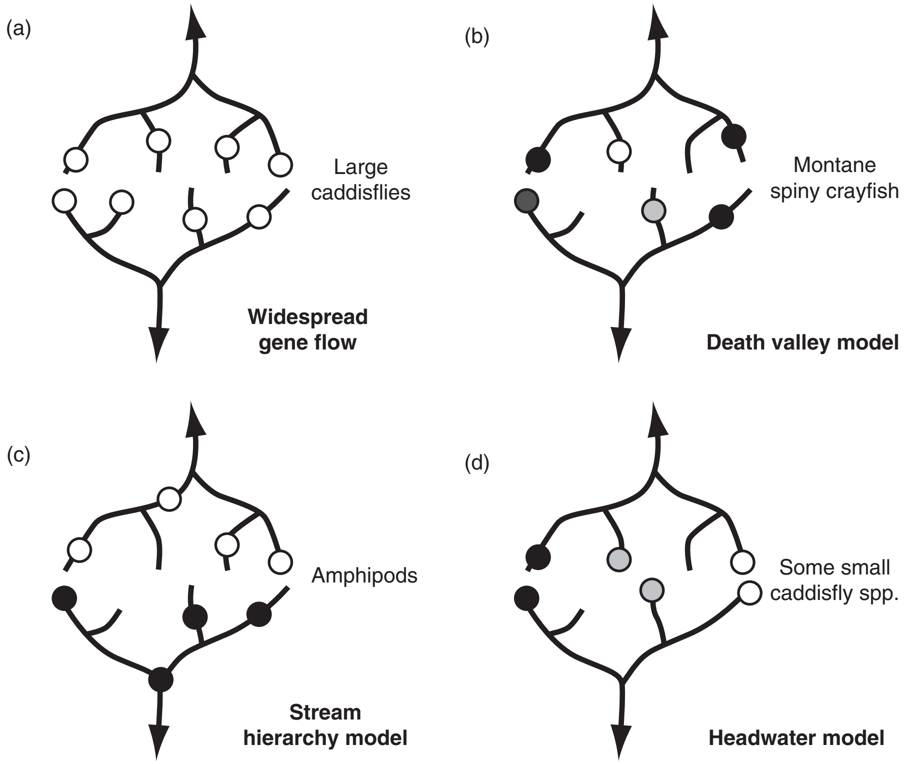

Figure 7.20 The molecular genetics of populations of stream invertebrates can be used to distinguish among different models of dispersal. Imagine two rivers (the black lines) flowing in opposite directions (arrowed) from the top of a mountain range, and inhabited by populations of taxa (examples are named next to each figure) whose genetic composition is represented by the shaded circles (same colour equals shared genetic composition). Dispersal patterns are implied by one of four alternative models: (a) widespread gene flow, where populations contain similar genetic diversity, being well mixed; (b) the Death Valley model, where each stream has a genetic diversity distinct from neighbouring streams, creating multiple genetically different populations; (c) the Stream Hierarchy model, where the two populations are isolated from each other by the mountain range but dispersal occurs along each stream (hydrological dispersal); (d) the Headwater model, where individuals in headwaters that are close together at the top of a mountain range overlap genetically but differ in genetic composition from populations further away, implying dispersal over only short distances. (Source: Adapted from Finn *et al.* 2007. Reproduced with permission of John Wiley & Sons.)

(Figure 7.20d). The genetic structures of populations of lotic Australian species studied so far generally fit one of these four models, allowing us to infer the likely pathways by which dispersal occurs. Further, we can also test whether potential connectivity among populations of aquatic organisms is actually realized (Hughes *et al.* 2013), and if not, explore why.

These differences in modes and capacities for recolonization and dispersal also have an evolutionary history. The distributions of aquatic species across Australia and at spatial scales among and within catchments reflect responses to disturbances over many millennia. Such disturbances include the formation of mountain ranges, changes in river courses, long periods of inundation by seawater and phases of massive floods, aridification and severe 'mega-droughts' as well as species interactions, including human activities (Chapters 9–12). Piecing together the effects of this long history of disturbances and inferring the causes of the present distributions of aquatic plants and animals in Australian rivers is a major challenge. Again, we can use tools such as molecular genetics to help us. But first we need to know a bit about Australia's geomorphic and climatic history.

7.7.3 Setting the biogeographic scene: ancient rocks, variable climates

It is often hard to grasp the dramatic geomorphic and climatic changes that have occurred across the continent during the many thousands of years before European settlement. The continent began to form after the breaking up of the ancient 'super continent' Gondwana some 167 million years ago. Cratons (old and very stable sections of the Earth's crust) from the Archean over 2500 million years ago persist in the western part of the continent as the Yilgarn and Pilbara Cratons, significant in the biogeography of groundwater fauna because of the geological stability of these formations (Section 8.5). In the eastern part, the rocks are younger (Phanerozoic, starting 540 million years ago) and there has been greater geological activity.

Over all this time, erosion by wind and water, the incursions and recessions of seawater as ocean levels rose and fell, and various forms of tectonic activity have been the major agents of change, significantly altering drainage basins and groundwater recharge zones at a vast scale. For example, the formation of the Great Dividing Range by progressive upwarping of the continent's edge some 80 million years ago enabled the hydrological charging of the Jurassic sandstone to become the Great Artesian Basin (White 1994). The formation of this mountain range also split coastal surface drainages from inland ones, isolating many aquatic species and leading to separate species (e.g. Murray cod, Eastern freshwater cod and Mary River cod, Rowland 1993) or genetically distinct populations of organisms such as the fish *Craterocephalus stercusmuscarum* (McGlashan and Hughes 2001). On the other hand, long periods of erosion and deposition have flattened the landscape across much of the continent (Chapter 1). There has also been a lack of recent glaciation or volcanic activity – a contrast to many parts of the Northern Hemisphere where these processes have had major effects on biogeographic patterns of the aquatic biota (as well as forming various types of deep lakes that are rare in Australia, Chapter 2).

Over millions of years, there have been alternating climatic extremes of prolonged 'mega-droughts' interspersed with wetter periods. For example, when glaciation was at its peak, much of the continent was extremely arid and deserts extended into northern Tasmania. At other times, large rivers and lakes have occupied the centre of the continent. In the last 350 000 years, there has been a trend towards drier and/or more variable climates (Kershaw *et al.* 2003). Not surprisingly, this trend of increasing aridity has had major implications for the biogeography of aquatic organisms as well as other key environmental features such as salinity and vegetation cover and type (e.g. more open and sclerophyllous vegetation).

At a continental scale, biogeographic patterns in aquatic plants and animals arising from this long history of continental isolation, periodic and extensive marine flooding, and changing landform and climate may account for some of regional differences in ecological processes occurring across Australia. Reviewing some of these biogeographic patterns helps us understand why some models developed overseas are inapplicable to many Australian running waters, and why we must temper our management strategies accordingly (e.g. native species translocations, Section 12.7).

7.7.4 Some biogeographic patterns in Australian inland waters

Rather than present the biogeographic patterns of all Australian aquatic groups, we only discuss flowering aquatic plants, macroinvertebrates and fishes here. Our intention is to illustrate the parallels among these groups that lead to the following generalizations: (1) relatively low species richness compared with equivalent-sized rivers overseas, (2) relatively high endemicity, (3) adaptive radiation and speciation within some families that are rare or absent in the Northern Hemisphere, (4) persistence of some Gondwanan relicts (those able to find refuge from aridity and changing sea-levels), and (5) often quite distinct regional patterns (e.g. south-western WA, Tasmania). These generalizations have their exceptions, and most biogeographic explanations should be viewed with healthy scepticism (Unmack 2013). Nonetheless, a long history of continental isolation and relative stability, periodic insertion of barriers to dispersal such as marine incursions and aridity, the formation of the Great Dividing Range, and the north-south trend in climate from wet-dry tropics to cool temperate zones probably led to many of the patterns we see today.

Broadly speaking, spatial patterns in the freshwater **flowering aquatic plants** (angiosperms) of Australia indicate two distinct elements – tropical and temperate – that are separated by a diffuse boundary interpreted by Jacobs and Wilson (1996) as forming a barrier to most groups. Although there is little exchange of aquatic plants between tropical and temperate areas, within each of these zones the species are mobile and appear to spread rapidly when provided with suitable habitats and dispersal opportunities. The aquatic flora of the tropics has evolved mainly from long-distance dispersal but some genera (e.g. *Nymphoides*, *Vallisneria*) show significant local speciation (Jacobs and Wilson 1996). At a global scale, species diversity of flowering aquatic plants is comparatively low in Australasia. Although most genera are globally widespread, about half of the 439 species are regional endemics (Chambers *et al.* 2008).

Australian freshwater **invertebrates** include many endemic taxa among the molluscs, crustaceans and insects. For example, the freshwater mussels are Gondwanan 'relicts', being part of a family (Hyriidae) shared with New Zealand and South America (Walker *et al.* 2013). Another relict is *Anaspides tasmaniae* (Figure 7.21), a shrimp-like syncarid crustacean from Tasmania (Camacho and Valdecasas 2008). Some mayfly families that dominate in the Northern Hemisphere are absent, or nearly so, leaving a cosmopolitan family, the Leptophlebiidae, to radiate into unoccupied niches, and similar radiations have occurred among certain families of caddisflies (e.g. Hydropsychidae, Leptoceridae) and stoneflies (e.g. Gripopterygidae). Other invertebrates, including some shrimps (Atyidae) and dragonflies, are immigrants from Asia via the Indonesian Archipelago; still others have invaded from the sea or land, or have been carried by wind, birds or other agents from the Northern Hemisphere (Williams 1983).

At a regional scale, south-western WA appears to have comparatively few species of mayflies, stoneflies and caddisflies. However, this region is a biodiversity 'hot-spot' supporting endemic species of other taxa such as dragonflies and damselflies (Theischinger and Hawking 2006), water mites, crayfishes and freshwater mussels (Morgan *et al.* 2011). Some old groups, including the amphipods and stoneflies, are confined mainly to cooler, wetter areas in the south, but there are exceptions – for example, there are amphipods in underground waters of the Kimberley region (Humphreys 2006, Section 8.5). Throughout Australia, lowland river communities are often sparse, especially in reaches affected by flow regulation, but they are complemented by the rich communities of floodplain wetlands. A few relictual species (e.g. water penny beetles) persist in the uncommon permanent streams in central Australia but stoneflies and amphipods are absent (Davis *et al.* 1993). In arid Australia, groundwater-dependent refuges such as springs and subterranean aquifers have persisted for millennia, supporting many short-range endemic aquatic taxa (Section 8.5.5, Box 8.11). However, these isolated communities are highly vulnerable because local extinctions may not be offset by dispersal from other sites (Davis *et al.* 2013b).

Figure 7.21 The endemic syncarid crustacean *Anaspides tasmaniae* closely resembles fossils in rocks over 250 million years old, and appears to be a Gondwanan relict that now persists only in permanent waters in Tasmania. (Source: Gooderham and Tsyrlin 2002. Reproduced with permission of John Gooderham and Eddie Tsyrlin.)

As we saw for the invertebrates, Australia's **freshwater fish** fauna differs markedly from that of rivers of the Northern Hemisphere. Acanthopterygian fishes (the spiny-rayed fishes) dominate the Australian fauna whereas ostariophysans (such as minnows and loaches) are predominant in freshwaters on most other continents (Unmack 2013). Australia has the only representatives of many acanthopterygian families in the world, and overall, about 90% of Australia's freshwater fish species are endemic (Allen *et al.* 2002). Recent thinking is that at least two families of Australian freshwater fishes evolved in fresh water (Unmack 2013). These two families (Osteoglossidae and Neoceratodontidae) contain the only three species of freshwater fishes with Gondwanan origins that were able to survive the climatic fluctuations and geomorphic changes described earlier: two species of saratoga (*Scleropages leichardti* and *S. jardinii*) and the Australian lungfish *Neoceratodus forsteri* (Figure 7.22). The Australian lungfish differs little from its fossil forebears that swam over 100 million years ago across much of the continent but today this air-breathing survivor is confined to rivers in south-eastern Queensland.

Four other families of Australian freshwater fishes may also have evolved in fresh water but the vast majority of our fish fauna evolved from marine ancestors or came from freshwater fishes with marine life-history phases (e.g. the eels, galaxiids and gobies). Because of the marine affinities of most species, a common misconception is that most of the Australian fish fauna evolved in the last few million years. Instead, it seems that much of the fish fauna has had a long exposure to the same pressures and barriers as the aquatic flora and macroinvertebrates. Regions with high endemicity have been historically fragmented by aridity, drainage divides and other barriers (Unmack 2001), and there are parallels in regional patterns with the ones we saw for the macroinvertebrates. For example, south-western WA is relatively poor in fish species but has high levels of endemism in species (79%) and genera (50%).

New species of freshwater fishes continue to be described (Box 7.15). For example, the book by Allen *et al.* (2002) listed 206 species whereas Unmack (2013)

Figure 7.22 The air-breathing Australian lungfish *Neoceratodus forsteri* closely resembles its fossil ancestors that inhabited Australian rivers over 100 million years ago. (Source: Darren Smallwood.)

Box 7.15 Discovery of new freshwater fish species challenges the notion of a 'depauperate' fauna

The freshwater fish fauna of Australia is often characterized as species-poor. Recent application of molecular techniques and more extensive targeted field surveys challenge this view. Species previously unrecorded from here are continually being discovered, species new to science are still encountered, and widespread species are increasingly found to comprise more than one species. For example, whole assemblages of sicydine gobies, previously unknown from Australia, have been described from torrent habitats of the wet tropics. Several undescribed species of tongue soles (Cynoglossidae) and an ariid catfish have been collected from the lower reaches of the South Alligator River. Genetic studies of northern fishes have identified a new species within *Mogurnda* in the Daly River, and new species within the rainbowfishes *Melanotaenia*. In southern Australia, molecular genetics has revealed new species within the smelt *Retropinna semoni*, the galaxid *Galaxiella pusilla* and the pygmy perch *Nannoperca australis*. A new diminutive pygmy perch has been discovered in south-western WA. The challenge ahead is now to formally describe these new species so that we can protect the diversity we never knew we had.

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listed over 310 species, including some 60 currently undescribed ones. Supplementing traditional fish taxonomy with molecular tools such as DNA analysis continually reveals degrees of genetic divergence within widespread species that, despite morphological similarities, are actually a complex of multiple cryptic species (e.g. carp gudgeons, Schmidt *et al.* 2011). Sometimes, these have major implications for conservation. For example, the trout cod *Maccullochella macquariensis* was not formally recognized as a different species from Murray cod *M. peelii* until it was verging on extinction.

7.8 SYNTHESIS

Unidirectional flow is the distinctive feature of running waters, structuring the channel and floodplains, transporting organic matter, nutrients and biota, and affecting virtually every ecological process. Parallels with standing waters are most marked where flow is slow or absent. However, changes to the flow regime (Chapter 9) alter most physical, chemical and biological attributes, affecting lotic plants and animals as well as changing the rates and efficiency of ecosystem processes such as organic matter breakdown and nutrient spiralling. To manage impacts on running waters effectively, we must understand how they function so that when we try to restore them, we are more likely to be reinstating the process rather than treating the symptoms.

A wide array of conceptual models to explain the factors affecting running waters and their ecology has been proposed over the last few decades. Although they have their limitations, these models help us generate hypotheses about how river ecosystems function in different parts of the world and when subjected to different disturbances, including from human activities. Most of these models pay particular attention to longitudinal trends from upland streams to lowland rivers and to lateral processes occurring between the channel and its floodplain and catchment. Less well understood are the vertical processes of exchanges of surface waters with groundwaters in both running and standing water ecosystems. This knowledge gap, coupled with the increasing importance of groundwater to Australia's economy and industries, prompts us to explore aspects of the ecology of groundwaters (Chapter 8) before investigating management issues associated with changes in water regime, physical features and water quality caused by human activities (Chapters 9–11).

CHAPTER 8

Groundwater processes and management

8.1 OUT OF SIGHT, OUT OF MIND?

So far in this book, we have dealt mainly with the ecology of surface waters. However, out of sight and usually out of mind lies groundwater, a vast resource that is often hydrologically connected to standing and running waters yet is frequently overlooked in discussions of their ecology and management. As mentioned in Chapter 1, most surface waters and groundwaters are a **single connected resource** (Winter *et al.* 1998) and must be considered together.

Our understanding of the ecology of groundwaters lags far behind that of surface waters. This is probably because most groundwaters are not evident to the casual observer. Furthermore, there has been a long-held belief that the saturated and lightless environment below the Earth's surface is an ‘aquatic desert’ where species richness is low, productivity is minimal and ecological processes, if they occur at all, are slow and of little relevance to surface ecosystems. Consequently, few limnology books devote much space to groundwaters and their ecology.

However, groundwaters are not ‘aquatic deserts’ devoid of life. In addition, many surface terrestrial and aquatic ecosystems rely on groundwater, either directly or indirectly. These diverse groundwater-dependent ecosystems are widespread across Australia, further underscoring the significance of protecting the physicochemical processes and ecological integrity of groundwater ecosystems. Effective management of aquatic ecosystems entails managing surface and subsurface waters as a single and connected entity, and is another example of our book's theme of the importance of linkages. As in surface waters, hydrological connectivity underpins the ecology of many subterranean waters and their dependent ecosystems (Figure 8.1).

In this chapter, after defining groundwaters from an ecological perspective, we review the main physical processes that control hydrological connectivity among aquifers and surface ecosystems. Chemical processes, frequently mediated by microbes and governed by subsurface residence time, parallel most of those found in surface waters (Chapters 3 and 6). Physical and chemical conditions interact to provide an environment that exerts strong selective pressures on many groundwater animals, many of which remain undescribed or new to science. Food webs and ecological processes occurring in many groundwaters appear to be as complex as those in surface waters. Much is yet to be learnt, and the research field of groundwater ecology is an exciting new discipline with major implications for our wise and sustainable use of a precious and limited commodity.

8.2 AN INTEGRATED DEFINITION OF GROUNDWATERS

Historically, groundwaters have been defined by hydrogeologists, whose main interests lie in mapping and explaining the distribution and movement of groundwater for extractive purposes. Consequently, traditional definitions of types of groundwaters tend to

Australian Freshwater Ecology: Processes and Management, Second Edition. Andrew J. Boulton, Margaret A. Brock, Belinda J. Robson, Darren S. Ryder, Jane M. Chambers, and Jenny A. Davis.

Companion Website: www.wiley.com/go/boulton/freshwater

reflect subsurface flow, recharge rates and the ease with which water can be extracted. One commonly accepted **hydrological definition** of groundwater is 'all water beneath the water table in soils and geologic formations that are fully saturated' (Freeze and Cherry 1979). Although this definition is useful in a general sense, it refers only to the *location* of the water and has limited ecological relevance (Tomlinson and Boulton 2008) because it overlooks the fact that groundwaters are ecosystems in their own right and that groundwater quality is influenced by its residence time underground and by subsurface conditions.

It also does not encompass the **capillary fringe** that lies immediately above the saturated sediments and is the subsurface layer in which groundwater seeps up from the water table by capillary action among porous unsaturated sediments. The capillary fringe is ecologically relevant because many plant species access water from it (Lamontagne *et al.* 2005), especially during extended dry periods (Jarvis 2011). Nor does this definition accommodate water in the **vadose zone**, the zone that extends from the ground surface down to the water table (the plane where water pressure equals air pressure), and that can contain water that would not be considered as surface water because it is underground and yet is not '**phreatic**' groundwater (i.e. within fully saturated sediments). Recharge by precipitation to most phreatic groundwaters primarily occurs via the vadose zone, and so this zone is also ecologically relevant as well as being a crucial link in the hydrological cycle (Section 1.5.3). Further, it can contain specialized fauna (e.g. epikarst fauna, Pipan *et al.* 2010) and also mediates transfers of energy and dissolved nutrients (Box 8.1).

Figure 8.1 Groundwater stream in Junee Cave State Reserve, Tasmania. This groundwater drainage system is fed by multiple surface streams sinking underground several kilometres away before converging to emerge at Junee Cave. The rapid through-flow of groundwater via large open conduits is typical of karst, a distinctive landscape characterized by water dissolving carbonate bedrock such as limestone, dolomite and gypsum. Many karstic systems are highly vulnerable to pollution and altered hydrological regimes in their surface catchments. (Source: Stefan Eberhard.)

Box 8.1 The vadose zone: a crucial link in many groundwater ecosystems

The vadose zone links infiltrating surface water with the saturated (phreatic) zone below the water table. Other than where aquifers intersect the surface, all terrestrial environments have a vadose zone. Infiltration of water across major environmental transition zones (typically between air, soil and bedrock) causes major changes in water chemistry that influence the receiving systems. The boundary between vadose and phreatic zones may fluctuate by tens of metres annually under natural conditions or through groundwater pumping. Unsustainable groundwater use gradually converts phreatic to vadose environments, potentially altering ecosystem functions and services. Vadose karst and non-karst conduit systems often contain substantial biodiversity and are crucial conduits of energy and dissolved nutrients from the unsaturated zone to the water table (Pipan and Culver 2005). Many are also sites of great geodiversity where irreplaceable formations of diverse rock types, structures and processes have developed over thousands of years. These warrant careful conservation to protect the water regime and chemistry of their environments (Houshold and Sharples 2008), especially because high accessibility for humans is both a threat and a saviour.

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Therefore, the definition of groundwater needs extension to integrate the hydrological, geological and ecological aspects into an **ecohydrological perspective**, and to also include water in the vadose zone. In this book, we define groundwater as: 'Water that is present in soils and geologic formations for sufficient time to undergo physical or chemical changes resulting from interactions with the aquifer environment.'

This broader definition includes vadose water as well as water emerging from spring-heads and cave streams, upwelling into rivers or carried by capillary action to porous sediments above the water table. The main criterion is that the water has been altered physically (usually thermally) or chemically by being below ground. Some groundwater has been below the ground for thousands of years ('fossil' groundwater) whereas other groundwater may be only a few hours old, having recently entered the sediments and yet already changed in physical or chemical quality.

Furthermore, this definition illustrates the artificiality of distinguishing 'surface water' from 'groundwater' based simply on location because, in many cases, it is the same water. The most familiar example is water that flows along a stream channel with a porous bed of gravels or coarse sand. 'Surface water' downwells into the saturated sediments, often at the heads of riffles or leading edges of lateral bars, travels underground for varying distances and times, and then upwells to the surface (Figure 8.2). Hydrologists and ecologists term this exchanged water '**hyporheic**' (literally 'below' + 'flow') and consider the zone of exchange as the 'hyporheic zone' (Section 7.2, Brunke and Gonser 1997). However, the definition of hyporheic water has troubled researchers for decades, largely because of the different disciplinary backgrounds of the researchers (hydrology, geology or ecology) and the different time-scales over which hyporheic exchange can occur (Gooseff 2010). Again, the key issue is that physical or chemical aspects of the water are altered by its time below ground and these, in turn, influence the biota and ecological processes occurring in this altered water.

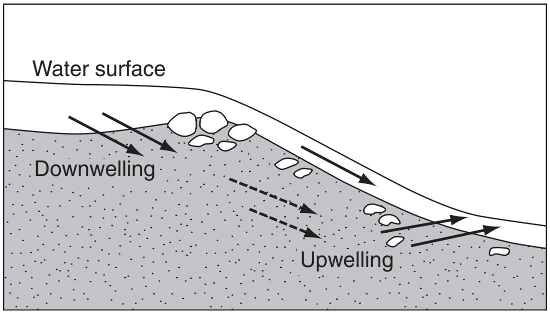

Figure 8.2 Hyporheic flow paths of water below the riffle of a gravel-bed stream. In reality, hydrological exchange occurs at multiple scales within riffles, producing a complex and dynamic mosaic of upwelling and downwelling zones.

Why give all this detail on defining groundwater? The main reason is the lack of a widely accepted ecological definition, hampered by the blurred boundaries (Section 4.3) between surface and groundwater. Another reason is that the legislative definition of groundwater varies between state jurisdictions in Australia (e.g. whether or not to include the vadose zone). Further work is still needed to settle on a satisfactory definition of groundwater that will meet all purposes and so, for this book, we have adopted an ecohydrological one.

8.3 PHYSICAL PROCESSES IN GROUNDWATERS

Recall the diagram of the hydrological cycle in Figure 1.8. That diagram needs refinement because the movements of water between the surface and groundwater compartments are much more complex than portrayed there. Two points are vital. First, groundwater and surface water interact at many places throughout the landscape, from mountains to oceans, swamps to rivers and karsts to sand beds. Second, these interactions occur at a variety of spatial and temporal scales. Subsurface flow paths range from less than a metre to thousands of kilometres; travel times range from minutes to millennia. Depth to the water table varies from zero (as in groundwater-fed wetlands) to hundreds of metres, and can vary seasonally and annually in response to recharge. This recharge is usually from precipitation, snow melt and runoff but can also be water carried by lateral throughflow from adjacent groundwaters.

The water table is the upper surface of the phreatic (saturated) zone. Below the water table, groundwater pressure is high enough for water to enter wells and be pumped out. To measure the location of the water table, we use special wells or pipes called **piezometers** whose perforated ends penetrate the top of the saturated zone far enough to hold standing water and to span the expected variation in saturated water level in

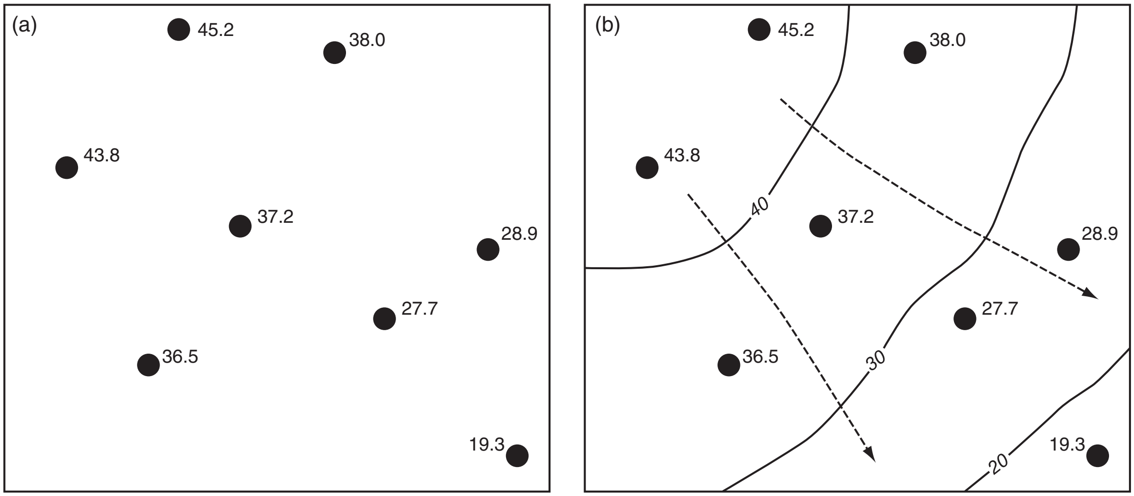

Figure 8.3 Looking down from above, in (a) we have an array of eight piezometers (circles) across the landscape and have obtained the depths to water table (expressed as metres above sea-level) indicated by the numbers next to the circles. In the second panel (b), contours (shown as solid lines with numbers) have been interpolated so we can draw perpendicular arrows (broken lines) to indicate the likely direction of groundwater flow. (Source: Adapted from Winter *et al.* 1998. Courtesy of the U.S. Geological Survey.)

the sediments (Gordon *et al.* 2004). With multiple piezometers (Figure 8.3a), we can map the water table profile and reference those depths to a common datum such as sea level to provide a contour map of the water table. This contour map can then be used to infer the direction of shallow groundwater flow by drawing lines perpendicular to the contours of the water table (Figure 8.3b). Don't forget that this map represents conditions only at that time – groundwater is a dynamic medium, and depths and flow directions can change.

The groundwater system is actually a three-dimensional flow field. What this means is that as well as the horizontal movements shown in Figure 8.3, we also have vertical movements in response to water pressure. A vertical section of the flow field (Figure 8.4) indicates how potential energy is distributed beneath the water table. This potential energy can translate into flow into the surface water (e.g. the upwelling zone in Figure 8.2) and is expressed as the **hydraulic head**. Groundwater flows from a high hydraulic head to a low one; the difference per unit distance is called the hydraulic gradient. To measure how hydraulic head varies with depth, we use a 'nest' of multiple piezometers inserted to varying depths (Figure 8.4), each of which has a screened opening to the groundwater at its base so that its water-level reading represents hydraulic head only at that screened depth in the groundwater system. The screen is to prevent sediments and other material filling the piezometer. By starting at a water table contour and using the water levels from the nested piezometers, we can estimate contours of equal hydraulic head (the dark lines with numbers in Figure 8.4). Then, as we did for the two-dimensional map, we can draw flow lines (the arrows in Figure 8.4) perpendicular to these hydraulic head contours to get the third dimension of downward and upward flows as well as lateral ones.

Of course, actual flow paths are more complex and occur at multiple scales. One widely used conceptual scheme involves three nested levels of '**flow systems**' first described by Tóth (1963). At scales of metres and often near the surface, 'local flow systems' include the exchanges of surface and groundwater that occur along rivers and with groundwater-fed wetlands. These local flow systems are underlain by deeper and larger 'intermediate flow systems' at a basin or catchment scale where flow paths are longer (multiple kilometres) and water may take decades or even centuries to travel

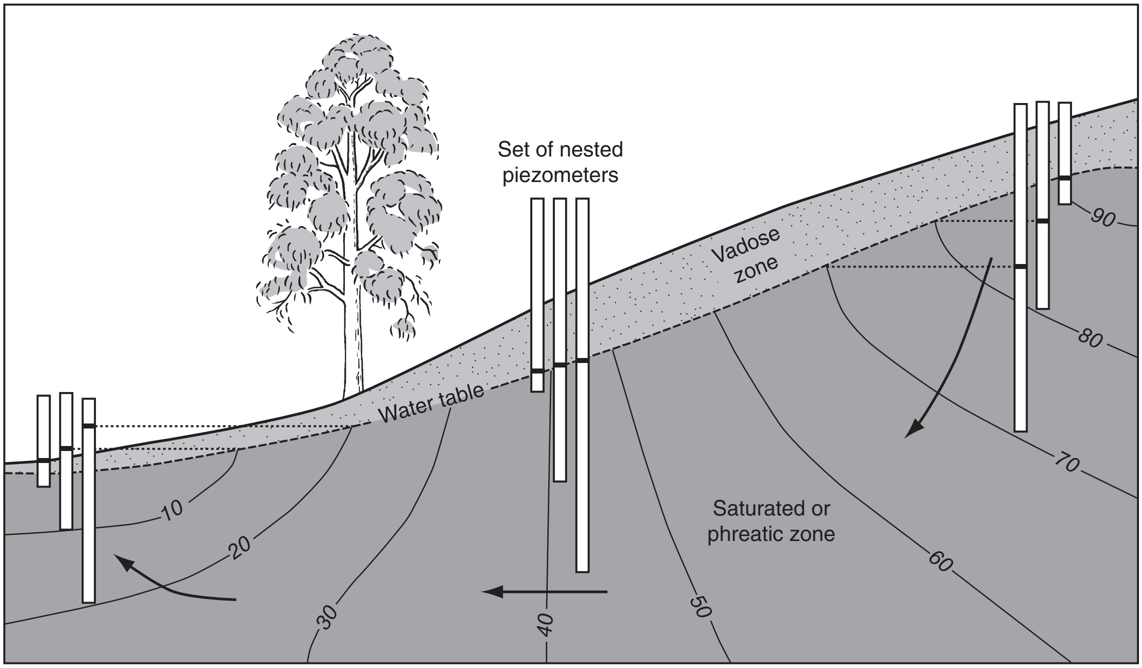

Figure 8.4 Multiple piezometers can indicate contours of equal hydraulic head (dark lines with numbers) and therefore indicate groundwater flow (solid arrows). Black lines within the piezometers represent the water levels in the wells and indicate the hydraulic head at the screened base of the piezometer where it is open to the groundwater. Water from the land surface infiltrates vertically downward to the water table and then moves downward and laterally in the saturated groundwater below the water table. Here, movement is downwards and laterally on the right-hand side, mainly laterally in the centre of the diagram, and then laterally and upward to the left, driven by differences in hydraulic head. (Source: Adapted from Winter *et al.* 1998. Courtesy of the U.S. Geological Survey.)

along them. Below these is the 'regional flow system', which is the largest scale, transcending basins and catchments across thousands of kilometres but ultimately discharging to surface waters. This nested hierarchy of flow systems has proved useful in conceptualizing the biogeochemical implications of groundwater interactions at multiple spatial scales (Hayashi and Rosenberry 2002) as well as their ecological repercussions for surface waters (e.g. wetlands in arid and semi-arid areas, Jolly *et al.* 2008).

By using data on groundwater levels collected over time from either individual or nested piezometers, groundwater models (Box 8.2) can be developed that provide powerful tools for research and management. For example, these models can be used to identify 'trigger levels' beyond which there is a strong chance that further groundwater extraction for human uses is likely to threaten groundwater-dependent ecosystems. Furthermore, modelling different scenarios can indicate the range of uncertainty around these 'trigger levels'. Models can also be used to study groundwater-surface water interactions at multiple scales, identifying hydrological connectivity and lags between, for example, river flows (Boulton and Hancock 2006) and the recharge or discharge of shallow alluvial aquifers (Vanderzalm *et al.* 2011).

8.3.1 Groundwater discharge, permeability, porosity and Darcy's Law

Groundwater discharge (termed 'flux' by hydrogeologists) into and from surface waters can be calculated for a known cross-section of aquifer by multiplying

Box 8.2 Groundwater models and their uses

Measurements of piezometric levels are essential to understand groundwater flow patterns and interactions between groundwater and surface-water systems. However, measurements alone have very limited use in making future predictions. Enter groundwater models! These are mathematical tools that combine the principle of mass conservation with Darcy's Law (Section 8.3.1) to develop equations that can be solved by computer to calculate piezometric levels as a function of space and time. Groundwater models are constructed by populating these equations with the hydrogeological parameters of the subsurface (e.g. the hydraulic conductivity appearing in Darcy's Law), known water levels and fluxes (including recharge and pumping rates). Values of the parameters in a model are adjusted until the model simulates observed groundwater conditions with a certain degree of accuracy. Once the modeller has confidence that the model is an adequate representation of the real world, future management scenarios can be simulated to assess their effect on piezometric levels and water fluxes. These can help to minimize impacts of pumping on streams by, for example, comparing different well locations and abstraction rates.

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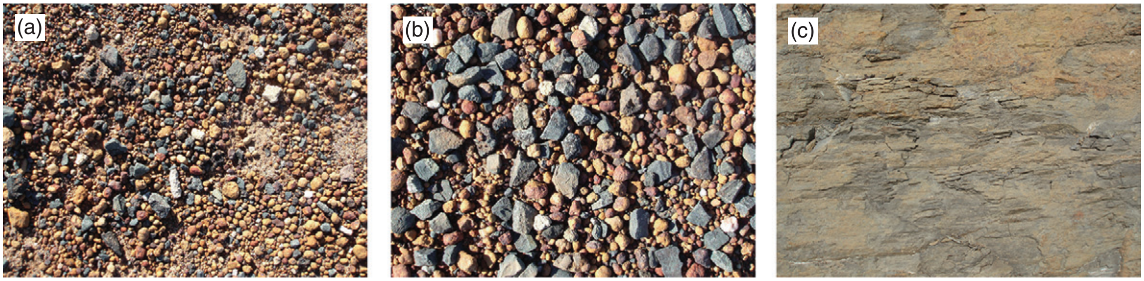

Figure 8.5 Poorly sorted sediments (a) have low porosity because finer materials fill the spaces among the larger particles whereas well-sorted sediments (b) have high porosity and high permeability. Shales (c) may have high porosity but permeability is often low because the spaces are poorly connected. (Source: Andrew Boulton.)

aquifer permeability by hydraulic gradient, derived from measurements of hydraulic head as described previously. **Permeability** describes how easily water moves through aquifers, and is related to the size and connectivity of spaces among the sediment particles which, in turn, depend on grain size and shape. For example, clay, with smaller and more tightly packed particles, is less permeable than sand. On the other hand, **porosity** is the volume of space among grains in an aquifer and is expressed as a ratio of the volume of open spaces to the total volume of material. Porosity is affected by the shape, arrangement and heterogeneity of grains. In poorly sorted sediments (Figure 8.5a), finer grains fill the spaces among coarser ones, reducing porosity compared with well-sorted sediments (Figure 8.5b). At first glance, you might think that porosity and permeability are always related. However, although an aquifer might be porous, if the spaces are not connected then water cannot move through it and the aquifer is not permeable. For instance, some shales can have high porosity but low permeability because the spaces are poorly connected (Figure 8.5c).

Porosity varies among aquifers. Unconsolidated aquifers consist of particles of gravel, sand, silt or clay that are not bound by mineral cement, pressure or thermal alteration (Freeze and Cherry 1979). They typically result from wind deposition (e.g. aeolian aquifers in sand dunes) or the action of water (e.g. alluvial aquifers). In contrast, fractured rock aquifers occur in consolidated sedimentary, igneous or metamorphic rock, and the spaces result from cracks along bedding planes or stress zones caused by pressure from factors such as tectonic movement or rapid changes in temperature. These cracks and fissures can be quite wide and can be further enlarged by solution in some rock types to form caves or solution conduits. In some karstic landscapes (Ford and Williams 2007), water action can create immense caverns (Figure 8.1) and solution holes, substantially increasing porosity. Thus, one can have **primary porosity** among the grains comprising the rock type and **secondary porosity** through the spaces dissolved in the rock. The size and connectedness of spaces in aquifers in different rock types play a major role in determining colonization potential and living space for fauna as well as influencing the ease with which water can be extracted from the aquifer.

Flow through an aquifer is described mathematically by **Darcy's Law**. The equation derived from this useful law expresses discharge (Q) in terms of the aquifer's hydraulic conductivity (K) and cross-sectional area (A), and the hydraulic head gradient ($h_a - h_b$) over a given distance (L) between points a and b:

$$Q = KA(h_b - h_a)/L$$

Hydraulic conductivity (K) is a function of the permeability of the aquifer as well as the density and viscosity of the groundwater. Darcy's Law elegantly summarizes two key properties of groundwater movement: (1) the greater the hydraulic head gradient, the greater the rate of discharge, and (2) even if hydraulic head gradients do not change, a reduction in permeability will reduce groundwater discharge. This equation is widely used to estimate groundwater discharge as well as being part of many groundwater models (Box 8.2).

8.3.2 Physical processes between groundwaters and surface waters

So far, our discussion has dealt with factors affecting flows *within* aquifers. These factors may also dictate how groundwaters interact with surface waters. For example, any variable that affects permeability or the pressure, density or viscosity of groundwater will affect hydrological exchange between groundwaters and surface waters.

Small-scale variation in permeability is common in many natural aquifers and governs groundwater discharge at multiple scales. The size, shape and packing of grains in an alluvial stream bed affect the amount of water recharged or discharged at a local scale. Reduced rates of stream flow may increase deposition of finer sediments and, in areas where groundwater exchanges with streamwater, reduce or even prevent the exchange. When a flash flood surges down a stream channel and water levels rise, water will often move into the banks (= bank storage), temporarily raising the local water table (Figure 8.6a). As water within the channel subsides, groundwater stored in the bank sediments returns to the stream (Figure 8.6b), often within days or weeks. When the flood extends onto the floodplain (Figure 8.6c), widespread recharge to the groundwater usually occurs (Doble *et al.* 2012). This infiltrated water may take years to return to the stream because flow paths are longer (Figure 8.6d).

At broader scales (local to intermediate flow systems), geologic units with different permeabilities can affect groundwater discharge. For example, there may be preferential flow through a layer of sand or gravel within an aquifer of silt (Figure 8.7). Layers with low or zero permeability can confine aquifers, holding groundwater under pressure until released, for example, by a bore sunk for agricultural purposes (Figure 8.7). We often call these **confined aquifers** to distinguish them from **unconfined aquifers** whose upper boundary is the water table. Many aquifers are actually semi-confined because of the complexity of the underlying geology and the existence of layers of varying permeability, especially in sedimentary rocks. (Sometimes, the term 'phreatic' is used to indicate that an aquifer is unconfined; in this book, we use the term in the broader sense to mean fully saturated sediments.)

Pumping groundwater can cause a **cone of depression** of the water table around the base of the well (Barlow and Leake 2012). Depending on the volumes extracted, these cones can be extensive and may persist for some time after pumping ceases. If pumping is done near a stream where groundwater discharges under natural conditions, the cone may be enough to reverse the groundwater flow path and draw water from the stream (Evans 2007), dramatically altering subsurface chemical conditions (e.g. introducing oxygenated, nutrient-rich water). Further, streamflow depletion

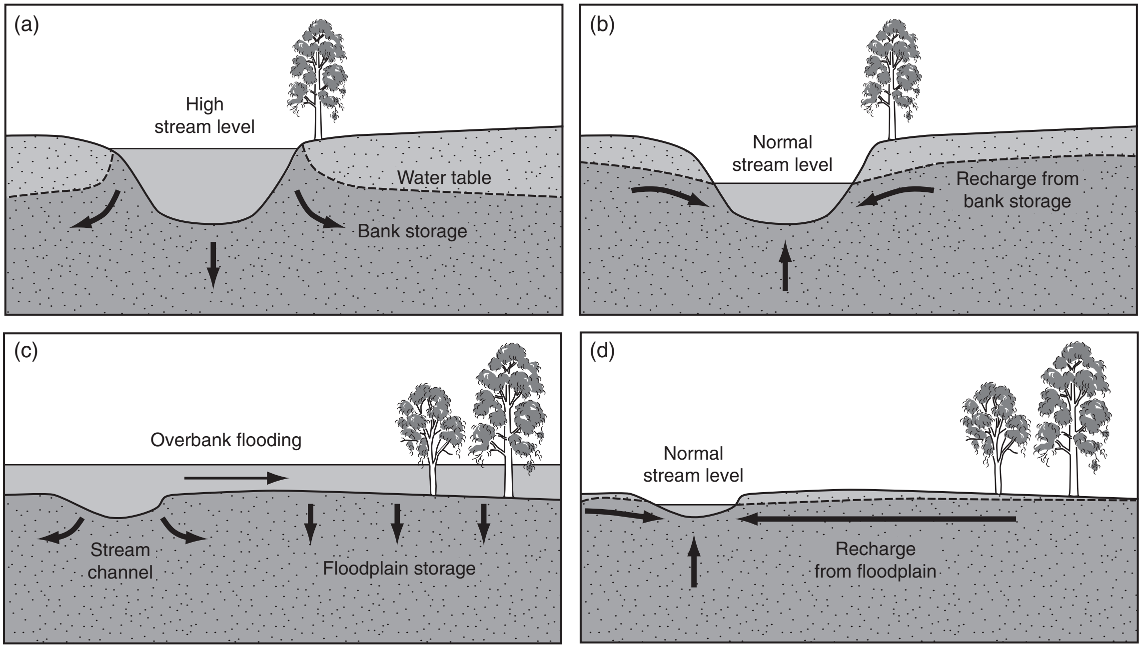

Figure 8.6 When stream levels rise higher than the local water table (dashed line), water can enter the banks as bank storage (a), returning to the stream days to weeks after stream levels fall (b). During overbank flows (c), water spreading onto the floodplain can recharge groundwater. Subsurface recharge (d) typically takes much longer than surface drainage to return to the stream. (Source: Image drawn by Belinda Cale.)

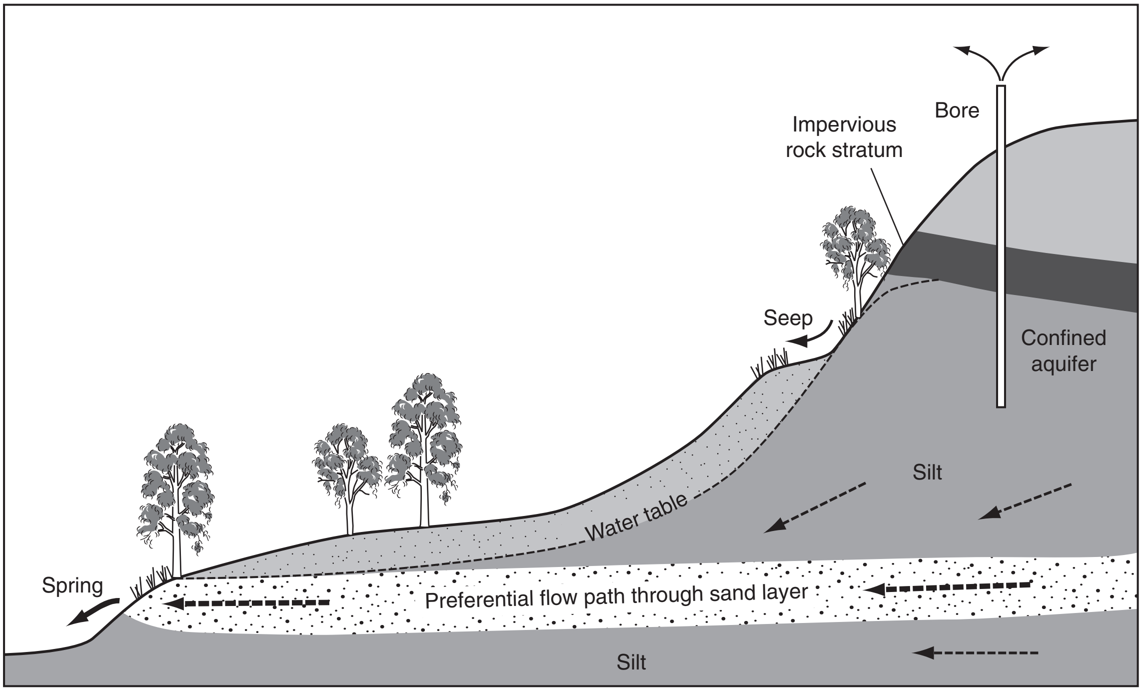

Figure 8.7 Preferential flow (thick broken arrows) through a sand layer in a silt aquifer can emerge as a spring whereas an impervious rock stratum can confine an aquifer so that water gushes out under pressure if a bore is sunk through the layer. (Source: Image drawn by Belinda Cale.)

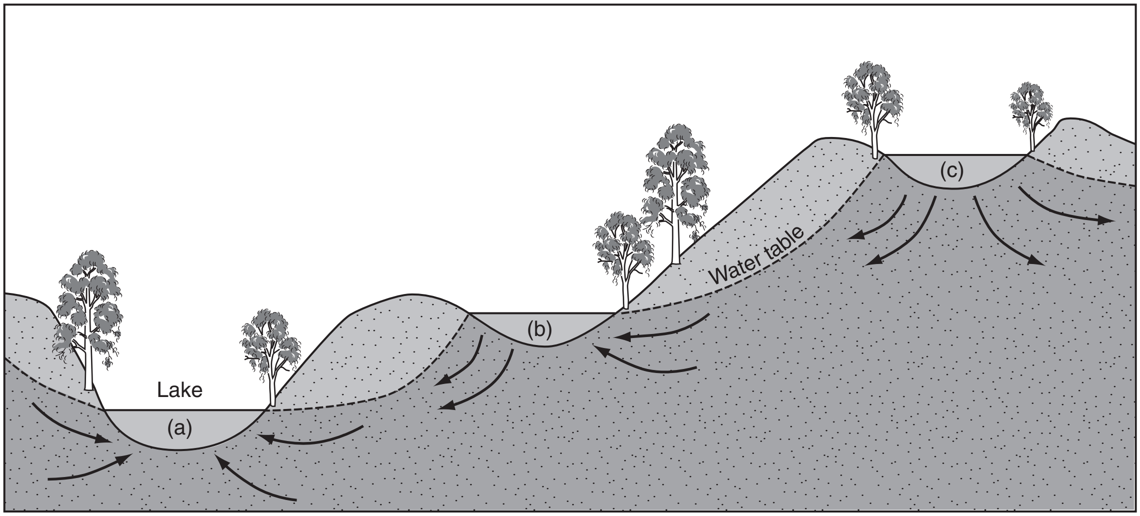

Figure 8.8 Lakes can receive groundwater (a), receive it on one side and lose it on the other (b), or only recharge groundwater (c). Some waterbodies (e.g. a and b, here) may also receive groundwater inputs from deeper aquifers, affecting their water chemistry and colour. (Source: Image drawn by Belinda Cale.)

will continue after pumping stops because it takes time for the cone of depression to refill and for the aquifer to recover. Such a situation nicely illustrates why groundwater and surface water must be considered and managed together. The complexity of these linkages coupled with the varying lag times and aquifer conditions create a challenge for water managers trying to predict timeframes for impact and recovery when groundwater near surface waters is extracted for human use (Section 8.6).

Lakes interact with groundwater either by receiving it as seepage through the bed (Figure 8.8a), losing it across the bed (Figure 8.8c) or, most commonly, receiving groundwater in one part of the lake and losing it in another (Figure 8.8b). However, the exchange patterns can be quite complex when groundwater enters from multiple aquifers at varying depths. For example, many shallow wetlands on the Swan Coastal Plain, WA, receive groundwater from shallow unconfined aquifers. These wetlands often contain highly coloured water because the shallow aquifers that feed them contain dissolved organic matter (Section 3.9.3) leached from the sediments. Most of them dry out during the rainless summer because of seasonal declines in the water table. In winter, when rain replenishes the groundwater, these wetlands may receive subsurface inflow along one edge of the lake and lose it from the opposite edge where the water table is lower than the lake surface. During summer, when groundwater tables fall, lake levels also drop and the flow-through process slows and may even cease (Searle *et al.* 2010). In larger lakes, such as Thomsons Lake, groundwater from deeper aquifers supplements inflows from the shallow aquifers, and the water in the lake is often clearer and remains for longer. Water chemistry of both deep and shallow groundwater-fed wetlands varies in response to the different sources and volumes of groundwater, and is further modified by inputs from direct rainfall and surface runoff.

To get a clearer impression of groundwater-surface water exchanges in these Swan Coastal Plain lakes and wetlands, Turner and Townley (2006) used chloride concentrations measured in nested piezometers beneath and beside different lakes and compared water chemistry in the surface water and at varying locations in the underlying aquifers. From these data, they developed numerical models of water exchange and subsurface flow to help managers make decisions about the types of land and groundwater use in this area, which is experiencing rapid population growth. Regional declines in groundwater tables and oxidation of acid sulfate sediments along the lake edges (Section 11.5),

Figure 8.9 Many lentic environments, such as this alpine wetland near Thredbo, NSW, are groundwater-dependent. (Source: Jane Chambers.)

coupled with urban and agricultural runoff, are impairing water quality and ecological values of these groundwater-dependent lakes on the Swan Coastal Plain (Searle *et al.* 2010, Section 9.4).

Many lentic environments, including those on hillslopes or on the saddles of drainage divides (Figure 8.9) are entirely groundwater-dependent, and the distribution of their often-distinctive flora and fauna is governed by groundwater quantity and quality (Section 8.5.6). Unfortunately, these groundwater-dependent standing waters are seldom adequately conserved. For example, only 0.2% of the fens on the New England Tablelands Bioregion in New South Wales are on reserved lands. Another 90% are on grazed land where they are threatened by damming, draining and grazing (Hunter and Bell 2009).

Groundwater-surface water interactions are a complex interplay of hydraulic pressure and groundwater flux, local and regional permeability, sedimentation of fine organic and inorganic particles, plant growth, and human activities that alter basin shape or infiltration properties of the catchment. For example, around the shores of open and exposed lakes, wave action can remove fine sediments, permitting surface and groundwater to interact readily. In other wetlands, accumulations of clay particles and highly decomposed organic material may clog interstitial spaces and slow the exchange of water and solutes between the surface waterbody and the groundwater. Sometimes, these waterbodies can be 'perched' above the water table because their fine sediments have such low permeability (Section 2.8.2). This has implications when dredging or deepening is suggested as a management option (e.g. as in some perched wetlands on the Swan Coastal Plain). Partial or total perching of standing waters can also occur when repeated wetting and drying combine with leaching of mineral-rich waters to produce 'hardpan' beds of soil particles bound with precipitated silica, iron oxide, calcium carbonate or organic matter.

However, even where fine sediments in the beds of wetlands restrict water exchange, water uptake by roots of emergent aquatic plants can facilitate the interchange of pore water and surface water. In some streams, for example, in the Flinders Ranges, SA, daily patterns of transpiration by river red gums can cause daily fluctuations in groundwater-fed surface flow, altering the area of the wetted channel by many square metres (Cooling and Boulton 1993). Such fluctuations have also been observed in cool temperate areas such as Mountain River in Tasmania, where transpiration by riparian mountain ash *Eucalyptus regnans* may reduce daytime water levels by a few centimetres. At a larger scale, the establishment of plantations of trees can have significant effects on water tables and groundwater-dependent surface waterbodies (Section 8.6). This varies during the life of the plantation. Young trees use large amounts of groundwater but as they mature, groundwater use slows. When the plantation timber is harvested, groundwater uptake ceases and water tables may rise. Similar processes occur when natural vegetation is cleared or killed by salinization (Section 11.4).

8.3.3 Groundwater temperature

One significant physical property affected by the varying depths and residence time of groundwater is its **temperature**. When residence time is short and the groundwater is highly connected with the surface, its temperature typically echoes diel and seasonal thermal cycles above ground, although with smaller amplitudes. Further, there is usually a slight time lag in the peaks and troughs of the dampened cycles in the groundwater, caused by the downstream displacement of groundwater in the sediments. These thermal patterns can be a useful indicator of groundwater flow paths and rates of transport in shallow aquifers because they can be easily measured with small and inexpensive data loggers. In combination with time-series data of surface water and stream-bed water levels, natural heat is a valuable tracer for measuring surface-groundwater exchanges in streams and their aquifers (Rau *et al.* 2010)

In deeper groundwater, water temperatures are relatively stable compared to surface waters. However, with every 100 m of depth, water temperatures rise by about 3°C. In some places, groundwaters rising rapidly from extreme depths can erupt as steam and boiling water. Steaming geysers are rare in Australia but hot artesian bores and springs are common, often accompanied by carbon dioxide degassing or a strong stench of hydrogen sulfide. As we have seen in earlier chapters, water temperature directly influences many ecological processes as well as governing the solubility of gases and solutes. Water temperature also affects the viscosity of water (Section 1.5.1) and may alter flow rates of groundwater through aquifers.

8.4 CHEMICAL PROCESSES IN GROUNDWATERS

The chemical composition of most groundwaters is primarily controlled by: (1) the geological characteristics of the aquifer materials, and (2) how long the water has been in contact with those materials. For example, the pH and chemistry of groundwater travelling through a limestone aquifer in a karstic landscape would be expected to differ from those of water in a fractured granitic rock aquifer. If the water has taken a long time to move through the limestone aquifer compared to, say, flowing quickly down a cave stream, the amount of chemical alteration is likely to be much higher. Of course, this chemical alteration also depends on the chemical reactivity of the aquifer materials with the adjacent groundwater.

Many of the same processes that affect the chemistry of surface waters (e.g. microbial activity and biodegradation, reduction-oxidation (redox) reactions, precipitation and dissolution) occur in groundwater. What differs is the predominance of certain types of chemical processes because of the low concentrations or absence of dissolved oxygen, reducing or nullifying its role as an electron acceptor. As we have seen in Chapter 3, under anoxic conditions, other electron acceptors such as nitrate, manganese, iron, sulfate and carbon dioxide are needed for microbial respiration. For example, many bacteria decomposing organic matter get their energy from redox reactions and can reduce sulfate (SO_4^{2-}) to sulfide (HS^-) when the organic matter is oxidized to CO_2.

Broadly speaking, different chemical processes occur with increasing time in the groundwater, and this often is evident as differences with depth. When water first infiltrates the ground surface, soil microbes immediately start to influence its chemistry (Figure 8.10). Most organic matter in soils is degraded by microorganisms, producing high concentrations of CO_2 that dissolves readily in the soil water, lowering its pH by increasing carbonic acid (H_2CO_3) concentrations. As this water seeps deeper, the carbonic acid can start to weather minerals and generate bicarbonate (Section 3.2.2).

In deeper groundwater, the contact time between the water and minerals is longer and so the initial importance of the microbial processes in the shallow groundwater tends to be superseded by geochemical **weathering** (Figure 8.10). As this weathering continues, the concentrations of dissolved salts increase and, depending on geology and residence time, the chemistry of the groundwater may be substantially altered. Carbon dioxide can also be produced by processes in the Earth's crust, generating an acid source from below. Rising through the ground in geothermally heated waters, it initiates weathering at depth by the same processes described previously.

8.4.1 Principal chemical processes in groundwater

Related to the weathering processes illustrated in Figure 8.10 is the process of **precipitation** of minerals. Precipitation is responsible for one of the visual wonders of the underground realm. When the calcite ($CaCO_3$) in limestone is dissolved by vadose water, calcium ions (Ca^{2+}) and bicarbonate ions (HCO_3^-) are released. The resulting solution may then drip from the roofs of caves and precipitate, creating beautiful formations of stalactites and stalagmites (Figure 8.11). A second example of precipitation associated with groundwater is that of iron, commonly seen in surface seeps as a rust-coloured iron hydroxide precipitate near the water's edge. This precipitate develops when groundwater comes in contact with atmospheric or dissolved oxygen, causing iron to precipitate out (Section 3.8).

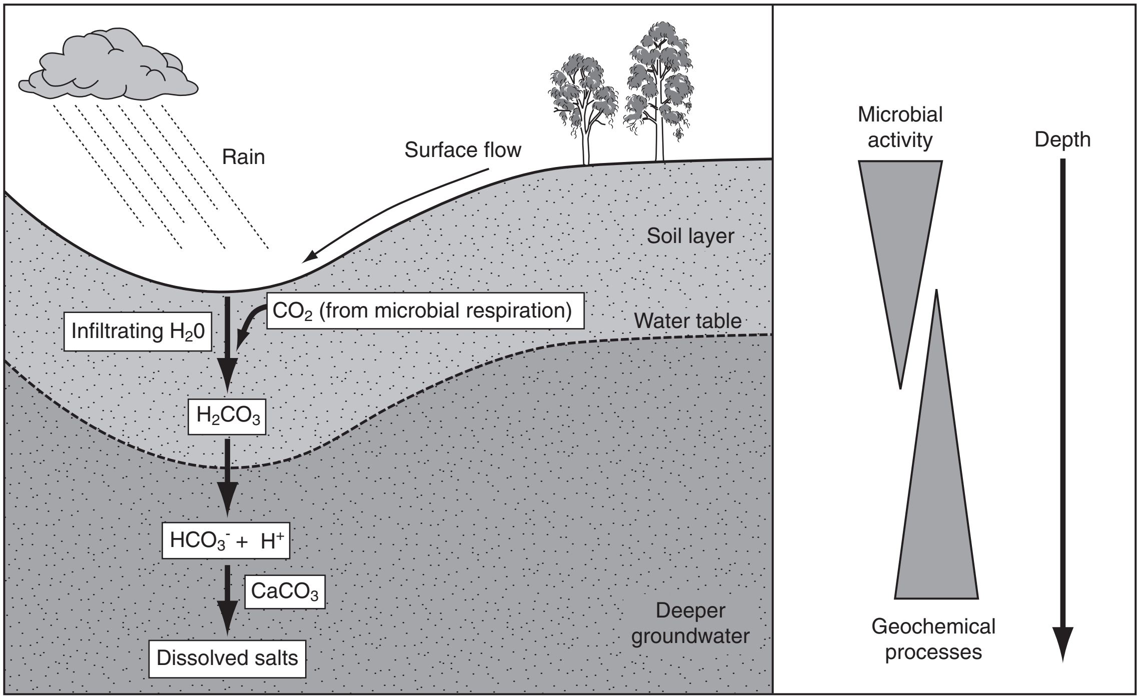

Figure 8.10 Transition in the relative contributions of microbial and geochemical processes with depth in groundwater. Typically, microbial activity (especially by aerobic microorganisms) predominates in shallow surface layers whereas geochemical weathering occurs at greater depths. (Source: Image drawn by Belinda Cale.)

Figure 8.11 The cave stream flowing through Croesus Cave, Mole Creek, Tasmania, is internationally significant for its diverse array of geological formations (Box 8.1). Water in this vadose system comes from dripping stalactites and percolation. (Source: Ian Houshold.)

Another chemical process common in groundwaters, especially in unconsolidated aquifers is **sorption** and its opposite, **desorption**. As groundwater carrying dissolved ions or molecules filters through the sediments, the solutes are sorbed (i.e. taken up) by the sediment particles, often as a result of electrostatic charges, as we saw in Chapter 3. This 'chemical filtration' is a key process capable of altering groundwater chemistry through ion exchange where ions in the water are exchanged for ions attached to the sediment surface. For example, when seawater percolates through a coastal limestone aquifer, some of the sodium ions are exchanged for calcium ions sorbed to the sediments of the aquifer.

The predominance of various chemical processes is dictated partly by the rate of movement of the groundwater. In unconsolidated sand and gravel aquifers where the groundwater moves relatively rapidly (Figure 8.7), chemical processes associated with sorption/desorption and redox reactions tend to be mediated by

Box 8.3 Groundwater chemistry and environmental tracers

Groundwater processes, flow paths and residence times can be revealed by measuring concentrations of environmental tracers in groundwater. Environmental tracers are natural or anthropogenic isotopes, elements or compounds that are widely distributed in the near-surface environment. Some tracers indicate groundwater age. For example, chlorofluorocarbons (CFCs) manufactured for industrial purposes from about 1950–2000 increased in atmospheric concentrations over this period. CFCs dissolve in rainfall, and can be used to determine groundwater residence times of water recharged between approximately 1950 and 2000. Other tracers operate over different time scales. Radon, for example, is naturally produced by radioactive decay of uranium-series isotopes, and can be used to estimate groundwater residence times of 1–20 days. Measurements of groundwater age on this timescale are useful in studies of surface–groundwater interactions such as hyporheic residence times (Lamontagne and Cook 2007). Other tracers do not provide information on residence time but reveal other groundwater processes. For example, proportions of the heavy isotopes of water (^{18}O and ^{2}H) can vary across precipitation events, and so concentrations in groundwater can indicate the source and intensity of precipitation recharging groundwater.

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microorganisms. Conversely, reactions involving dissolution or precipitation of minerals are more common in aquifers where porosity and permeability are low and the groundwater moves more slowly.

Rates and directions of groundwater movement can be determined using chemical or environmental ‘**tracers**’, many of which occur naturally and can be used to indicate sources and residence times of groundwater (Box 8.3). Using stable and radio-isotopes in the Australian arid zone, hydrogeologists have been able to determine the age of groundwaters, the significance of large floods for groundwater recharge, and the use of groundwater by vegetation (Herczeg and Leaney 2011). Co-injection of solutions containing ‘conservative’ tracers that are virtually inert (e.g. bromide) along with biologically active tracers such as nitrate can reveal groundwater flow paths as well as rates of nutrient transformation along the same flow paths. For example, co-injections of bromide and nitrate into a perched riparian aquifer of an ephemeral stream in south-eastern Queensland indicated how hydrological exchanges between stream and groundwater affected nitrate dynamics in the riparian aquifer (Woodward *et al.* 2009).

8.4.2 Chemical processes along gradients of dissolved oxygen

Groundwater and surface waters exchange in many lentic and lotic environments. This creates gradients of chemical conditions along the pathways of exchange, illustrated by the hypothetical example of a gravel bar at the edge of a river (Figure 8.12). Downwelling or inwelling surface water carries dissolved oxygen and organic matter into the sediments (Figure 8.2), generating ‘**hot-spots**’ of biogeochemical activity where aerobic bacteria thrive. These bacteria preferentially use oxygen as an electron acceptor, so it is used up soon after inwelling (Figure 8.12). Along this gradient of declining oxygen concentrations, the abundance and activity of anaerobic microorganisms increase, metabolizing nitrate, sulfate and other solutes in place of oxygen. In turn, their activities cause gradients in these solutes. Thus, there is a trend of increasing amounts of reduced forms of nutrients (e.g. ammonium) and decreasing amounts of oxidized nutrients (e.g. nitrate) along subsurface flow paths (Figure 8.12).

However, the dynamic changes in groundwater flow paths, especially in response to surface water fluctuation and sediment heterogeneity, mean that these gradients often fluctuate at a microscale (less than millimetres) while at broader scales (greater than metres), there may be longer gradients of alternation of surface and groundwater such as through gravel bars (Figure 8.12) and riffle beds in the hyporheic zone (Figure 8.2). In this way, physical groundwater processes interact with chemical processes, often mediated by microbes, to produce dynamic gradients of intensive biogeochemical activity across a range of spatial scales. These chemical gradients provide a constantly shifting mosaic of environmental conditions and promote the

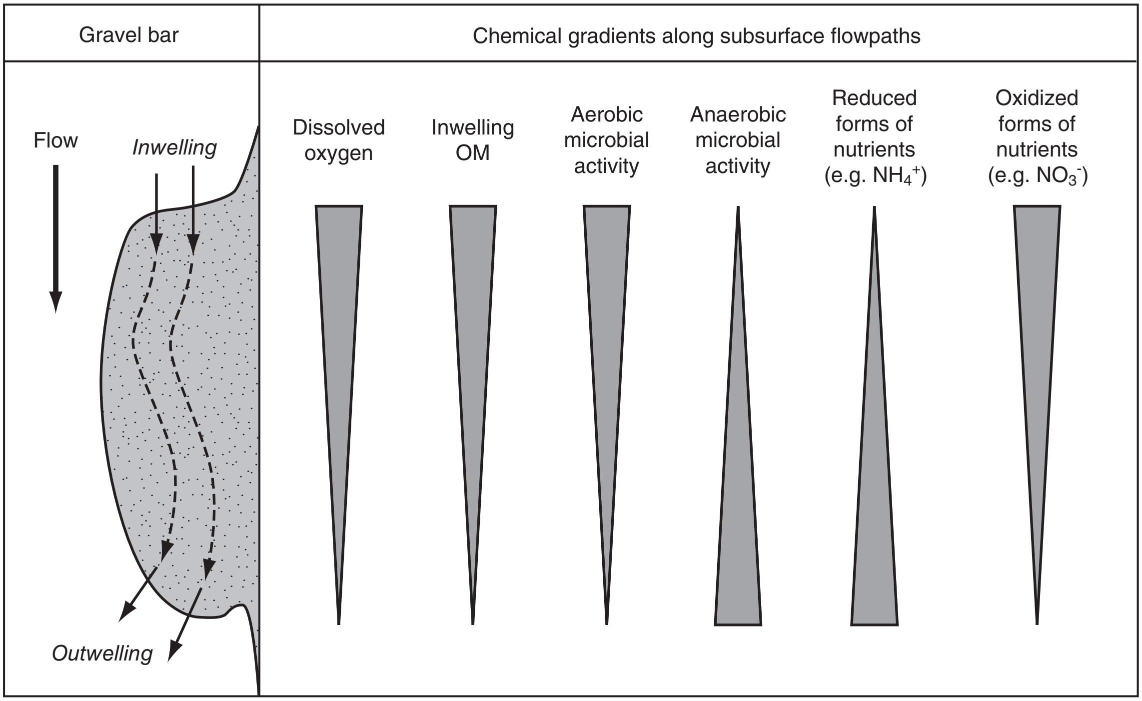

Figure 8.12 A bird's-eye (plan) view of the way that downwelling surface water enters a gravel bar at the river's edge and travels along subsurface flow paths, creating gradients in dissolved oxygen, microbial processes and the concentrations of different ionic forms of nutrients.

great diversity of biogeochemical reactions in many aquifers. Localized 'hot-spots' of biogeochemical transformations and the dynamic gradients in groundwater chemistry also influence many ecological processes in groundwaters because they can govern the distributions of groundwater invertebrate fauna as well as influencing (and being influenced by) subsurface microbial assemblages.

Similarly, upwelling groundwater containing dissolved nutrients such as ammonium may create 'hot-spots' of algal production in nutrient-limited surface waters. Often, bright green patches of filamentous algae such as *Spirogyra* indicate upwelling zones at the tail-end of gravel bars or the heads of seeps in sand and gravel bed rivers. Other aquatic plants also take advantage of this bounty, and groundwater inputs can explain some of the patchy distribution of particular reeds and sedges along the shoreline of surface waterbodies. Biogeochemical and microbial processes that alter groundwater chemistry have major implications for many surface aquatic and terrestrial systems. Two of the most severe and widespread examples are salinization and acidification (Degens *et al.* 2012, Chapter 11), again illustrating the significance of surface-subsurface linkages and the need to manage our water resources as a single connected resource.

8.5 BIOLOGICAL PROCESSES IN GROUNDWATERS

By now, you have a good idea of the parallels and contrasts in physical and chemical features between surface and groundwaters, and will be inferring some of the likely biological processes based on what we covered in Chapters 2–7. For example, the lack of light in groundwater environments means that photosynthesis is unlikely to take place and therefore groundwater food webs rely on organic matter imported from the surface or on producers that do not require light. What are the implications of this for the diversity and types of organisms in groundwater environments? How might food-web structure differ? While you read the next few sections, consider the constraints imposed by lightless environments on the biota and ecological processes in groundwaters, and how these compare with those in surface waters.

8.5.1 Groundwater microbiology

Bacteria and other microorganisms play vital roles in many ecosystem processes occurring in groundwaters. Most groundwater microbes are associated with the surfaces of sediment particles; relatively few occur in the free water. Early investigators of the microorganisms of groundwater collected water samples, often from long-standing wells, and many samples were not collected with due care to avoid contamination from surface waters (Gounot 1994). Consequently, some of the initial work on groundwater microbiology was biased by poor data. Reliable studies of microbial ecology must ensure that samples are uncontaminated, undisturbed and representative of groundwater sediments – a challenge, especially for deep groundwater where techniques are needed to minimize the effects of drilling tools and fluids. Where existing wells or bores are sampled, any stagnant water must be removed first. Even so, there will always be some uncertainty as to the exact source within the aquifer of the microbes collected.

Until recently, the ecological roles of groundwater microorganisms were seldom considered. Where microbiological samples were collected, it was usually to detect pathogens or pollution indicators from groundwater intended for human use. Therefore, the discovery of substantial microbial diversity, especially in waters from several kilometres deep (Krumholz 2000), was unexpected and exciting. Molecular analyses of DNA and 16S ribosomal RNA from samples in deep aquifers indicate the absence of any strains identical to those of microbes in surface waters. This implies a long period of isolation and evolution within the groundwater environment.

Often, diverse microbial assemblages occur across multiple scales within the same groundwater ecosystem. For example, in the Bundera Sinkhole, a groundwater system in north-western Australia with a highly stratified water column, diverse vertical sequences of populations of heterotrophic, phototrophic or chemoautotrophic microorganisms occupy discrete microbial habitats associated with physicochemical strata (Seymour *et al.* 2007), revealing the extraordinary spatial complexity to be found in some groundwater environments (Box 8.4). Another remarkable example of chemoautotrophic communities occurs in the

Box 8.4 Microorganisms in Bundera Sinkhole

Bundera Sinkhole, north-western Australia, is a groundwater ecosystem characterized by intense density stratification resulting from the subterranean intrusion of seawater from the coast. In addition to stratification by salinity, several other chemical and physical properties of Bundera Sinkhole are also stratified. This complex physicochemical profile influences and is influenced by the ecology of a diverse community of planktonic microorganisms. In the upper depths of the sinkhole, where light penetrates, phytoplankton photosynthesize and aerobic bacteria recycle organic matter. However, a few metres deeper, where light levels drop and oxygen is reduced, the microbial community shifts to one dominated by anaerobic and chemolithotrophic microbes, including sulfur-oxidizing, denitrifying and nitrifying bacteria. Each of these groups is spatially constrained within tight horizontal layers of the water column, resulting in discrete microbial niches, often separated by distances of only a few centimetres. Consequently, intense peaks in the abundance of specific microbial populations occur, sometimes evident as visible veils of organisms, including sulfur-oxidizing bacteria. The unique conditions within Bundera Sinkhole support and are supported by a rich and ecologically diverse microbial community, which ultimately underpins the productivity and function of this amazing ecosystem.

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water-filled passages of caves deep below the dry and flat Nullarbor Plain. In these caves, such as Weebubbie Cave, hang 'slime curtains' bathed in groundwater rich in nitrite and nitrate but isolated from any photosynthetically derived carbon. Using molecular methods of genome sequencing, Tetu *et al.* (2013) showed that the diverse microbes in these slime curtains apparently obtain their energy from metabolizing inorganic nitrogen.

Not surprisingly, photosynthetic microorganisms are absent from most groundwaters. The few phototrophs that are collected occur either just below downwelling or recharge zones in unconsolidated aquifers interacting with surface waters or are near the entrances of caves or various karstic systems and sinkholes. However, virtually every other functional group of microorganisms can be found in most groundwaters where they play ecological roles similar to those of their surface relatives (Chapters 3, 4 and 7). For example, groundwater bacteria and Archaea (Box 3.4) are directly involved in nitrification, denitrification, oxidation and reduction of sulfur, and the breakdown of organic matter. By altering ambient chemical conditions, as described earlier, they indirectly govern rates of many processes such as precipitation and dissolution, redox reactions, and sorption and ion exchange.

Bioavailable organic carbon is a rare commodity in most pristine groundwaters, unlike surface waters. Except for those driven by chemoautotrophs, most aquifer ecosystems are **heterotrophic** and rely on organic matter imported from photosynthesis at the surface. Generally, this organic matter either infiltrates as dissolved organic carbon or is particulate organic matter trapped within the sediments. However, where tree roots reach groundwaters in caves such as those at Yanchep, south-western WA, fungal associations (mycorrhizae) in the roots provide enough carbon and other nutrients to support complex and diverse aquatic food webs where invertebrate densities may be as high as 350 animals per gram dry weight of root mat (Jasinska and Knott 2000). Another example is in Jewel Cave, also in south-western WA, where root mats snake along the cave floor (Figure 8.13) and contribute carbon to aquatic and terrestrial food webs within the cavern.

Although organic carbon is often rare, iron and manganese are usually abundant in groundwaters. In aerobic environments, soluble Fe^{2+} and Mn^{2+} are oxidized, and the oxides or hydroxides readily precipitate. Under anaerobic conditions, these materials are reduced by microbes, just as we saw in surface waters. Also, as in surface waters, oxides of Fe^{2+} and Mn^{4+} can bind with a variety of toxic trace metals in the sediment, which are then remobilized as a potential hazard when these iron and manganese compounds are reduced in groundwater ecosystems.

Figure 8.13 Living tree roots such as these snaking across the floor of the Jewel Cave karst system, WA, provide carbon and other nutrients that support diverse assemblages of subterranean aquatic invertebrates. However, availability of water rather than carbon is the main constraint in some of these systems now. In 2000, a survey of the aquatic assemblage revealed some 15 species including at least two endemic crustaceans. By 2010, the surface area of water in this cave had shrunk by 99% and the aquatic community had all but gone (Box 8.10). (Source: Stefan Eberhard.)

Despite being oligotrophic, pristine aquifers still support a high biodiversity of bacteria. The productivity of these bacteria appears primarily limited by the supply of substrates on which to act. When organic pollution of groundwaters occurs (e.g. infiltration of sewage effluent, excessive fertilization of crops above shallow porous aquifers, Section 11.3), microbial activity is typically stimulated. Groundwater bacteria are able to degrade many natural organic compounds as well as some anthropogenic ones such as pesticides and industrial chemicals (Naidu *et al.* 2012). Microbial responses to enrichment of groundwater with organic compounds tend to be almost instantaneous, presumably taking advantage of any fleeting bioavailability of carbon in this oligotrophic environment. Injection of air ('air sparging') can also be used to enhance groundwater microbial degradation, and shows promise in the

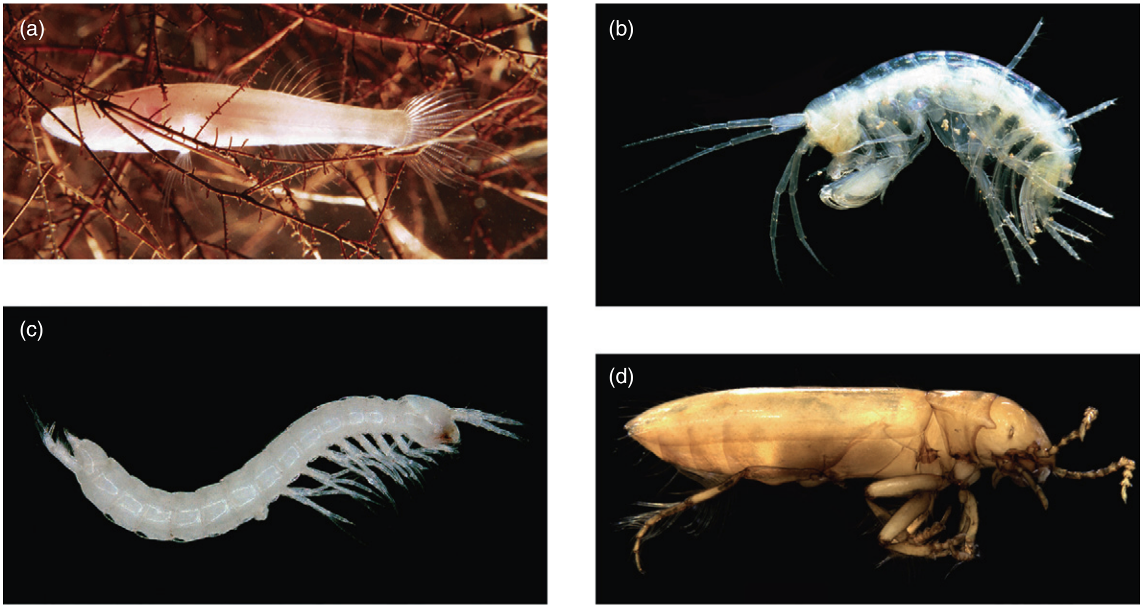

Figure 8.14 Representatives of Australian groundwater fauna: (a) blind cave gudgeon *Milyeringa veritas* – 4 cm long; (b) amphipod *Nurina poulteri* (body length 5 mm) endemic to groundwater of the Roe Plain, Nullarbor, WA; (c) undescribed species of syncarid (Parabathynellidae, body length 4 mm); (d) a new species of dytiscid beetle *Paroster* endemic to a single calcrete aquifer in the Goldfields region, WA (body length 4.5 mm). (Source: (a) and (b) Stefan Eberhard; (c) and (d) Subterranean Ecology Pty Ltd.)

bioremediation of volatile organic compounds derived from residual gasoline in sand aquifers. One of the most rapidly growing fields in groundwater research is that of bioremediation, where microbes are being cultivated to enhance this valuable ecosystem service (Section 8.7) provided by many aquifers.

8.5.2 Buried treasures in Australia: groundwater invertebrates and fishes

Until the 1990s, most groundwaters were assumed to be largely devoid of fauna. This assumption arose from the seemingly minimal habitat diversity (because of the constrained physical size of most interstitial spaces), the lack of light as a source of energy, the low dissolved oxygen and the limited food supply. However, sporadic investigations in cave streams and saturated karsts of Europe over a century ago had revealed the existence of several species of unusual invertebrates and even small vertebrates (e.g. the cave salamander *Proteus anguinus*). These animals were unpigmented, had lost their eyes and generally had elongated sensory appendages and limbs (Figure 8.14), interpreted as modifications for life underground. This fauna was collectively termed **stygofauna**, a word derived from the mythical River Styx across which spirits of the dead must travel to enter the underworld of Hades. The global diversity of stygofauna is much greater than initially thought and there is growing interest in understanding their ecological roles and significance in groundwater ecosystems (review in Larned 2012).

In Australia, several species of groundwater crustaceans had been described by the early twentieth century but over the next hundred years, only occasional studies were published on stygofauna (review in Humphreys 2008), focusing on descriptions of unpigmented shrimps and other aquatic crustaceans, and even groundwater fishes – a blind cave gudgeon (with a second species described by Larson *et al.* 2013, Figure 8.14a) and a blind cave eel. It was not until systematic surveys in the 1990s in north-western WA that the true extent of the biodiversity of our stygofauna began to emerge. These surveys revealed a number of unusual higher-order taxa, such as the class Remipedia and the orders Spelaeogriphacea, Misophrioida and Thermosbaenacea (Humphreys 2012), along with many new species of stygal isopods, amphipods and syncarids (Figure 8.14b,c). Within some groups, especially microcrustaceans (e.g. ostracods and copepods), the diversity is extraordinary (Guzik *et al.* 2011). Even some insect groups, such as stygofaunal dytiscid diving beetles (Figure 8.14d), have proven remarkably diverse with over a hundred new species being described.

Many of the new species discovered appear to be 'short-range endemics' (Harvey 2002), occurring only in a very restricted area and often known from only a few specimens. This has implications for their conservation (Section 12.6.5) but in some cases may also reflect limited sampling (Eberhard *et al.* 2009). No doubt there are many more species of stygofauna to be discovered (Box 8.5), and intriguing groundwater environments such as the perched aquifers of karst regions (epikarst) that have yielded a diverse and unique fauna overseas (e.g. Pipan *et al.* 2010) remain virtually unstudied in Australia.

8.5.3 Biodiversity and ecology of Australian groundwater fauna

The high stygofaunal biodiversity in some of the aquifers in Australia partly reflects the long persistence of relatively stable environmental conditions below ground compared to the surface where there have been major episodes of regional aridity and marine intrusions (Section 7.7.3) and, in Tasmania, glaciation. Many of these aquifers have been described as 'living museums' (Humphreys 2009) containing examples of lineages that comprised the fauna from various geological periods.

Although the groundwater environment might be persistent, it can be hydrologically dynamic and creates a mosaic of living conditions underground. As we have seen, complex biogeochemical gradients occur across multiple spatial and temporal scales while interstitial spaces in the different aquifers can range from tiny pores to massive caverns and sinkholes with varying hydrological connectivity. When local hydrological connectivity is disrupted, speciation may occur and, over long enough time, give rise to rich pockets of stygofaunal biodiversity (Guzik *et al.* 2011, Box 8.6). For example, in north-western Australia, assemblages of many groundwater species have been discovered co-occurring in sequences of aquifers below the drainage lines of ancient rivers ('paleochannels'). Using molecular techniques, Finston *et al.* (2007) showed that populations of blind amphipods living in separate groundwater tributaries of paleodrainages with episodic surface flow had been separated from between 2.0–8.9 million years.

We know very little about the biology of any individual species of groundwater invertebrates in Australia. However, extrapolating from studies of stygofauna

Box 8.5 Exciting discoveries of new stygofauna

Finding new species or even new genera is always thrilling but when you record a whole new order, the excitement rises a notch! On my first aquatic collecting trip to the Pilbara for the Western Australian Museum in 1991, I sampled water in a cave at Cape Range, inland from Ningaloo, and found *Halosbaena*, representing the crustacean order Thermosbaenacea, a new record of this order for the Southern Hemisphere. This was just the first of many extraordinary findings that fellow collectors and I would make of a hitherto unexpected diversity of stygofauna (Humphreys 2008, 2012). Over the years, from various groundwater habitats, including the marine layer of Bundera Sinkhole (Box 8.4), we have found further higher taxa that were new records for the Southern Hemisphere, such as the class Remipedia, the order Misophrioida and the families Epacteriscidae and Ridgewayiidae. Later, using a special net hauled through the water in a borehole in the Fortescue Valley, WA, I collected a spelaeogriphacean, another crustacean order new for Australia and previously known only from caves in South Africa and Brazil, indicating a Gondwanan origin. Who knows what we'll find next?

Bill Humphreys, Western Australian Museum

Box 8.6 The biodiversity and uniqueness of Australian stygofauna

Drop a net down a well in some of the driest places in Australia and you have a good chance of sampling a new groundwater species. Stygofauna occur throughout arid Western Australia in various groundwater habitats such as calcrete aquifers and ancient fractured-rock aquifers. This region is a biodiversity hotspot for stygofauna, predicted to harbour over 4000 new and endemic species of which only about 10% are described (Guzik *et al.* 2011). In eastern Australia, groundwater habitats like the spectacular Jenolan Caves and alluvial habitats of rivers in the Great Dividing Range are also sites of stygofaunal biodiversity. Australia's stygofauna arose during a period of major climatic change. Inland Australia was once wet, but during the late Miocene/Pliocene (14–2 million years ago), much of the continent started to become increasingly arid. This process probably favoured groundwater organisms and appears to have driven an explosion in subterranean speciation. Interestingly, Australia's stygofauna also have direct faunal links to ancient Pangaea and Gondwana (e.g. Abrams *et al.* 2012). Such a long and complex evolutionary history has probably contributed greatly to the extraordinary biodiversity we see today.

Michelle Guzik, University of Adelaide

overseas and from the sparse data available from laboratory studies of several Australian groups, it seems that most species are slow-growing, long-lived and have few young compared to their surface counterparts. These attributes would help stygofauna cope with the restricted sources of energy in most groundwater ecosystems. Overall densities of stygofauna are also usually very low. Many groundwater invertebrates lack resting or dispersal stages, interpreted as the result of life in a relatively persistent aquatic environment. However, this means that they are slow to recover from drying or fluctuations of the water table or from reductions in their populations (Humphreys 2009). This has obvious implications for their vulnerability to natural and human disturbance of the groundwater regime.

Groundwater fauna can be classified by their affinity to groundwater (Gibert *et al.* 1994). Animals that are surface dwellers but accidentally occur in caves or alluvial sediments are termed **stygoxenes** (e.g. larval hydroptilid caddisfly in Figure 8.15) and are relevant because they can influence groundwater food webs either as predators or prey. **Stygophiles** have some affinity for groundwater, appearing to actively exploit subsurface resources such as food or shelter and may spend part or all of their life cycle in aquifers, usually those with close hydrological linkages to surface waters. Animals that are obligate inhabitants of groundwater are called **stygobites** (Figure 8.15). Stygobites typically share features of being blind and unpigmented with elongated appendages and sensory structures (Figure 8.14) and tend to predominate in aquifers with limited hydrological linkages to surface waters.

This ecological classification acknowledges the crucial biotic linkages between surface and subsurface environments that occur in many groundwater ecosystems. For example, many stream insects are stygophiles because their small aquatic stages occur within the hyporheic zone where they can reach high densities, protected by the sediments from surface predators and nurtured by food carried in downwelling zones. Similarly, aquatic nematodes, worms, mites, copepods, cladocerans, ostracods, tardigrades and even some small snails may be present in all life stages in the groundwater as stygophiles, even though they are capable of living in surface habitats. As a result, prey and predators in many groundwater and hyporheic food webs span surface and subsurface waters, mediating substantial transfers of energy and carbon between the two systems (Boulton *et al.* 2010).

Most groundwater food webs are truncated because primary producers are absent and, by extension, so too are herbivores (except in downwelling zones where surface algal cells enter the sediments). Predators are usually rare and the food web is dominated by detritivores (Gibert and Deharveng 2002). These detritivores obtain their carbon from particulate material (e.g. buried leaf litter) or from grazing microbial biofilms on sediments. As in surface systems (Chapters 4 and 7),

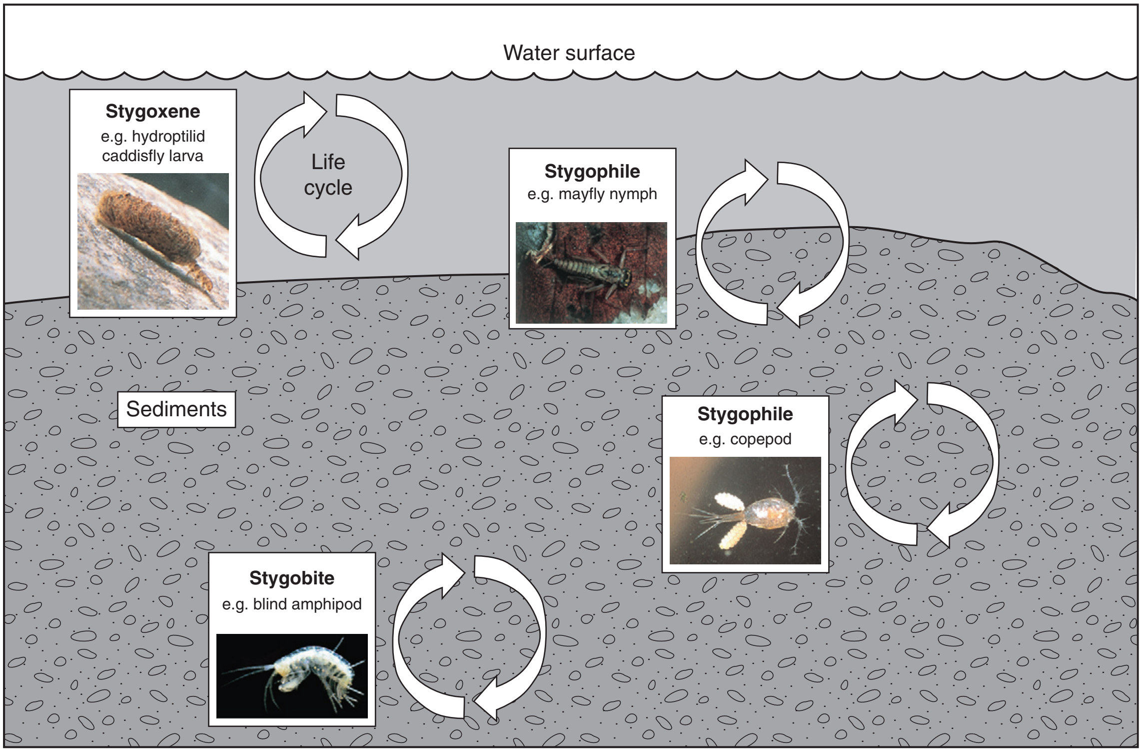

Figure 8.15 Groundwater fauna can be classified into stygoxenes that accidentally occur in groundwater but whose life-cycle is completed in surface waters, stygophiles that can (but do not have to) complete their life-cycle partly or entirely in groundwater, and stygobites that are obligate residents of groundwater for their entire life-cycle. (Source: (top three) Gooderham and Tsyrlin 2002. Reproduced with permission of John Gooderham and Eddie Tsyrlin; (bottom) Stefan Eberhard.)

groundwater microbes take up dissolved organic carbon and nutrients from the surrounding groundwater and are then grazed by protists and invertebrates. Most groundwater food webs appear to be controlled from the 'bottom-up' by organic matter supply (except, of course, the chemoautotrophic systems described in Section 8.5.1). Carbon-isotope tracer experiments demonstrate that microbial biomass and activity in aquifers are predominantly controlled by the supply of dissolved organic carbon whereas grazing activities of stygobitic amphipods appear to exert little or no 'top-down' influence (Foulquier *et al.* 2010). In areas where organic pollution from sewage infiltrates into shallow aquifers, fluorescence and stable isotope signatures have been used to show how food webs are affected (Box 8.7).

8.5.4 Physical, chemical and biological drivers of groundwater ecological processes

As in surface waters (Chapters 4 and 7), many groundwater ecological processes are influenced by the prevailing suites of physical and chemical conditions across a range of spatial and temporal scales. These interact to provide a much more complex environment in groundwater ecosystems than once thought. Further, the activities of microbes and possibly stygofauna (Boulton *et al.* 2008) also modify the environmental conditions, in turn influencing ecological processes. Hydrological linkages with surface waters provide complex gradients in space that vary over time in response to varying surface conditions, rainfall and infiltration, catchment land-use and vegetation, and of

Box 8.7 Tracing effects of sewage-derived organic matter in stygofaunal food webs

The extent of trophic interactions in groundwaters is virtually unknown. Stable isotopes offer perhaps the most promising tools for understanding flows of matter and energy in these systems. Therefore, in our efforts to assess the likely effect of sewage on groundwater assemblages below a treatment plant in the South Island of New Zealand (Hartland *et al.* 2011), it seemed a great idea to use the isotopic signature of sewage as a baseline against which to assess the structure of the groundwater food web. However, we found that the carbon isotopes in the sewage were too variable to provide a reliable baseline for the food source and that the biofilms in the groundwater had a low nitrogen content, precluding an assessment of the microbial basis of the food web. Nonetheless, it was clear that groundwater fauna receiving sewage were less diverse and were dominated by resilient taxa. Encouragingly, recent advances in compound-specific stable isotope techniques (McCarthy *et al.* 2013) offer new opportunities for distinguishing between changes in trophic status and food source composition in groundwaters – a challenge awaiting inquisitive researchers of means!

Adam Hartland, Waikato University

course, climate change (Ali *et al.* 2012). Finally, many of the effects lag in time, sometimes by decades to centuries. As a result, interactions may not be evident for some time and cause-and-effect relationships can be difficult to discern.

Physical and chemical factors at multiple scales affect the **groundwater regime** (flow, pressure and water table), water quality and biota (including micro-organisms) (Figure 8.16). In concert, these create environmental gradients from minute redox gradients of a few millimetres up to the changes along paths within regional flow systems of many thousands of kilometres. Conditions along these gradients dictate the nature of biogeochemical and ecological processes in groundwaters. Groundwater ecosystems are clearly just as complex as surface ones and, by and large, the processes are driven by the same environmental variables and biogeochemical pathways.

Three broad-scale drivers – climate, aquifer geology and geomorphology, and catchment vegetation and land-use – govern recharge rates and volumes of terrestrial inputs to groundwater and the chemistry of the water (Figure 8.16). The climate, through its influences on temperature and seasonality of rainfall and snowmelt, affects the input of atmospheric fresh water (recall the hydrological cycle from Section 1.5.3). However, for this fresh water to enter the groundwater, it must traverse the terrestrial components of the recharge area, affected by catchment land-use, soil types and vegetation. These, of course, are also influenced by climate, and the relationship is a complex one governing rates and timing of infiltration and evapotranspiration. Surface relief can affect hydraulic head (and hence pressure and flux rate) while aquifer geology and geomorphology control groundwater residence times, largely through void size and connectivity (porosity and permeability). In turn, residence time and aquifer geology affect groundwater chemistry and biogeochemical gradients (especially redox gradients) at a range of spatial scales within the aquifer.

Groundwater residence time, flux, pressure and the dynamics of the water table can be grouped into a complex factor termed ‘groundwater regime’ in Figure 8.16. Groundwater regime controls ecological processes via the supply of water, nutrients and biota as well as their removal and redistribution among adjacent aquifers. Analogous to the water regimes of surface waters, the groundwater regime is the outcome of the processes supplying and transporting incoming water and, in turn, largely regulates biogeochemical and ecological processes throughout the aquifer. For example, stygofaunal and microbial distribution, activity and assemblage composition are governed by the supply of water, nutrients and energy. Dispersal and colonization rely on the groundwater regime and connectivity among aquifers, and the groundwater regime dictates the availability of habitats, the access to food resources and the removal of excretory products.

Groundwater chemistry directly controls many ecological processes either through the chemical form (i.e. reduced or oxidized) and amount of particular materials or via physiological constraints on the components

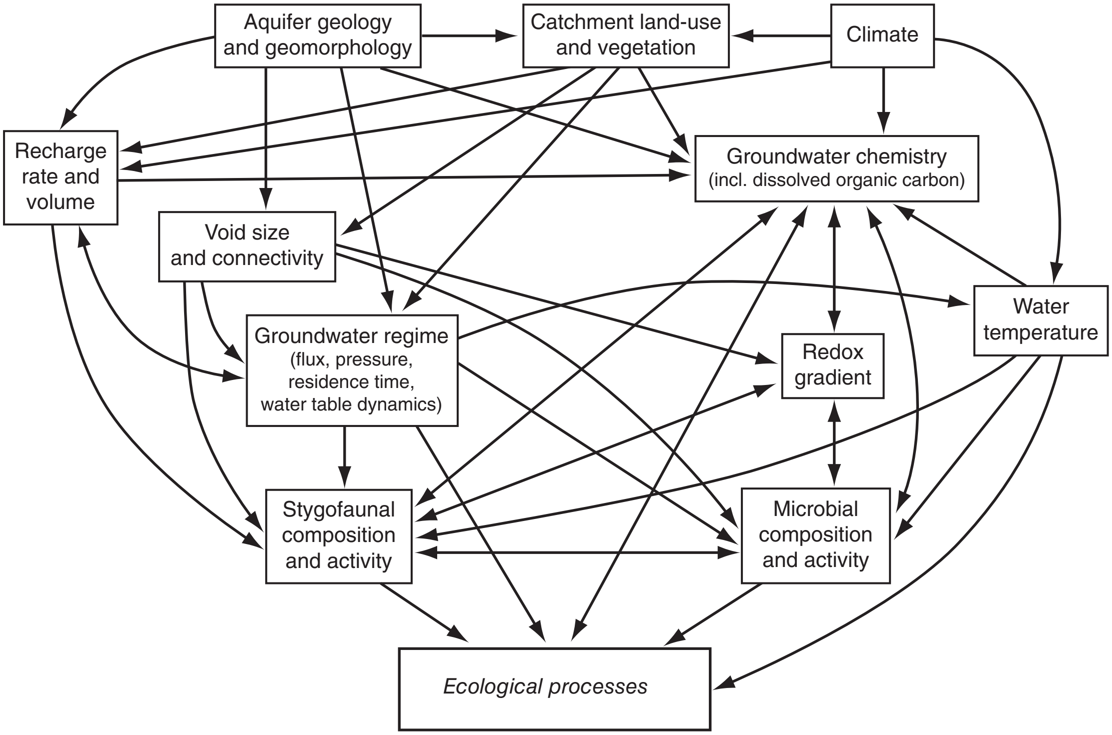

Figure 8.16 Physical, chemical and biological factors affecting ecological processes in fresh groundwaters. Two-way reciprocal interactions are shown as double-headed arrows. Marine influences have been omitted.

of specific ecological processes (e.g. oxygen for aerobes). Chemical products and transformations from the ecological processes feed back to groundwater chemistry, hence the two-way interaction shown in Figure 8.16. Similar feedback loops occur for microbial and stygofaunal activity, and in many aquifers, ecological processes probably play a major role in the chemical and biological filtration of groundwater.

Given the focus of this book, we have not discussed the interactions of groundwater with marine or estuarine ecosystems but we should not overlook these aspects when studying coastal groundwaters. For example, changes in groundwater regime such as reduction in pressure and flux can promote the intrusion of marine groundwater (review in Werner 2010). Given the density differences in saline and fresh groundwater, the intruding marine water may enter below overlying fresh groundwater in unconsolidated porous aquifers with only limited mixing at the interface (e.g. the Bundera Sinkhole). Land-locked waterbodies with a subterranean connection to the sea are termed **anchialine**, and are commonly associated with coastal aquifers.

8.5.5 Groundwater-dependent ecosystems (GDEs)

Surface and subsurface ecosystems that rely entirely or occasionally on groundwater (including vadose water) are termed **groundwater-dependent ecosystems** (GDEs). These include aquifer and cave ecosystems, many wetlands fed by aquifers, river base-flow systems and often their riparian zones, many terrestrial ecosystems (especially their vegetation), and even some estuarine and marine ecosystems (Sinclair Knight Merz 2001). Given the ubiquity of groundwater, it comes as no surprise that Australia has a rich and diverse array of GDEs, many of which only rely on groundwater during the dry season or in extreme drought. They range from an obligate dependency (e.g. aquifers and their stygofauna, Humphreys 2006) through to facultative dependency (e.g. *Melaleuca* swamps in the NT). Dependency by facultative GDEs varies over time. For example, in arid-zone streams, flow may depend entirely on groundwater input (baseflow) during the dry season but show little dependency under wetter conditions.

Not every component of a GDE must depend on groundwater. For example, the vegetation communities that comprise the GDE relying on the Gnangara Mound near Perth (Box 8.8) are often dominated by species of *Banksia* (Figure 8.17) that are groundwater-dependent for much of the time whereas other plants in the association have no requirement for groundwater. Some plant species will be obligate phreatophytes (plants associated with groundwater), others will be facultative and yet others will be variously obligate or facultative, depending on their position in the landscape (Groom *et al.* 2000). Clear boundaries seldom delimit GDEs, and sometimes groundwater dependency is not evident until deep into a severe drought when other sources of water are absent or when extended groundwater extraction and steadily falling water tables start to affect susceptible species (Box 8.8).

Ecological processes in GDEs appear to be governed by complex requirements for particular combinations of groundwater quantity, pressure, depth, timing of supply, and water quality. Theoretically, attributes of GDEs such as biodiversity, rates of particular ecological processes and measures of ecosystem health (Section 11.8) could be represented by an **ecological response function** that illustrates the relationship between the attribute of interest and groundwater availability (Murray *et al.* 2003). However, ecological response functions of GDEs to these different elements of groundwater regime and quality are poorly known,

Figure 8.17 Open banksia *Banksia* woodland above the Gnangara groundwater system near Perth, WA. (Source: Andrew Boulton.)

Box 8.8 Declining groundwater levels and vegetation health on the Gnangara Mound

Management of groundwater-dependent vegetation (phreatophytes) relies on knowledge of their eco-hydrological habitats. One way to gain this knowledge is by assessing community change associated with altered hydrology. Change in the availability of groundwater because of extraction and drought can promote the development of alternative vegetation states, represented by a shift in community composition, structure and function (Froend and Sommer 2010). The Gnangara groundwater system on the Swan Coastal Plain, WA, supports phreatophytic vegetation already affected by a progressive decline in average annual rainfall and groundwater drawdown since the 1970s. Using a 30-year dataset of the response of phreatophytic plant communities to reduced water availability, we found that depth to water table and rate of drawdown are the dominant biophysical determinants of ecohydrological state (Sommer and Froend 2011). At sites with slower rates of groundwater drawdown (9 cm per year), there was a reduction in species density rather than species turnover in each plant community. In contrast, where rapid hydrological change occurred (50 cm per year), there was species turnover, with increased representation of facultative xerophytic (drought-tolerant) species and loss of drought-susceptible ones.

Ray Froend, Edith Cowan University

Box 8.9 Allocating water to maintain groundwater-dependent ecosystems

What is an environmental allocation for groundwater? In surface waters, setting environmental water allocations is underpinned by the concept of an ecological response function (e.g. a flow-fish spawning relationship). However, we know little about the timing, volume and quality of groundwater needed to support ecological processes and biodiversity in GDEs. Simple ecological response functions for GDEs relate groundwater levels or depth to water table with the occurrence of vegetation types or particular species. The next step is to consider other aspects of groundwater regime such as the patterns of surface water–groundwater connectivity, the magnitude and timing of groundwater discharge and recharge, and fluctuations in water level or pressure. Establishing ecological response functions for groundwater requires long-term data sets. Ecological responses may vary across a range of hydrological conditions, multiple and interacting components of the groundwater regime are likely to be ecologically relevant, and there are ecological and hydrological time lags between disturbance to the groundwater regime and ecological response. We need to coordinate monitoring nationally to generate adequate data to test hypotheses about ecological response functions among different GDE types and ecohydrological settings so that groundwater allocations in future water management plans can be refined to better protect GDEs.

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even though this is crucial information for their effective management and protection.

These ecological response functions are difficult to derive because GDEs rely on more than simply availability of groundwater. Water quality (especially salinity), timing and spatial location of groundwater supply, and fluctuations of water table (including waterlogging) are also likely to matter. For example, terrestrial vegetation GDEs in parts of south-western Australia may have adequate groundwater but, if the salinity is too high, the plants will die. Response functions are also probably controlled by various parameters such as the species composition, and the age structure, condition and physiology of the species in the ecosystem as well as the location and connectivity of the GDE in the landscape. Nonetheless, broad ecological response functions can be discerned in some cases. On the sandy soils above the Gnangara groundwater system described in Box 8.8, species of *Banksia* differ in their sensitivities to changes in groundwater depth. This has made them a useful indicator of impacts on the structure and function of this ecosystem in response to anticipated drawdowns of groundwater for human use (Groom *et al.* 2000) against a backdrop of increasing aridity as a result of climate change (Ali *et al.* 2012).

Identifying GDEs, especially facultative ones that depend on groundwater only in extreme drought, can be challenging and often reliant on integration of hydrogeological data, tracer studies of the incorporation into the ecosystem of materials from groundwater, GIS mapping and predicted response functions. The difficulty of linking groundwater regime and ecosystem requirements hinders effective management of sustainable volumes and timing of groundwater extraction. Currently, the states and territories in Australia use different methods and criteria in assessing GDEs and also make different allocations of water to maintain their health (Nevill *et al.* 2010). We urgently need to learn more about the groundwater requirements of most GDEs to improve this situation (Box 8.9) and to have a more effective approach for rapidly assessing the health of groundwaters (e.g. Korbel and Hose 2011) and managing them accordingly. One obvious example is the groundwater contribution of baseflow to rivers. Can we effectively manage environmental flows and govern surface water allocations without a good working knowledge of groundwater movements into and out of our rivers?

8.6 MANAGEMENT ISSUES IN AUSTRALIAN GROUNDWATERS

In the next four chapters of this book, we review management issues of water regime, physical structure, water quality and biodiversity in Australian aquatic ecosystems. Groundwater processes and groundwater-dependent ecosystems (GDEs) are an integral part of all these issues. In many cases, the management of surface waters influences associated groundwaters and *vice versa* because the systems are frequently connected hydrologically. For example, pumping water from a shallow aquifer such as the Gnangara groundwater system below Perth will affect the water regime in groundwater-fed wetlands overlying the aquifer (Section 9.4). At the same time, pollutants entering surface waters (Section 11.6) will enter groundwater recharge zones and contaminate the aquifers. Thus, effective management and conservation of aquatic ecosystems (Chapter 12) involve both surface and subsurface waters.

It is helpful at this point to summarize the major ways that human activities potentially threaten groundwaters and their dependent ecosystems in Australia (Table 8.1). Broadly speaking, these threats involve changes to the quantity, timing, flux and pressure of groundwater, its physical matrix and its water chemistry, either singly or in combination. In turn, these threats affect the natural physical, chemical and biological processes within the groundwater ecosystems and are likely to impair their microbial and stygofaunal biodiversity. One recurring theme in this book is that effective management seeks to address the causes of the problems rather than simply treating the symptoms. To do this, we need to understand the **mechanism** of the effect. In groundwaters, this is complicated by the substantial time that can elapse between a disturbance such as over-extraction and the ecological response (sometimes decades). Furthermore, with groundwaters being ‘out of sight’, we seldom notice the impacts until long after the event. For example, an algal bloom as a result of high nutrient concentrations in a surface lake will be evident long before we are aware of the impacts of nutrient-rich water on stygofauna in an underlying aquifer.

Rather than go through each issue covered in Table 8.1, we highlight several to provide examples from across Australia. In many parts of the country, water tables are falling because of a combination of groundwater and surface water extraction as well as changes in vegetation, often coupled with reduced rainfall and runoff associated with climate change (Ali *et al.* 2012). These declines in water tables are leading to caves drying out, threatening aquatic communities associated with root mats (Jasinska and Knott 2000) as well as the aesthetic appearance of some of the grandest tourist attractions such as the reflected images of stalactites in the limpid waters of Lake Cave (Figure 8.18).

Figure 8.18 Lake Cave in the Margaret River region of WA is an impressive tourist attraction with its spectacular reflections. However, natural groundwater recharge to the lake has declined due to a drying climate and possibly other anthropogenic stressors. (Source: Lindsay Hatcher.)

Immediate efforts to conserve the remnants of these threatened GDEs include gravity-feeding rainwater into drying caves and installation of retention basins. Longer-term management options involve revegetation of overlying recharge zones and tighter controls on groundwater and surface water extraction as well as vegetation management in the catchment (Box 8.10). Other threats to cave systems accessible to the public include graffiti, removal and damage of stalactites and other structures, trampling, sedimentation and even dumping of rubbish and pesticide drums. Efforts to control public access by building mesh gates across cave entrances risks also excluding bats and other fauna, potentially removing vital sources of organic matter to aquatic ecosystems within caves. The dominant threats to karst and other groundwater ecosystems are generally those operating at larger spatial and temporal scales, and include groundwater abstraction for water supply, effects of mining and mine dewatering, forestry and agriculture, industrial contaminants, limestone quarrying and climate change.

Another issue is management of groundwater extracted by industries such as mining and gas extraction. In areas where minerals are to be extracted, strict regulations control the amount of groundwater that can be removed and where it can be deposited. Often, this extracted water is saline or its chemical composition differs from surface waters and so it cannot simply

Table 8.1 Potential effects of human activities on groundwaters and groundwater-dependent ecosystems. The relative severity of these effects on groundwater regime (i.e. quantity, timing, flux and pressure of groundwater), physical matrix (i.e. aquifer structure and stability) and water quality are estimated as: x = mild or temporary; xx = moderate; xxx = severe or permanent.

Human activity	Groundwater regime	Physical matrix	Water quality
Direct extraction of groundwater, including rapidly removing large volumes and creating cones of depression or promoting marine intrusion	xxx	x	xx
Direct extraction of surface water, especially where surface waters are hydrologically connected to GDEs	xx	x	x
Modification of surface flow or runoff, especially into groundwater recharge zones or GDE groundwater sources	xx	x	x
Vegetation change, including clearing, planting trees in areas that were once grasslands, and introducing exotic vegetation (e.g. pine plantations)	xx	x	x
Poorly managed catchment clearance and timber harvesting in recharge zones, promoting sedimentation, altering nutrient dynamics, etc.	xx	xx	xx
Cropping and other intensive agricultural activities, including irrigation, nutrient enrichment, soil compaction and application of pesticides and herbicides in recharge areas or karstic systems	xx	xx	xx
Activities promoting salinization and acidification	x	x	xxx
Poorly managed tourism in 'wet' caves	x	xx	xx
Urbanization, including construction of underground fuel storage tanks, poorly managed land-fill, altered drainage and increased runoff of pollutants such as heavy metals	xx	x	xxx
Poorly managed groundwater 'aquifer-recharge' schemes, including aquifer water transfers, groundwater storages and disposal of contaminated water or treated water	xxx	x	xxx
Unconventional gas (e.g. coal seam gas) extraction, including depressurization of coal seams and adjacent aquifers, extraction and disposal of low-quality water, effects of hydraulic fracturing ('fracking') on aquifer connections and groundwater quality	xxx	xxx	xxx
Gravel extraction, mining (including pollution, acidification and dewatering of aquifers) and dredging, especially on floodplains, recharge areas and shallow alluvial aquifers	xxx	xxx	xxx

Box 8.10 Climate change and other stressors on cave stygofauna

Stygofauna in south-western WA are threatened by climatic drying, which has caused a progressive decline in groundwater levels and loss of aquatic cave habitat. In some cases, groundwater decline is hastened by additional stressors including pumping and increased evapotranspiration from tree plantations. In the Margaret River region, the altered groundwater regime has dried out lakes and streams in many caves including Jewel Cave and Lake Cave, both major tourist attractions once famous for their spectacular underground lake reflections. Between 2000 and 2010, the stygofauna community in Jewel Cave dwindled as the surface area of its groundwater shrank by 99% (Figure 8.13). Imminent extinction of this community was predicted if recovery actions were not immediately implemented (Eberhard and Davies 2011). In Lake Cave, the rate of groundwater decline was ameliorated by capturing winter rainfall and releasing it to trickle into the cave during the summer dry season. Meanwhile, water quality was monitored to ensure it was adequate for the stygofauna. Although not ideal, these measures seem to have forestalled extinction of the Lake Cave stygofauna but are probably too late for the stygofauna of Jewel Cave.

Stefan Eberhard, Subterranean Ecology Pty Ltd

be added to existing wetlands or streams. The remarkable biodiversity of many short-range endemic stygofauna in mineral-rich areas has sometimes led to frustration in the mining industry because of the delays caused by the time-consuming process of sampling, identification and environmental assessment.

Gas extraction poses similar management issues, especially the extraction of 'unconventional gas' that requires pumping (as distinct from conventional gas that seldom needs pumping). The most contentious of these is **coal seam gas**, an unconventional gas that is pumped out and chilled into liquefied natural gas. Associated with some of Australia's aquifers lie seams of coal, with the coal seam gas trapped in the pores of the coal along with huge volumes of groundwater. Wells are sunk down to the coal seam, and are cased with cement and steel to minimize mixing among overlying aquifers. To release the gas and water in the coal seam, a mixture of water and chemicals is sometimes pumped under high pressure into the seam in a process called hydraulic fracturing ('fracking'). A mixture of water and gas flows to the surface where the gas is extracted. The by-product, called 'co-produced water', is often very salty and may contain toxic chemicals from the fracking process as well as those naturally present in the coal seam.

Substantial amounts of this poor-quality co-produced water are predicted in Australia. Over 25–35 years from 2010, more than 300 GL per year of co-produced groundwater is expected from known reserves of coal seam gas (RPS 2011), compared to the approximate annual groundwater extraction of 540 GL per year from the Great Artesian Basin. Although this industry offers substantial economic benefits to Australia, there are likely significant risks to groundwater and nearby surface waters, both from the extraction process as well as the need to deal with huge volumes of co-produced water. Risks from the extraction step include cross-contamination of aquifers, disruption of the aquifer matrix by fracking and extraction, changes to groundwater pressure and flux in the mined aquifer and connected GDEs, and alteration of the quality of water remaining in the aquifer.

The large volumes of co-produced water pose their own problems. Most management options involve some form of water treatment prior to use or disposal. Although urban and industrial supply would seem ideal for water re-use, the variable yields and short supply period from individual wells and fields discourage major investment in pipeline infrastructure. Aquifer recharge is technically possible and affordable but, unless there is a good knowledge of the hydrological connectivity among adjacent aquifers, it risks contamination of good quality groundwater as well as likely severe impacts on ecological processes and biota in any receiving aquifers, especially shallow ones. Finally, discharge of large volumes of groundwater to surface waters is likely to cause problems by altering water regimes (Chapter 9) and water quality (Chapter 11).

8.7 ECOSYSTEM SERVICES AND CONSERVATION OF AUSTRALIAN GROUNDWATERS

Groundwaters perform four main **ecosystem services** (Table 8.2, Tomlinson and Boulton 2010). The most obvious service is provisioning. In Australia, groundwater comprises some 20% of total consumptive water use, and this percentage is likely to rise as available surface waters deteriorate in quality and volume. The second type of service is a supporting one, where biogeochemical processes (mainly involving microbial activity, Section 8.5.1) facilitate supporting services such as nutrient transformation and cycling, bioremediation, and organic matter dynamics. The aquifer matrix also harbours stygofauna and other biota, acting as a refuge from extreme conditions at the surface (Section 7.7). Groundwater pressure is also essential for supporting and maintaining the physical matrix of many aquifers; in some areas, excessive groundwater extraction has led to land subsidence, illustrating the importance of this supporting service. Hydrological connectivity allows aquifers to support associated GDEs with water and nutrients as well as the third service of regulating flooding or erosion by storing runoff. Finally, many groundwaters have great cultural significance. Indigenous traditions are often associated with GDEs such as rivers, mound springs and caves (Moggridge 2007), and most of these GDEs are also popular tourist attractions (Box 8.10).

Table 8.2 Main categories and some examples of ecosystem services provided by groundwater.

Type of service	Examples
Provisioning	Water for drinking, irrigation, stock and industrial use
Supporting	Nutrient cycling; denitrification; bioremediation; supporting linked ecosystems (GDEs); refugia for aquatic fauna from linked ecosystems; preventing land subsidence
Regulating	Mitigation of flooding and erosion by absorbing and storing runoff, buffering water levels in groundwater-fed wetlands and rivers (including baseflow)
Cultural	Indigenous spiritual values; scientific values; tourism to caves, mound springs and natural spa waters; recreational values such as kayaking and fishing in rivers that are largely fed by baseflow

In light of these ecosystem services and our increasing awareness of the vulnerability and biodiversity of many Australian groundwaters, their effective **conservation** is essential and urgent (Boulton 2009). For many decades, groundwater has been perceived as an infinite resource that can be used when surface water is scarce. Clearly, this is not true. In Australia, a lack of metering of licensed groundwater extraction in many areas, provision of free or under-priced groundwater, and a failure of many water resource management plans to adequately recognize the connectivity of groundwater with surface water all threaten current groundwater resources (Nevill *et al.* 2010). Furthermore, ecological conditions and threats to most Australian GDEs are incompletely understood or documented, and this lack of basic data severely hampers conservation efforts.

These problems are being partly addressed by the development of a national atlas of groundwater-dependent ecosystems (www.bom.gov.au/water/groundwater/gde/index.shtml) as well as management strategies as part of federal water reforms. Groundwater management priorities proposed at a national level include identifying connected surface-groundwater systems, assessing sites for managed aquifer recharge and recovery, determining vulnerability of GDEs to human activities and climate change, and developing conservation and management plans for major groundwater basins such as the Great Artesian Basin. Various government agencies have also released discussion papers and proposals for managing connected surface water and groundwater resources (e.g. in Tasmania: www.dpiw.tas.gov.au/inter.nsf/WebPages/JMUY-8U37ZR?open).

Policies and legislative protection are also being developed, especially in light of the rapid development of industries such as coal seam gas extraction. Although some policies at the state level have been successful in promoting knowledge, understanding and partial protection of some elements of groundwater ecosystems (e.g. stygofauna in WA, EPA 2007; several groundwater assemblages listed as Threatened Ecological Communities under the EPBC Act, www.environment.gov.au/cgi-bin/sprat/public/publiclookupcommunities.pl), current national groundwater legislation tends to be piecemeal, poorly coordinated and reactive. Sustainability of groundwaters needs to be assessed in all management plans, and Australian governments must develop appropriate compliance programs to achieve this. Worldwide, groundwater conservation still lags far behind that of surface waters. Given that surface and subsurface aquatic systems are often linked, such a lag in groundwater conservation potentially jeopardizes effective protection measures for many surface waters as well (Chapter 12).

8.8 SYNTHESIS

As we have seen, most groundwaters and surface waters are parts of the one resource – water. These two systems are linked although the linkages are often subtle, gradual, indirect and variable in time and space. Most groundwater ecosystems rely on provision of water, materials and energy from the surface. Quantity, timing, flux and pressure (groundwater regime) and quality of the groundwater are the results of complex interactions among climate, surface and aquifer geology and geomorphology, land use and vegetation. In turn, these dictate the composition and activity of groundwater microbial assemblages, many of which mediate key biogeochemical processes along environmental gradients at multiple spatial scales. Often, a diverse fauna with varying affinities for groundwater also occurs in the voids of aquifers as well as the considerable volume of the vadose zone. Many of the ecological roles of this fauna await discovery.

The availability and quality of groundwater govern the distribution and ecological condition of groundwater-dependent ecosystems across Australia. These GDEs are diverse, and many of them include surface waters that we have already discussed in this book (Chapters 2–7). However, the exact nature and degree of their dependency on groundwater availability and quality are seldom known, hampering efforts to protect and manage many of them. Again, there is much to learn about these systems and how their linkages with groundwater control their ecological processes. Furthermore, many of these GDEs, such as the SA mound springs fed by the Great Artesian Basin (Figure 8.19), have unique and often endemic invertebrate assemblages whose location-specific population structures and dispersal mechanisms must be understood to inform effective spring restoration and conservation (Box 8.11).

Box 8.11 The unique invertebrate fauna and conservation issues of South Australian mound springs

The mound springs fed by the Great Artesian Basin flow into the deserts west of Lake Eyre in SA. They provided a permanent water source for indigenous Australians and enabled early European development of pastoralism in this region. These aquatic 'islands' in the desert have also long fascinated biologists because the permanent isolated habitat allows a suite of endemic animals and plants to persist. Genetic studies reveal numerous cryptic invertebrate species and evolutionary lineages, including phreatoicid isopods and hydrobiid snails. Isolation of these springs apparently led to short-range endemism, and many species exist only in single springs. Some species evolved after being 'trapped' within these springs, but much of the diversity arose long before the formation of this habitat, when central Australia contained large permanent swamps and rivers. Mound springs are almost all that remains of this surface water. Habitat degradation threatens species with such limited distributions but although these springs are listed for legislative protection, few lie within conservation reserves. As the pressure for groundwater extraction increases in SA, competing interests threaten these springs and the evolutionary relics that inhabit them.

Nick Murphy, LaTrobe University

Figure 8.19 Oasis in the desert: collecting invertebrate samples from a SA mound spring yielded many endemic species including these unique isopod crustaceans (inset). (Source: Nick Murphy.)

Although often out of sight, groundwater is no longer out of mind. Aquatic ecologists now have a greater appreciation of the importance of groundwater for many surface ecosystems in terrestrial, marine and aquatic landscapes. The vertical component of connectivity in the hydrological cycle is no less a crucial linkage than lateral and longitudinal linkages when it comes to understanding and managing aquatic ecosystems. In the next four chapters, we see how these three vectors of hydrological connectivity are affected by human activities and the repercussions of these on water quality and aquatic biodiversity against a background of climate change and increasing population pressure in Australia.

PART II

MANAGEMENT OF AQUATIC ECOSYSTEMS

In Part I of this book, we reviewed the **physical**, **chemical** and **biological** processes that characterize standing and running waters and groundwaters (Chapter 2–8) in Australia. In particular, we saw how **water regime** (Chapter 1) largely controlled these processes, interacting with the physical structure of the water bodies and their catchments to influence water quality as well as the organisms in and around different aquatic ecosystems.

Human activities such as urbanization, farming, forestry and mining inevitably change water regimes, the physical structure of the basin, channel and catchment, and aspects of water quality, usually all at once. These changes may be **intentional** or **unintentional**. For example, an impoundment may be built across a river to intentionally alter the water regime to provide water for irrigation but, in doing so, unintentionally alters water quality downstream because the properties of the water released from the impoundment have been changed by its retention behind the wall. In the coming chapters, we will see that management of aquatic ecosystems involves having to weigh the benefits and costs of our actions and trade them off against the desired ecosystem services. To effectively manage aquatic ecosystems, we need to understand the associated hydrological and ecological processes and how they have been affected by one or more human activities. That way, we can seek to **remedy the causes rather than simply treat the symptoms**. At the same time, with wise planning, we can learn more about the ecological processes themselves and how they operate and interact at different scales in space and time.

Successful management of aquatic ecosystems is complex and must be underpinned by rigorous science. Many human activities occur together, creating **multiple stressors** that affect water regime, physical structure and water quality of surface and groundwaters. Furthermore, there are other issues such as the influence of invasive species and climate change that are superimposed on the effects of altered water regime, physical structure and water quality. Finally, social, economic and political components of management must also be considered when proposing viable solutions to problems caused by human activities.

Building on the process-based approach in Part I of this book, we have grouped the major management issues arising from human activities in Australia into issues associated with changes in **water regime** (Chapter 9), **physical structure** of the water bodies and their catchments (Chapter 10) and **water quality** (Chapter 11). We then explore, using examples, the causes or drivers of the major problems, the mechanisms by which they affect the ecology of surface and groundwaters, how the drivers potentially interact, and what solutions might be feasible in the short and long terms. Chapter 12 reviews **conservation** aspects and the effects of **invasive species**, paying particular attention to how management options are influenced by projections of **climate change** in northern and southern Australia (Chapter 12). The book concludes with a brief synthesis (Chapter 13) that reiterates the main themes and explores approaches to **strategic adaptive management**, explicitly integrating social, economic and political components in our ecological framework of the processes and management of aquatic ecosystems in Australia.

Australian Freshwater Ecology: Processes and Management, Second Edition. Andrew J. Boulton, Margaret A. Brock,
Belinda J. Robson, Darren S. Ryder, Jane M. Chambers, and Jenny A. Davis.

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CHAPTER 9

Management issues: water regime

9.1 'WHEN THE WELL IS DRY ...'

We have all heard the adage attributed to Benjamin Franklin: 'When the well is dry, we know the worth of water.' This simple line captures three key points: the importance of the amount of water available for our use, the relevance of water regime to its availability, and the fact that we usually appreciate neither of the first two until we face scarcity. The previous eight chapters have dealt with physical, chemical and biological processes in surface and groundwaters; it is now time to explore how humans have affected these processes and how we can manage and protect them before it is too late and the metaphorical well is dry.

The **water regime** and its components underpin almost every physical, chemical and biological process in all aquatic ecosystems. Recall from Section 1.4, the water regime referred to 'where, when and to what extent water is present', or putting it more formally: the spatial aspects of water extent and depth, volume, variability and, in lotic waters, discharge, and temporal ones of timing, frequency, duration and variability of the presence of water (Table 1.1). These components interact to produce the diversity of water regimes throughout Australia, and are altered by many human activities (Figure 9.1), with subsequent effects upon most physical, chemical and biological processes in aquatic ecosystems. These effects occur together as **multiple stressors** and, in turn, influence ecosystem components such geomorphology, water quality, biodiversity and ecological processes. The main point is that these effects typically interact and, quite often, the outcomes are unexpected and unpleasant. For example, the well may become saline before it goes dry!

This chapter explores how human activities in Australia have altered components of the water regime and, in many cases, continue to do so. Drawing on information from Chapters 1–8, the effects of these changes in water regime on ecological processes in lentic and lotic waters are reviewed, along with options for their effective management. We need to understand how ecological processes have been affected and changed so that we can address the causes of the problem rather than merely treat the symptoms. In most cases, there are multiple causes. For example, human changes to water regime seldom occur in isolation of other multiple stressors such as impaired water quality, changing climate and invasive species. This is why management of aquatic ecosystems is so complex. Not only are there social, economic and political dimensions to all water management issues (Chapter 13), the ecological interactions are often poorly understood and their outcomes are difficult to predict reliably. In most cases, human alterations to water regime are adversely affecting the native biota and ecological processes of inland waters (Figure 9.1), and that is why we start our exploration of management issues in Australian aquatic ecosystems with this fundamental driver.

9.2 CHANGES TO WATER REGIMES BY HUMANS IN AUSTRALIA: A BRIEF HISTORY

For thousands of years, Aboriginal Australians living in the driest regions modified inland waters to help ensure a reliable supply of drinking water (Smith

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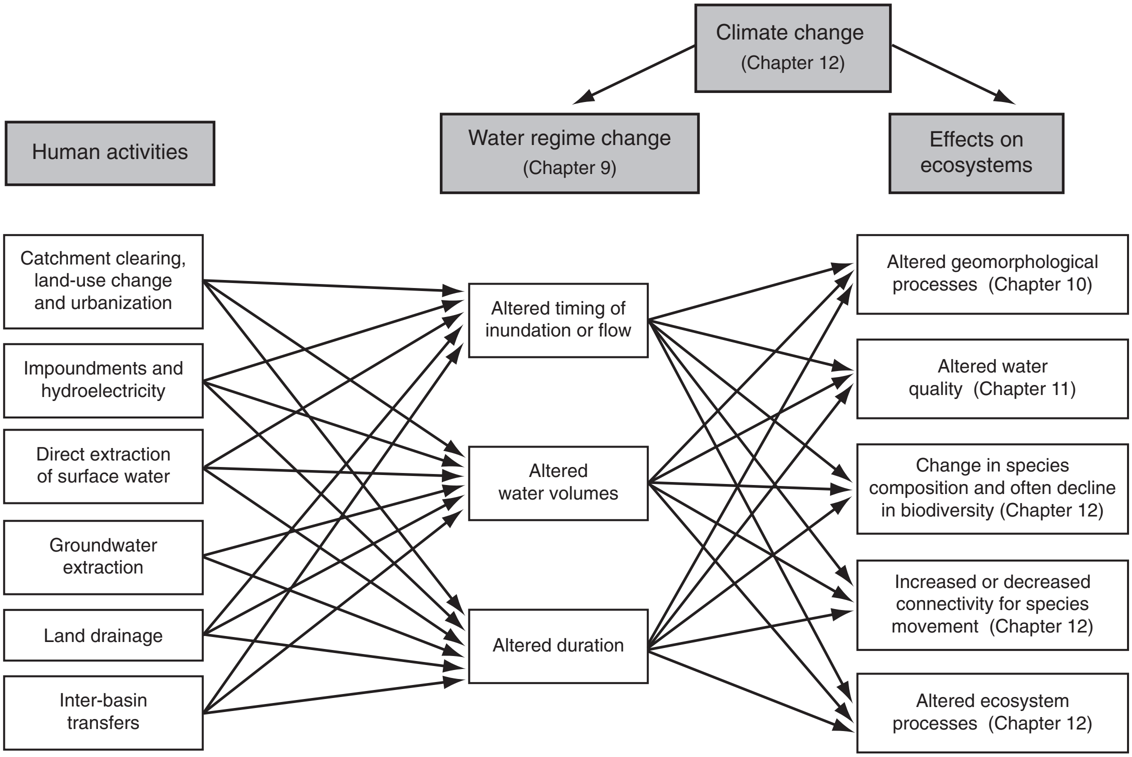

Figure 9.1 A web of interactions among some of the principal human activities that affect three key aspects of water regime and their likely effects on aquatic ecosystems (discussed further in Chapters 10–12).

1998). These modifications included scooping out sand in a seepage area until a large pool of clean water accumulated. On rock outcrops, water regimes of rockholes and gnammas would be altered by funnelling water into the depressions and covering deeper holes with stones to limit evaporation. A nomadic lifestyle meant that there was seldom sustained heavy pressure on individual water supplies. Consequently, these changes to water regimes were very modest and localized.

These modest changes did not continue after Europeans arrived and spread across much of Australia, usually accompanied by sheep and cattle. In most places, the new arrivals exploited and developed water supplies that had been previously used by Aboriginal Australians. Thousands of small and large dams were built for stock and domestic supply, affecting water regimes in headwater streams as well as larger rivers and their floodplains, wetlands and associated creeks. Wells were dug to obtain shallow groundwater. Deeper groundwater was accessed with bores and windmills, often altering the local groundwater regime and creating cones of depression during drawdown (Section 8.3.2). Shallow standing waters were drained to increase agricultural land (Brock *et al.* 1999) or were excavated to provide more permanent water. In other places, levee banks were built to divert floodwaters away from floodplains where crops were planted and towns were built. All these drainage and embankment schemes intentionally altered water regimes but there were unintended changes as well, often transferred far downstream or to the groundwater where recharge patterns had been affected.

Towns grew into cities, needing larger impoundments to provide reliable supplies of drinking water. Industries such as mining and power generation also needed water. Where water was scarce, channels and pipelines were constructed to carry it from wetter locations. For example, the 500-km pipeline from the

Perth hills to Kalgoorlie to supply water to the arid goldfields was completed in 1903, and changed the water regimes at both ends (Smith 1998). Mundaring Weir, the supplying impoundment, reduces flows and floods down the Helena River while the water diverted from along the pipeline has increased the number of permanent standing waters across much of the distribution network.

River flows were also harnessed for power. One example is the largest infrastructure project in Australian history, the Snowy Mountains Hydroelectric Scheme, which commenced in 1949 and took over 20 years to complete. It comprises 16 major impoundments, seven power stations and over 200 km of pipelines that divert water from rivers such as the coastward-flowing Snowy River inland to the Murray-Darling Basin to generate hydroelectricity and supply irrigation water (Ghassemi and White 2007). As a result, flows in the Snowy River were severely reduced, changing the volumes of flows in the receiving channel of the Murray. Almost all the rivers of the Murray-Darling Basin have now had their water regimes altered by impoundments, weirs, levees, channelized sections and direct extraction. Between the 1950s and 1980s, storage capacity steadily increased six-fold (Figure 9.2), enabling massive increases in irrigated agriculture.

However, dam-building activity across the Basin has slowed since the 1980s, probably as a result of increased public and political awareness of the environmental costs as well as fewer suitable unused dam locations. In some parts of the Basin, when it became clear that government investment in dams had ceased, there was increased construction of large on-farm storages (up to 500 000 ML) on floodplains to capture seasonal high flows for use in irrigated crops such as cotton.

Where impoundments are being built or enlarged, there may be efforts to minimize their ecological effects by altering their infrastructure. For example, the size of release valves may be increased to enable large releases of impounded water for environmental purposes, and locations of outlets in the wall can be raised to improve the quality of released water (Section 9.5.2). In other cases, impoundments may even be modified to enhance their potential role as refuges for threatened fishes (Box 9.1, Figure 9.3).

Since the 1990s, there has also been more focus on increasing access to groundwater resources for industry, agriculture and domestic supply. Most major Australian cities now experience water shortages, and in coastal cities, costly desalination plants are used to derive fresh water from seawater. Northern Australia is the only region where many waterbodies have so far

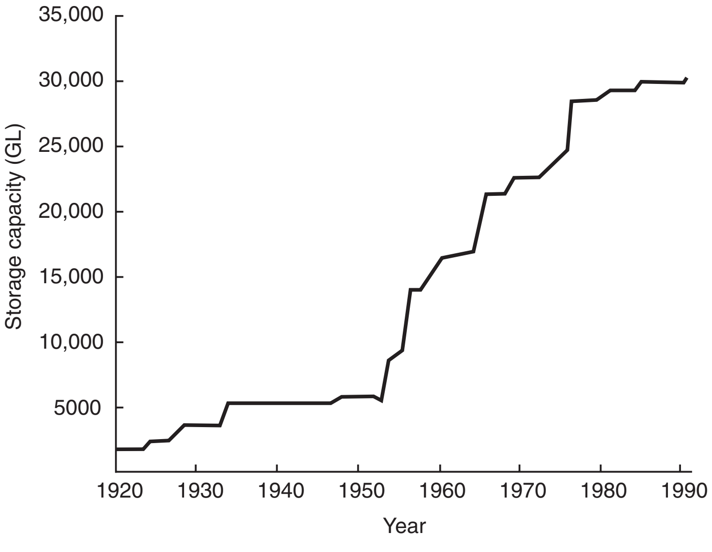

Figure 9.2 Growth in water storage capacity in the Murray-Darling Basin from 1920–1990. (Source: Redrawn with permission of the Murray-Darling Basin Authority.)

Box 9.1 Creating a Macquarie perch habitat on the enlarged Cotter Reservoir, ACT

As rivers become increasingly degraded, reservoirs may be significant refuges for populations of threatened fishes. Cotter Reservoir contains the only self-sustaining population of Macquarie perch *Macquaria australasica* in the ACT. Enlarging its storage capacity from 4 to 78 GL will increase the maximum depth 50 m, and the operational water regime will change from mostly stable to fluctuating. A band of emergent plants around the edge of the reservoir currently protects adult fishes from predatory birds but will be lost on filling, and is unlikely to re-establish because of the fluctuating water levels (Lintermans 2012). Consequently, three types of refuge habitat were trialled: pipe reefs, pipe reefs with a cormorant-exclusion grill and rock reefs. Using radiotelemetry for adult fish and underwater video for all size classes, Lintermans *et al.* (2010) showed Macquarie perch preferred rock reefs (Figure 9.3) with large interstices. Seven kilometres of rock reefs have now been built, constructed in horizontal bands at 5-m depth intervals across the modelled drawdown range to allow some reefs to remain inundated at any drawdown level. An ongoing monitoring program will measure the success of this habitat augmentation.

Mark Lintermans, University of Canberra

Figure 9.3 Rock-reef habitat created for Macquarie perch in the Cotter Reservoir, ACT, prior to enlargement and filling. (Source: Mark Lintermans.)

escaped development (Leigh and Sheldon 2008) but pressure is building from sectors such as large-scale mining and irrigated agriculture. Water shortages in rural areas have led to programs updating irrigation infrastructure to maximize the efficiency of water use. Each of these developments comes with its own environmental costs (e.g. groundwater extraction, Section 8.6), and we deal with some of these costs next. First, let's review the ecological importance of the water regime before exploring the effects of impoundments on water regimes and aquatic ecosystem processes.

9.2.1 Changing water regime, changing processes

Chapters 1–8 reviewed the central role played by water regime in virtually every physical, chemical and biological process in surface waters and groundwaters. Changes to natural variability in water extent, depth, volume and, in lotic environments, discharge, have direct effects on food supply, living space and dispersal of most aquatic plants and animals (Bunn and Arthington 2002). Similarly, alteration of natural patterns of timing, frequency and duration of the presence of surface water and groundwater directly influences almost all ecological processes in aquatic ecosystems, either directly or through multiple interacting effects on the physical and chemical environment.

For example, in rivers, reduced volumes of discharge usually change channel form (Section 10.2.2) and geomorphological processes such as floodplain formation. River regulation and water extraction may lead to the drying of once permanent streams and rivers (e.g. Mackie *et al.* 2013) or cause water quality to deteriorate (e.g. Lind *et al.* 2007). Rivers used to carry irrigation water often have their natural seasonal flow regime almost reversed because water is transported down the channel during times when flow would usually be low or absent. Other changes to flow regime, especially in impounded rivers, include reductions in annual and inter-annual variability. These hydrological changes are associated with changes in fundamental ecological processes such as primary and secondary production (e.g. Burford *et al.* 2008, Robson *et al.* 2008a).

Human activities that remove flood peaks (Section 9.3) limit floodplain inundation in lowland rivers. Floodplains are highly productive environments where many riverine species feed and reproduce (Chapter 7) but this productivity is underpinned by connectivity to the river (Bunn *et al.* 2006). In some lowland rivers of southern Australia, changes to water regimes have prevented some floodplain wetlands from being inundated by river water for decades. Without riverine flushing, the water quality of these wetlands declines over time, affecting species diversity. In other places, irrigation flows may inundate parts of the floodplain but the duration of flooding is shorter. This may cause the floodplain to dry out before species of fishes, waterbirds and aquatic plants can reproduce, leading to high mortality or reduced recruitment (Figure 9.1).

Changes to the water regime of lentic environments may be caused by urbanization. For example, temporary waters may become permanently inundated, changing the composition of communities of native plants and animals (e.g. Davis and Froend 1999). In urban and rural areas, standing waters are often drained to obtain productive land. Paved surfaces and cleared catchments alter runoff to surface waters and groundwaters, changing water regimes and infiltration processes. Prolonged groundwater extraction has extinguished some groundwater-dependent wetlands, and in coastal areas, sometimes led to the intrusion of seawater into local aquifers (Section 8.6). Elsewhere, rising groundwater levels owing to irrigation and clearance of deep-rooted vegetation is causing widespread waterlogging and salinization (Figure 9.1; Section 11.4).

These are just a few of the anthropogenic changes in water regime of surface waters and groundwaters that affect physical, chemical and biological processes in aquatic ecosystems. These changes arise from one or more activities, including the construction of impoundments, direct extraction of surface water and groundwater, transfers of water among waterbodies, alterations to catchment vegetation and land use (including urbanization) and changes to channel or basin shape (Figure 9.1). Most of these changes occur together and their effects interact, usually with diverse ecological outcomes.

9.3 DIVERSE IMPOUNDMENTS WITH DIVERSE EFFECTS

Impoundments range from small farm dams on temporary headwater streams to large impoundments across permanent rivers that retain water used for urban and irrigation uses as well as hydroelectricity generation (Figure 9.4). In addition to changing the water regime, impoundments across channels also influence the **sediment regime**, the size, nature and transport of sediments downstream. In running waters, changes to the sediment regime affect physical processes in the channel and its floodplain (Section 5.7), with implications for chemical and biological processes associated with sediment and nutrient storage and transport (Chapters 6 and 7). Chapter 10 reviews the effects of changes to the natural sediment regime in lotic (and lentic) environments, emphasizing the management significance of these linkages between water regime and sedimentation.

As we saw in Section 5.5, the hydrograph of a river tells us a lot about its catchment run-off and the variability of river discharge in response to climatic conditions and groundwater contributions. The terms *rising limb*, *crest* and *falling limb* were introduced in Section 5.5, and it is now time to look at some of the other features of the hydrograph that comprise a river's flow regime, including the flood pulse. This allows us to better describe how impoundments alter specific **flow components**, especially changes in their size, timing, variability and duration.

Many running waters in Australia cease flow at some time, and the timing, variability and **duration of zero flow** (Figure 9.5, sometimes called 'cease-to-flow') periods have major implications for many physical, chemical and biological processes (Boulton *et al.* 2000, Table 9.1). The timing, variability and duration of floods are also ecologically significant (Chapter 7). The **interval since the last flood peak** can govern successful reproduction and recruitment by many aquatic organisms (Table 9.1), and alteration of this by impoundments may cause local extinction of some species. Obviously, the size of the flood governs how far it will spread across the floodplain and the sediment dynamics of the process. However, the **slopes and amplitudes of the rising and falling limbs** are also ecologically important and these, too, are affected by impoundments as well as water diversion and extraction during the flood. Further details of the association of flow components with ecological processes described

Figure 9.4 Diverse impoundments: (a) small farm dam on a headwater stream, (b) small weir, (c) large weir on the Gwydir River, NSW, (d) Bendora Dam on the Cotter River, ACT, (e) hydroelectricity generation outlet on the Hume Dam, NSW. (Source: (a) Ty Matthews; (b) Belinda Robson; (c), (d) and (e) Darren Ryder.)

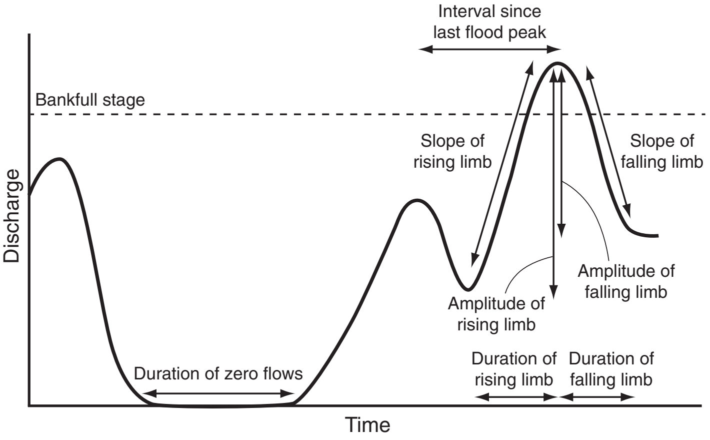

Figure 9.5 Hypothetical hydrograph of some flow components of a floodplain river. When water exceeds bankfull stage (dashed line), the floodplain is inundated. Aspects of the ecological significance of these flow components are given in Table 9.1. (Source: Walker *et al.* 1995. Modified and redrawn with permission from John Wiley & Sons.)

Table 9.1 Ecological significance of the flow components shown in Figure 9.5, and consequences of changes to them by impoundments and other human activities. (Source: Boulton and Brock 1999.)

Flow components	Ecological significance of flow components and the consequences of changes to them
Duration of zero flow	Duration of zero flow (= cease-to-flow duration) affects water quality and persistence of aquatic biota in remaining pools, and influences establishment of terrestrial floodplain vegetation. Extended duration typically eradicates or reduces densities of aquatic species intolerant of drying. Viability of seeds and resting eggs of aquatic organisms declines over time. Changing the cease-to-flow duration alters the extent of isolation and drying of channel and floodplain wetlands and the composition of aquatic biota when flow resumes.
Interval since last flood peak	The interval since the last flood peak affects drying regimes of floodplain waterbodies and the establishment of most floodplain plants. Changes from natural patterns affect recruitment of biota with seasonal life-cycles (e.g. some native fishes). Longer intervals promote sediment drying and cracking, affecting floodplain saturation and sometimes causing banks to slump on re-wetting (leading to major sedimentation, Section 10.3). Longer intervals may also increase the likelihood of blackwater events when flows increase. The capacity of populations to respond to flooding (resilience) may decline.
Amplitude of the rising flood limb	The amplitude of the rising flood limb is related to pre-flood river level and size of flood. Big floods may facilitate breeding and recruitment of many river and floodplain species, and inundate large areas of floodplain, hydrologically reconnecting the mosaic of floodplain waterbodies. Changes to this amplitude affect the extent of nutrient release from floodplain sediments and the success of hatching of eggs or resting stages of aquatic animals and germination and growth of some floodplain plants.
Amplitude of the falling flood limb	The amplitude of the falling flood limb affects the degree of isolation of floodplain wetlands from the main channel. It influences fish recruitment (with cascading effects on invertebrates and waterbirds) and germination and growth of some floodplain plants. Changes to this amplitude typically alter the extent of inundation of littoral and floodplain habitat, and the immersion of sessile and sedentary biota.
Durations of rising and falling limbs	Durations of the rising and falling limbs of the flood pulse together influence inundation time of the floodplain (i.e. duration of period above the dashed line in Figure 9.5). Consequently, they affect the time for recolonization of floodplain waterbodies, growth of fishes, invertebrates and plants on the floodplain, changes in water quality, dissolved oxygen and temperature, and successional changes in the biota responding to flooding. Changing these durations alters the persistence and composition of floodplain assemblages.
Slopes of rising and falling limbs	Rates of change (slopes) of the rising and falling limbs of the flood pulse affect the responses by different groups of species to flooding. For example, steeply rising limbs may flush out lentic biota, whereas steeply falling limbs during drawdown may strand slow-moving animals, including juvenile fishes. Changes to these slopes affect survival and recruitment of many aquatic species, rates of erosion and deposition of sediments, and the speed of changes in water quality during flushing and drawdown in the main channel and floodplain waterbodies.

in Table 9.1 and their potential use in environmental watering (Section 9.5) are reviewed by Watts *et al.* (2009), Robson *et al.* (2009), Rogers and Ralph (2010) and Arthington (2012).

There are two key points to take from this consideration of flow components and the ecological consequences of changing them. The first is that all the components **interact** with each other. Changing one will influence many of the others, which means that we can seldom manipulate individual components of a flow regime independently (Section 9.5). Therefore, we seek to protect the components and their interactions because we recognize their ecological significance – where possible, water should be diverted with minimal ecological impact.

The second point relates to our theme of the importance of **variability**. Most impoundments reduce annual and inter-annual variability in nearly all of these flow components, and some impoundments (e.g. for hydropower and irrigation) increase the variability at finer time-scales such as days. There may be a complete seasonal reversal of the natural flow regime (Section 9.4.1) where steady and consistent flows are released for irrigation at a time of year when the channel would be naturally dry or experiencing variable flows. Then, when large floods would usually extend down the channel and replenish the floodplain, they are held back by the impoundment for release later in the year. For example, Lake Hume, an irrigation reservoir on the Murray River, is used to hold back peak natural flows in winter and spring for release in summer and autumn during the irrigation season. The flow regime below Hume Dam has undergone a seasonal flow reversal.

In the different types of rivers in tropical northern Australia, natural patterns of variability in water regime components such as wet-dry seasonality and the permanence and regularity of flow govern ecological processes and ecosystem function (Leigh and Sheldon 2009). Human activities that change water regimes by altering this natural variability have serious negative effects on the water quality and aquatic life in these types of rivers. Seasonal cycles of hydrological linkages and disconnections to floodplain waterbodies and shallow groundwater are also likely to be affected (Leigh and Sheldon 2009).

Rapid short-term fluctuations in water levels downstream from impoundments used for producing hydroelectric power pose a particular problem for the biota and ecological processes. During periods of power generation, especially where demands peak at different times of the day, volumes of discharge can fluctuate daily or even hourly (Watts *et al.* 2011). This repeatedly wets and dries sections of the riverbed frequently, potentially stranding and desiccating benthic biota. Over longer periods, biofilm composition may shift from a diverse assemblage of species towards one dominated by cyanobacteria (Ryder *et al.* 2006) that can tolerate repeated drying. Changes in rates (slopes) of the rise and fall also affect sedimentation processes, water quality and recruitment by some species (Table 9.1). Sometimes, where there is a sequence of hydropower impoundments along a river system, they may be managed collectively to try to replicate features of the natural flow regime while still meeting the fluctuating demands for irrigation or hydroelectricity generation (Watts *et al.* 2011). Alternatively, small 're-regulation dams' can be used to store water downstream of the hydropower impoundment and release it in more constant volumes (Watts *et al.* 2011). Although this may partly address the water regime issue, there remains the problem of a barrier across the channel, impeding not only water but also sediment and biota.

9.3.1 Impoundments as ecological barriers

Impoundments act as barriers to the ecological needs of plants and animals that depend on hydrological connectivity (e.g. for movement, dispersal, food supply). In Australia, impoundments have been associated with lower native fish diversity and abundance, and led to contractions in the geographic range of many species (Gehrke and Harris 2001). One of the most common situations occurring in nearly all impounded rivers throughout Australia is the unnaturally large aggregations of fishes downstream of dam walls, increasing their vulnerability to predation by birds and other carnivores (Morgan and Beatty 2006). Downstream passage of fishes over or through weirs often causes significant mortality or injury (Baumgartner *et al.* 2006, Lintermans 2013). Impoundment walls limit access to fish spawning and nursery habitat or to refuges from floods and drought. They can also result in isolation of populations and loss of genetic diversity, limiting population viability. In Australia, the proliferation of impoundments and other river barriers has been implicated in the decline of several native fish species, including Macquarie perch and golden perch (Beatty *et al.* 2013).

Although attention tends to focus on the effects on fishes, other biota are also affected. For example, freshwater mussels have larvae (glochidia) that are parasitic on fishes. Impoundments may exclude the fish hosts for larval development and dispersal, so that recruitment falters, the population becomes dominated by older individuals and eventually may go locally extinct (e.g. Walker *et al*. 2001). The significance of these kinds of impacts on river fauna is reflected in the recognition of instream barriers as a 'Key Threatening Process' under legislation (Section 12.1.1) in New South Wales and Victoria.

Ecological effects of impoundments extend upstream as well as downstream. Usually, the change from flowing to standing water upstream of the barrier alters the species of fishes and invertebrates that are found there. For example, the benthic fauna within and immediately upstream of the impoundment may become dominated by oligochaete worms and chironomid midge larvae that prefer soft sediments to hard substrata. Consequently, the biota no longer resembles that of the unimpounded river – a result of the shift from a lotic to a lentic system.

In some of Australia's larger rivers, impoundments occur along many hundreds of kilometres of the river's course. This creates a sequence of alternating lentic and lotic conditions down the river, substantially changing its ecology (Box 9.2). In the Murray River, for example, several once-common riverine species that played key roles in the ecosystem have become rare, often being replaced by their floodplain counterparts that are better adapted to lentic conditions. For example, the habitat of the river mussel *Alathyria jacksoni* has declined and the floodplain species *Velesunio ambiguus* has proliferated in the weir pools. Another example is the Murray River crayfish *Euastacus armatus* that has virtually disappeared from the lower Murray below the Darling River confluence (Zukowski *et al*. 2012) whereas the yabbie *Cherax destructor* has become common in weir pools (Figure 9.6).

9.3.2 Impoundments and estuaries

Water regimes and discharge of exorheic rivers largely govern hydrological and ecological processes of their estuaries (Section 1.5.4). Impounding and extracting river water upstream removes the supply of water and nutrients to highly productive coastal estuaries. Altered water regimes and inadequate flushing by freshwater flows can result in sedimentation and nutrient enrichment (Section 11.3), causing toxic algal blooms and fish kills. Most Australians live near the coast, and estuaries are a focus for urban development, fishing and recreation. Maintaining the water regimes of the rivers supplying these estuaries is essential to sustain their ecosystem services. However, all too often, the very impoundments that supply urban development also harm its estuarine support systems, depriving them of fresh water, nutrients, sediments and biota.

During the 'Millennium Drought' (1997–2010) in south-eastern Australia, some of the impacts of large impoundments on the estuaries became especially evident (Bond *et al.* 2008, Kingsford *et al.* 2011a).

Box 9.2 Ecological effects of weir pools in the Murray River

Rivers are a conduit for water, of course, but they also transport sediment, salt and nutrients, and they are a corridor for dispersal of animals and plants. It is not difficult then to imagine the effects of a barrier across the channel. Even a small weir impedes the passage of water, as intended, but it also blocks the transport of materials and the movements of organisms. You might suppose that the effects of one weir could scarcely rival those of a big dam, but what if there are weirs in series, so closely spaced that the pool behind one nearly overlaps its neighbour? Along the Murray below the Darling confluence, there are 10 3-m high weirs along 830 km of channel, and their effects are compounded by river-mouth barrages and floodplain levees (Walker 2006). The river is robbed of its power to transport material that now must accumulate. Meanwhile, deposition and erosion above and below each weir are reforming the channel as a long staircase with 3-m risers. The weir-pool margins have been colonized by wetland species, displacing their riverine counterparts. River and floodplain are transformed.

Keith Walker, University of Adelaide

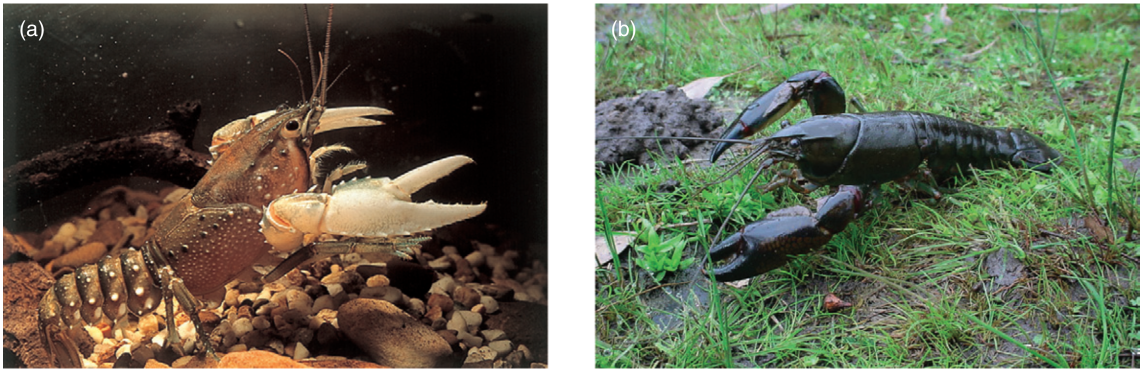

Figure 9.6 Species differ in their responses to river impoundment. Densities of Murray River crayfish *Euastacus armatus* (a) have declined whereas those of the yabbie *Cherax destructor* (b) have increased in weir pools of the Murray River. (Source: (a) Gooderham and Tsyrlin 2002. Reproduced with permission of John Gooderham and Eddie Tsyrlin; (b) Kerrylyn Johnston.)

Coupled with water diversions for irrigation, the drought prolonged periods of low discharge, curtailing freshwater flows into estuaries, including many sandbar estuaries. These are estuaries where a bar of sand forms across the river mouth each year during natural low flows. When discharge increases, the bar is breached and connectivity is re-established between the river and nearshore environment, renewing water quality and allowing many diadromous fish species such as the common galaxias (Figure 9.7) to complete their life-cycle. During the drought, many sandbar estuaries remained closed to the sea all year. Water quality deteriorated and the estuaries became increasingly saline, sometimes saltier than seawater (hypersaline) through evaporative concentration of salt. One of the most severe cases was at the mouth of the Murray River where the Coorong and Lower Lakes, a National Park and Ramsar-listed site, steadily grew hypersaline, productive fisheries all but collapsed, and there were serious impacts on aquatic plants, invertebrates, waterbirds, fishes and turtles (Kingsford *et al.* 2011a).

9.4 ECOLOGICAL EFFECTS OF WATER EXTRACTION

Obviously, water regimes can be greatly affected by direct extraction of water. The ecological effects depend

Figure 9.7 The common galaxias *Galaxias maculatus* is a native diadromous fish that relies on the annual cycle of river flows and estuary closure in sandbar estuaries. The fish spends most of its life in freshwater rivers but migrates downstream to estuaries during autumn to spawn. It arrives when the sandbar blocks the estuary mouth and water levels are high, and lays its eggs on inundated vegetation in the wetlands and margins of the estuary. Winter rains increase river discharge, the sandbar is breached and fresh water flows out to sea. At this time, the eggs hatch and the larvae are carried out to sea. In the nearshore environment, the larvae develop into juveniles that then migrate upstream through the open estuary mouth in spring to mature as adults in the freshwater river (Barbee *et al.* 2011). (Source: John Gooderham and Scott Hardie.)

on the volume, timing and rate of extraction. In standing and running waters, extraction can turn perennial systems into temporary ones. Organisms that rely on permanent water disappear and the fluctuations of water around the shoreline can slow growth and prevent recruitment of littoral species such as some plants. In temporary streams, the duration of cease-to-flow periods can be prolonged and the rate of drying accelerated because peak extraction for irrigating crops usually coincides with drier weather.

Where surface and groundwaters are connected, water extraction from the surface can reduce recharge to the groundwater and alter its flux and pressure. Conversely, groundwater extraction lowers the groundwater table for an area around the extraction point ('cone of depression', Section 8.3.2), affecting nearby connected surface waters. Lowering the groundwater table may change a stream from a gaining to a losing one (Figure 5.9). When the groundwater table is reduced for long enough, the stream may change from flowing perennially to flowing only when supplied by rainfall and runoff. This has dramatic effects on the biota and predominant ecosystem processes (Chapter 7). The loss of permanent streams in drier regions owing to direct extraction of groundwater may also remove major sources of dispersing invertebrates, having a disproportionately large effect on catchment biodiversity (Chester and Robson 2011).

Water extraction can affect the entire food web. For example, water extracted from streams in the Grampians National Park, Victoria, is used to supply several towns. Once permanent, these modified streams now flow seasonally and have longer dry periods than nearby unmodified temporary streams. The change to the flow regimes of these streams has altered algal growth rates and species composition. Cyanobacteria able to withstand prolonged drying now dominate the benthic biofilms in the modified streams. These cyanobacteria are unpalatable to grazers, affecting the rest of the food web (Robson *et al.* 2008a).

There are also effects of direct extraction on water chemistry. Reducing water volume often increases the concentrations of dissolved substances and reduces the pH, and these changes in water quality have ecological consequences (Chapter 11). For example, declining water quality in dwindling pools of temporary waters may eliminate all but the most tolerant aquatic plants and animals (Section 4.7). Sometimes, there is an interaction between deteriorating water quality and the shrinking aquatic habitat caused by water extraction. In western Victoria, the Glenelg and Wimmera Rivers both have impoundments in their headwaters for rural and urban water supply, reducing flows downstream. Saline groundwater intrudes through the riverbed into deep pools in the lowland sections of both rivers leading to salinity stratification (Coates and Mondon 2009). At low flows, runs and pools shrink, reducing habitat area. The upper layer of fresh water flowing over the saline pools also becomes thinner, reducing the only habitat available for most freshwater organisms because the deeper water is too salty and hypoxic. When low flows were compounded by water extraction, freshwater invertebrate densities escalated as animals crowded into the last remaining habitat. Further downstream in the Wimmera River, diversity declined because pools became saline (Lind *et al.* 2006).

Many standing waters are surface expressions of the groundwater table for at least part of the year (Figure 8.8). When the groundwater table is lowered, these surface waters are inundated less often and for a shorter time. Water levels of many wetlands of the Swan Coastal Plain, WA, fluctuate in response to fluctuations in groundwater level driven by seasonal rainfall. Historically, there was a natural mosaic of inundation patterns, with some wetlands being permanent and others seasonally filled for different periods depending on basin location and shape (Figure 9.8). Groundwater pumping now occurs year-round (Horwitz *et al.* 2009), lowering the water table to an extent equal to or greater than the original annual fluctuations. Since the 1970s, annual rainfall in south-western WA has declined steadily as a result of climate change (Section 12.9). This reduced rainfall coupled with sustained groundwater pumping has lowered groundwater tables across the entire region (CSIRO 2009), decreasing water depths and increasing periods of drying in many Swan Coastal Plain groundwater-fed wetlands (Figure 9.8). Separating the impacts of this alteration of water regime on the biota from the effects of urbanization and eutrophication (Section 11.3) is difficult (Davis *et al.* 2010), further complicated because many Swan Coastal Plain wetlands are now filled by stormwater and other urban drainage rather than groundwater inputs (Figure 9.8). Given the predicted climate change scenarios for the region, this change to their water regimes is likely to be permanent, and will require different management strategies to protect and sustain the biodiversity of native aquatic biota.

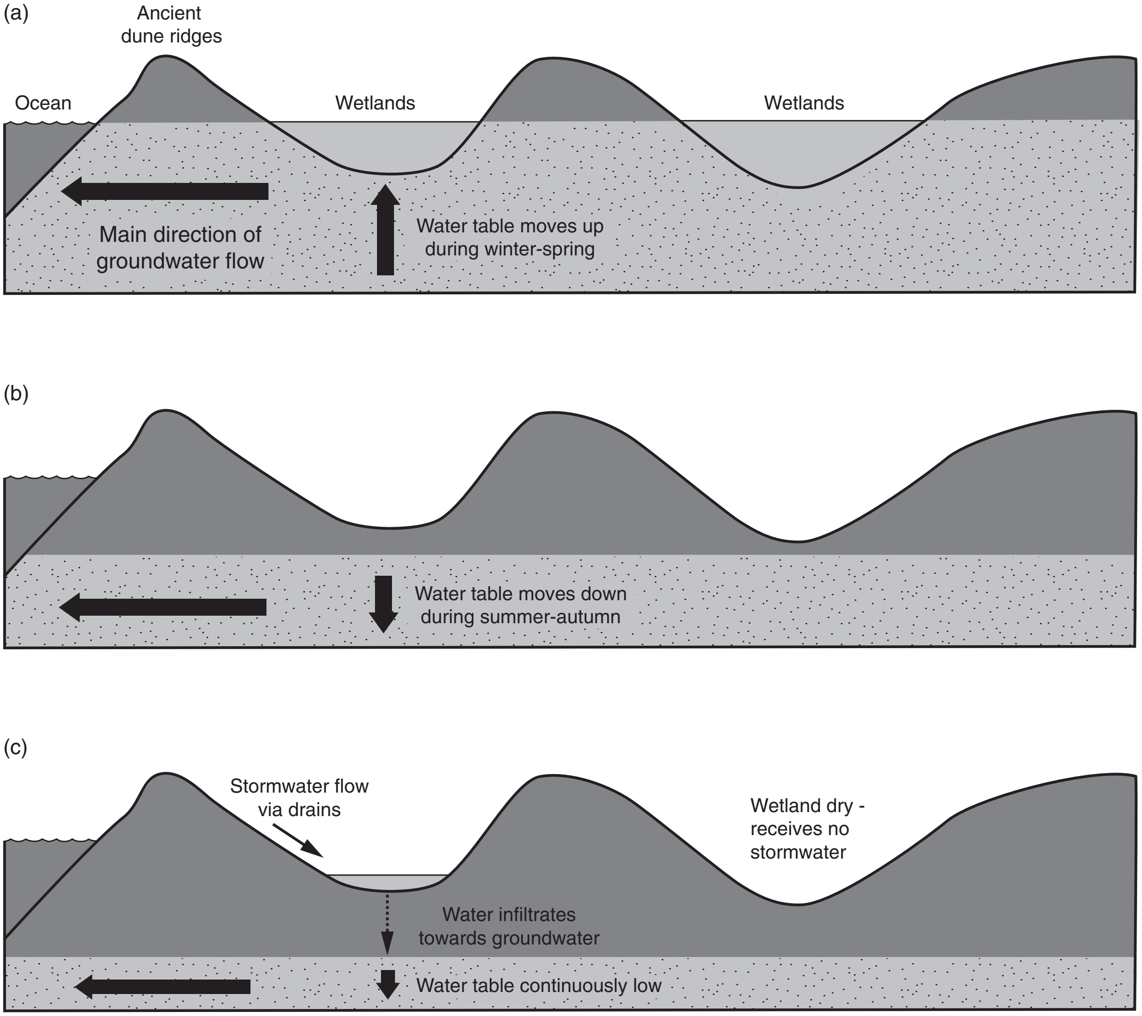

Figure 9.8 Cross-sectional diagram of the changes in groundwater surface expression on the Swan Coastal Plain. Groundwater, stippled, moves vertically and horizontally through permeable sand beds. (a) During the wet winter-spring, recharge from rainfall raises the groundwater table, filling the wetlands lying between ancient dune ridges. (b) During the hot, dry summer-autumn, groundwater levels decline and the wetlands dry. (c) The current situation is that in some areas, groundwater levels are now permanently lowered, and wetlands fill only when they receive surface inputs such as stormwater.

9.4.1 Ecological effects of drainage and irrigation

Another form of water regime change is the drainage of land for agriculture, industry or settlement. Drainage water is usually discharged into nearby rivers or lakes, altering the water regimes of recipient waters as well as the drained areas. Thousands of kilometres of drainage ditches have been constructed all over the world to drain urban and agricultural land. In some heavily modified landscapes, such as parts of the Netherlands, drainage ditches now harbour most of the remnant freshwater biodiversity (Vermonden *et al.* 2009). Less is known about the biodiversity of drainage ditches in Australia, although some are significant refuges for waterbirds (Paton 2010) or assist movements of frogs (e.g. Wassens *et al.* 2008) and other freshwater species (including invasive ones, Section 12.8) across modified landscapes.

Drainage for urbanization and agriculture has removed natural waterbodies from many parts of Australia. For example, more than 70% of the natural wetlands across the Swan Coastal Plain of Western Australia (Davis *et al.* 2001), the New England Tablelands of New South Wales (Brock *et al.* 1999) and much of western Victoria (Robson and Clay 2005) have been drained. Most drainage schemes destroy shallow standing waters across the landscape, affecting patterns of groundwater recharge and reducing the natural variability of surface water regimes. Under natural conditions, these waterbodies usually support species-rich plant and animal communities, and their loss severely reduces regional biodiversity. Amphibious habitats and their biota are particularly vulnerable to water regime change (Chapter 4). Finally, removal of such a large percentage of natural wetlands by drainage has likely interrupted broad-scale processes such as the movement of waterbirds across the landscape, impairing associated aquatic-terrestrial subsidies (Section 4.6.5).

Land that has been drained is often levelled and used for irrigated agriculture. Irrigation requires water to be moved around the landscape, again altering the water regimes of receiving waters as well as the irrigated areas. Often, high flows are stored and then released on demand during the dry season, reversing the natural water regime (Section 9.2.1). Furthermore, when this irrigation water has been released from deep in a thermally stratified reservoir, it is often colder than would be usual in the dry season (thermal pollution, Section 11.6.2). This combination of unseasonal high flows and cooler water temperatures adversely affects the life-cycles and reproduction of many native plants and animals in river sections that previously experienced natural low summer flows and warm water (reviewed in Olden and Naiman 2010).

Earthen irrigation infrastructure such as open channels and ditches inevitably change local water regimes of both surface and groundwaters, especially where seepage is substantial. Seepage and other releases of irrigation water can cause waterlogging in agricultural soils, often introducing salt, fine sediments and pesticides into surface waters as well as affecting the water quality of shallow groundwater (Section 8.6). All these changes to the water regime are usually accompanied by other stressors such as altered water chemistry and water temperature, and we expand on these issues in Chapter 11.

9.4.2 Ecological effects of inter-basin transfers

Inter-basin transfers involve moving water from one river basin to another, usually by modifying existing river channels to divert their courses or by transferring the water in pipes or open channels (Ghassemi and White 2007). Occasionally, this term is also used for transfers among tributary catchments within a basin. In Australia, the persistent plea to 'turn the rivers inland' seeks inter-basin transfers from coastal rivers east of the Great Dividing Range to the semi-arid plains inland, but reveals a lack of awareness of the threats of such schemes to the native biota and ecology of coastal and inland ecosystems. One unusual example of an inter-basin transfer is that of the Glenelg and Wimmera Rivers in western Victoria (Figure 9.9). The Glenelg River flows south to the coast whereas the Wimmera River is part of the Murray-Darling Basin and flows north. Both rivers have large reservoirs in their headwaters, but the Wimmera River also receives 'environmental water' (defined in Section 9.5) from the Rocklands Reservoir on the Glenelg River (Lind *et al.* 2007). Depriving one river of water to provide environmental water for another river in a different catchment is contentious, and exemplifies the 'trade-offs' between environmental and exploitative needs faced by water resource managers.

Figure 9.9 The Wimmera River, western Victoria, receives environmental water from the Glenelg River via an inter-basin transfer. (Source: Peter Lind (GHD).)

Like irrigation channels, inter-basin transfers increase hydrological connectivity for many aquatic organisms. However, the transfers typically connect different catchments that have either never shared hydrological connections or have not done so since the basins were isolated by past geological events. Populations of native species that may have been isolated for millennia may mingle and interbreed. Invasive species, especially fishes, frequently invade new catchments via inter-basin transfers. For example, the Glenelg River did not contain common carp (Chapter 12) before 2001 when they were found in Rocklands Reservoir and then in the river downstream. Although the species may have been deliberately introduced to Rocklands Reservoir by anglers, it likely entered from the Wimmera River via the inter-basin transfer. Special screens are now used to prevent more adults (but not their larvae or eggs) entering the lower Glenelg River.

Inter-basin transfers also change the water chemistry of receiving rivers, with implications for their aquatic ecology. For example, if dissolved nutrients are originally present or are imported into a system at the same time that turbidity declines because of the influx of fresh clear water, algal blooms may occur. There may also be changes in salinity, dissolved gases and concentrations of toxicants such as herbicides and pesticides (Section 11.6). The decision to transfer water among basins should not be taken lightly, especially as ecological effects on the receiving waters are seldom reversible.

9.4.3 Ecological effects of urbanization

Over 85% of Australia's population now lives in urban areas. Not surprisingly, water regimes of standing and running waters in these areas are highly modified, often intentionally to prevent flooding of infrastructure. Flashy hydrographs (Section 5.5) typify urban streams as a result of the vast areas of impervious surfaces (e.g. roads, car parks), drained by engineered structures to remove stormwater runoff as rapidly as possible (Figure 9.10, Box 12.2). Baseflow levels may be so reduced that the stream does not flow for weeks

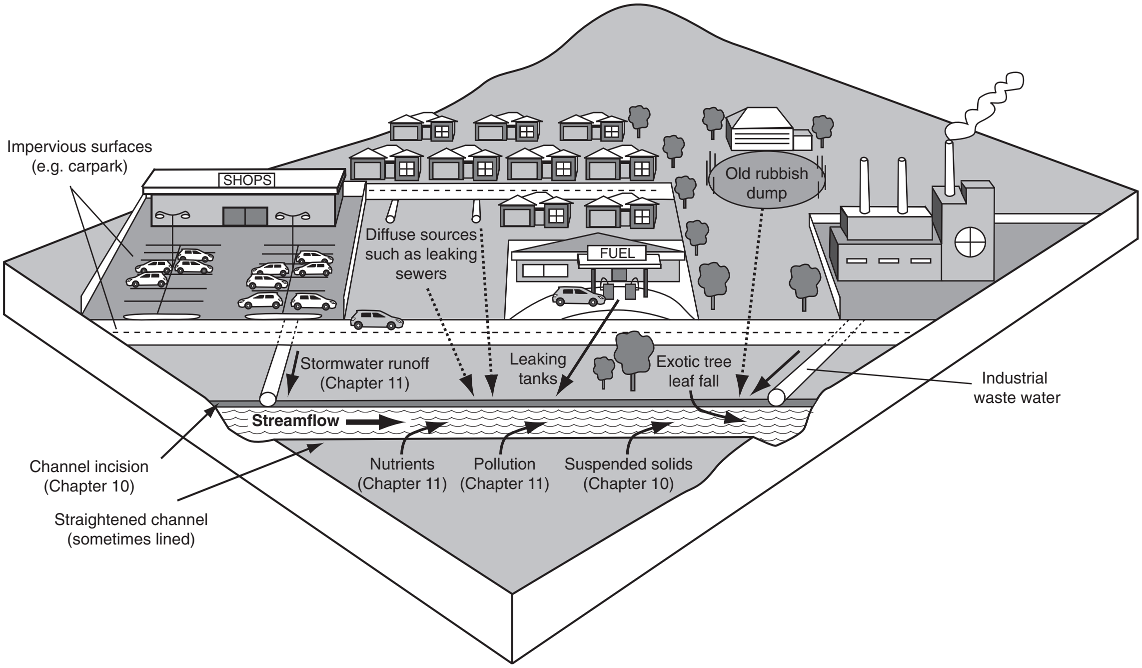

Figure 9.10 Potential effects of urbanization on poorly managed streams. Dotted arrows are diffuse pollution sources, solid arrows are point sources. Impervious surfaces and piped stormwater drainage create a more flashy flow regime. Other effects of urbanization are discussed in Chapters 10 and 11. (Source: Image drawn by Belinda Cale.)

or months. However, during storms, stream water levels and velocities rise swiftly before declining again, almost as quickly. The flashy water regime, combined with channelization (Section 10.2.2) and poor water quality (Chapter 11), creates challenging conditions for most aquatic life. Native species diversity in these systems is usually low, dominated by hardy opportunists with brief life-cycles (e.g. chironomid midges).

The multiple stressors affecting urban streams ('urban stream syndrome', Walsh *et al.* 2005a) entail the interaction of a flashy hydrograph with elevated concentrations of nutrients and contaminants and simplified channel morphology (Figure 9.10). To reduce the frequency of hydrological extremes, Walsh *et al.* (2005b) proposed that stormwater drainage should be disconnected from the pipe systems that deliver it directly into streams. Instead, stormwater should be allowed to drain into the soil so that it enters streams more slowly, allowing natural biogeochemical filtering processes in the soils to improve water quality (Box 12.2). This is just one of the many strategies of **water-sensitive urban design** whereby ecological processes are used to reduce the effects of urbanization on water regime and water quality in an effort to improve biodiversity and other ecosystem services.

9.5 WATER REGIMES AND ENVIRONMENTAL WATERING

Given the central importance of water regime to all aquatic ecosystems, it seems logical that if most ecological damage results from changes in water regime, then management efforts should focus on trying to restore the regime to a more natural state, if possible. The predominant tool used by water resource managers to achieve this is the allocation of **environmental water**. As this is a book on aquatic ecology, we define 'environmental water' from an ecological perspective, emphasizing the importance of the water regime (Section 1.4) but not overlooking the biological relevance of physical and chemical features of its water quality.

Environmental water is water that is intended to support biodiversity and ecological processes in surface waters, groundwaters and all water-dependent ecosystems. Under Australian Commonwealth legislation, the provision of environmental water is explicitly recognized in all statutory water plans, and water entitlements for the environment have the same security as any other consumptive use. Various terms describe the different types of environmental water according to whether it is 'held' or 'planned' (see National Water Commission 2012 for examples) but the most important aspect is the **water regime** when developing strategies to provide environmental water to an aquatic ecosystem.

Provision of environmental water, termed **environmental watering**, aims to protect or restore the water regime, especially ecologically relevant components such as peak flows, small floods and natural low flow periods. Environmental watering includes releasing impounded water, preventing extraction of some or all of the water at certain times or under particular hydrological conditions, protecting natural run-off and groundwater recharge processes, and other strategies to achieve particular environmental objectives. The process is guided by various hydraulic models and habitat assessment approaches (see review in Arthington 2012) as well as discussions with all stakeholders when water plans are being developed. Determining how much water should be reserved for the environment and judging the success of this compromise is especially challenging across much of Australia where natural water regimes are inherently variable and unpredictable, complicating efforts to classify them to guide appropriate provisions of environmental water (Box 9.3).

In addition to the scientific challenges of environmental watering and the assessment of its success in meeting ecological objectives, water resource managers need to assess the social, political and economic implications of the 'trade-offs' usually required to provide the environmental water. Social issues arise because people value rivers for different reasons. Some people may wish to have a near-natural river where they can enjoy recreational pursuits such as kayaking or bushwalking, whereas irrigators along the river must derive their income by extracting the water. They may enjoy those recreational pursuits just as much but feel threatened by demands to 'give up' water for the environment unless they can be convinced that there is some benefit, especially during drought (Box 9.4).

Even if there is public agreement about the need for aquatic ecosystems to have an environmental share of water, there is then the complex debate about the volumes, strategies and timing of environmental watering. Political issues reflect public values but are also heavily influenced by economic aspects. Putting a dollar value on environmental benefits is more difficult

Box 9.3 Classification of river flow regimes to support environmental water strategies

Hydrological classification involves systematically arranging streams and rivers into groups that share particular hydrological characteristics or environmental determinants of their flow regime. Such a classification plays a key role in helping us to understand spatial patterns in riverine flow variability, explore the influence of streamflow on biological communities and ecological processes, aid hydrological modelling in regional analyses, and prioritize conservation efforts for freshwater ecosystems (review in Olden *et al.* 2012). Hydrological classification also informs environmental flow management by providing a spatially explicit understanding of how much and when flow regimes vary within and among rivers. For example, Kennard *et al.* (2010b) classified flow regimes for rivers across Australia based on 120 metrics describing ecologically relevant characteristics of the natural flow regime derived from discharge data for 830 stream gauges. They distinguished 12 classes of flow regimes differing in the seasonal pattern of discharge, degree of flow permanence, variation in flood magnitude and flow predictability and variability. This classification can now be used to enhance our understanding of flow-ecology relationships in Australian rivers and improve our prescriptions of environmental flows.

Mark Kennard, Griffith University

Box 9.4 An experimental environmental water release

Although environmental watering strategies are developed based on scientific understanding of ecosystem processes, they must also incorporate human water requirements. Water resource plans include allocations of water for environmental purposes but specific criteria for using environmental water are often undefined. During the summer of 2006–2007, an experimental flood release from Lostock Dam on the Paterson River, NSW, was proposed to test its potential ecological consequences. The local water user association raised several concerns, primarily regarding use of the release during a drought and the risk to irrigators of lower water allocations in future years. Complex negotiations among irrigators, water management agencies and scientists eventually led to a consensus to release a smaller volume. This enabled the experimental flow, albeit reduced, to proceed whilst satisfying the water users' concerns about social and economic risks. When planning releases, sufficient time is needed for discussion amongst stakeholders to achieve viable compromises and to encourage participants to experiment so that more can be learned about both positive and negative effects of environmental flows. This developing scientific evidence can then be used to improve management practices (e.g. King *et al.* 2010, Rolls *et al.* 2011).

Rob Rolls, Griffith University

than on, for example, farm produce from an irrigated field, and the economic assessment of environmental watering strategies is very challenging. These aspects are discussed in Chapter 13 but we make the point here that aquatic scientists contributing to these debates on environmental watering should be fully aware of all the other pressures on decision-makers.

Often, quite a gap exists between the minimum volumes estimated by scientists to be needed by a waterbody and the volume that is considered acceptable from various social, political and economic perspectives. Negotiations where scientists contribute to the debate on an equal footing with other interests seek to achieve some form of '**environmentally sustainable level of extraction**'. This is the level of extraction that, if exceeded, would compromise key ecosystem functions, environmental assets or environmental outcomes for a water resource or impair the productive base of the water resource. It is intended to indicate the volumes that can be taken so that water does not have to be returned to the system as an environmental allocation. The major challenge is assessing whether these levels of extraction are ‘environmentally sustainable’ in the short and long terms, ensuring that some critical component of the ecosystem is not overlooked.

9.5.1 Environmental watering: ecological objectives and outcomes

Strategies for environmental watering often seek to enhance particular components (Figure 9.5) of the water regime, and usually have clear environmental objectives by which to judge the ecological success of the process (Table 9.2). In any assessment, it is essential to specify the **mechanism** by which an environmental watering regime is intended to achieve a given outcome because this helps devise monitoring programs and survey designs that will best test the effectiveness of the allocation (Downes *et al.* 2002, Section 11.8). Timing, volumes and water quality of the environmental watering are all important considerations, and different combinations favour different parts of the ecosystem (Table 9.2). Various watering strategies are intended to restore or enhance particular flow components to achieve certain ecological outcomes. For example, flushing flows and sustaining flows are often aimed at improving water quality as well as altering sediment deposition patterns and the physical structure of riverbeds to enhance habitat complexity. Overbank flows are intended to restore river channels and inundate floodplains (Table 9.2).

A crucial point to reiterate is that different organisms and ecological processes benefit from different aspects of the water regime. Responses to particular features of the flow regime vary widely among species

Table 9.2 Efforts to restore particular flow components have specific environmental objectives and watering strategies. Table modified from Robson *et al.* (2009), which also has case studies exemplifying each of these strategies, and reproduced with permission from the National Water Commission, Australia. (Source: Modified from Robson *et al.* 2009. Reproduced with permission from National Water Commission, Australia.)

Flow component to be restored	Flow regime prior to environmental watering	Environmental objective	Environmental watering strategy
Duration of zero flow	Prolonged zero flow	Restore water quality and inundate habitat, including pools	Provide sustaining flows
Presence of zero-flow periods	No zero-flow periods	Restore natural variation in flow cessation	Stop releases
Dry-season low flow	No low flow in dry season	Restore natural seasonal variation	Reduce releases in dry season
Presence of freshes (small floods)	No freshes	Restore refuge pools, trigger specific ecological processes, and flush sediment	Provide short-term releases, passing flows
Wet-season base flows	Wet-season base flow not above dry-season low flow	Inundate specific habitat (e.g. woody debris for fish spawning)	Provide wet-season releases
Presence of bank-full flows	No bank-full flows	Increase fish diversity and restore bed complexity	Provide large releases
Presence of large floods (overbank flows)	No overbank flows	Reconnect floodplain, refill wetlands, recharge shallow groundwater, trigger breeding by birds and native fishes, and improve floodplain tree health	Provide over-bank flows with large releases or ‘piggy-back’ on smaller freshes

Box 9.5 Reproductive responses by native fishes to a flood prolonged by an environmental water release

In October–December 2005, 513 GL of environmental water was used to extend a natural spring flood in the Barmah-Millewa Forest on the Murray River floodplain. Flooding from August-December included several natural flood peaks, and its recession matched that before impoundment (King *et al.* 2009, 2010). Drifting eggs and larvae of four native fish species were netted throughout the 2003, 2004 and 2005 spawning seasons. Young-of-the-year (YOY) were also collected the following autumn each year. Golden and silver perch increased their spawning activity during the 2005 flood compared to the previous two seasons. There was no change in Murray cod and trout cod spawning activity among years, but their YOY were more abundant after the 2005 flood season, implying that flooding enhanced larval and juvenile survival of these two species. Subsequent monitoring also found high abundances of YOY cod during low flows. Our study provides scientific evidence of a link between environmental watering and native fish spawning and recruitment, and highlights the variable responses among fish life-history strategies and the importance of all hydrological characteristics for maintaining fish populations.

Alison King, Charles Darwin University

(Box 9.5), and maintaining the full suite of hydrological components is a common strategy to retain near-natural biodiversity and a range of ecosystem processes. However, one principle of ecologically successful restoration is that no lasting harm should be caused (Palmer *et al.* 2005). The suite of multiple stressors (Section 11.9) acting upon rivers with modified flows may mean that restoring certain flow components might actually cause lasting harm (e.g. Lind *et al.* 2007). Therefore, all stressors and the present ecological condition of a waterbody must be assessed before any decision to implement an environmental watering strategy (Robson and Mitchell 2010).

However, not all environmental watering strategies are completely successful. Sometimes, unintended adverse consequences occur as a result of incomplete understanding of the system's ecological interactions. At other times, the volume of water available is insufficient to meet the environmental objective, or factors unrelated to the water regime may limit the ecological response (Robson *et al.* 2009). For example, an environmental water release into the Snowy River downstream of Jindabyne Dam in 2002 used water from a tributary, the Mowamba River. The objectives were to improve environmental condition and restore pre-regulation ecological and physical qualities as much as possible (Brooks *et al.* 2011). Although discharge in the Snowy River increased during the flow release, it did not reach levels comparable with nearby unregulated rivers. However, the release did increase flow variability and produced higher spring flows. Brooks *et al.* (2011) found no obvious effect of the environmental flow on invertebrates in the Snowy River and concluded that the released volume was too small to create the intended environmental changes (e.g. reduced silt levels) required to trigger changes in the invertebrate fauna. Barriers to invertebrate recolonization such as weirs remained in the river system and may also have limited the invertebrate response. It is also possible that the long period of reduced flow before environmental watering affected the capacity of invertebrates to respond.

In another study, Mackie *et al.* (2013) examined the effects of small environmental flow releases (0.4 ML per day) during summer on invertebrates in two headwater streams downstream of weirs in the Victoria Range, Victoria. In one stream, invertebrate composition shifted towards that observed in nearby unregulated streams, whereas in the other stream, invertebrate composition did not change. In the first stream, water was released directly through a pipe in the weir wall (Figure 9.4b), allowing invertebrates to drift downstream through the weir. However, in the second stream, released water had to pass along a pipe and then bubble up through the streambed sediments, probably preventing invertebrate drift. This illustrates how the mode of release and the effects of weirs likely govern the success of environmental watering strategies for restoration of invertebrate assemblages in different streams.

9.5.2 Environmental watering: risks and tactics

All environmental watering strategies entail some degree of risk and most strategies include formal **risk assessment frameworks**. One source of risk is the quality of the environmental water. Different sources of water (e.g. reservoirs, inter-basin transfers, mine waters, discharge from wastewater treatment plants or industrial processes) all vary in water quality and may not be suitable for particular environmental objectives. For example, some water sources (e.g. certain discharges from wastewater treatment plants or industry) will be too pure, lacking necessary nutrients or sediment particles to supply aquatic ecosystems. Other released waters may have such poor water quality that although the water regime is partly restored, problems associated with nutrient enrichment or salinization may arise (Chapter 11).

A second risk arises from constraints on the capacity of the infrastructure to provide the intended water regime or a particular flow component. These constraints may arise from limited channel capacities (e.g. the Barmah Choke on the Murray River) or transmission times and losses of environmental water before it reaches its target system. Another major limitation is 'valve constraints' on impoundments because these physically limit the volume of environmental water that can be released within a short period of time to simulate, for example, a large flood downstream at a time when the dam is not spilling over. Even if a large environmental release (e.g. to simulate a flushing flow) is possible, another risk arises from potential damage to bridges and land-owners' property downstream.

A third risk is the uncertainty arising from the different modelling approaches used to determine environmental water strategies, and the influence of incomplete data sets, non-linear ecological responses, and the natural complexity and variability of aquatic ecosystems. Bayesian modelling has been proposed as a powerful tool for risk-based environmental water strategies (Hart and Pollino 2009) and shows considerable promise because of its capacity to integrate hydrological and ecological models, compare outcomes from various water regime scenarios and trade-offs, and prioritize areas where further research is needed, especially into the success of different tactics for environmental watering.

These tactics are often aimed at enhancing particular flow components to achieve specific environmental outcomes (see reviews in Watts *et al.* 2009 and Arthington 2012). For example, in impounded systems, environmental water can be stored across several years so that large volumes are available for release to increase the size of natural flood events or to prolonging the duration of flooding (Box 9.5) to enable aquatic organisms to reproduce before floodwaters retreat (Robson *et al.* 2009). Wetlands can be topped up either via river diversion (e.g. Chowilla floodplain on the Murray River – Holland *et al.* 2009) or by pumping from the groundwater (e.g. Swan Coastal Plain wetlands, Figure 9.8). Water from wastewater treatment injected into groundwater aquifers is being trialled as a potential method of providing environmental water for groundwater-dependent ecosystems on the Swan Coastal Plain.

Existing infrastructure on impounded waterways can sometimes be modified to help restore a near-natural water regime. For example, outlets of impoundments across large rivers may be modified to permit the release of warmer, oxygenated surface waters rather than deeper hypolimnetic releases of poor-quality water low in oxygen. Where variable-level release outlets cannot be retrofitted, special aerators may be installed within or near the outlet to increase oxygen concentrations. Some valves can be modified to spray the water as it emerges from the outlet but this can severely accelerate evaporation, especially in arid and semi-arid areas. In other cases, the timing and method of water release can be managed across a sequence of pre-existing dams down a river to mimic more closely the natural water regime (Box 9.6).

Some dams can be operated differently to allow a particular discharge through at all times and maintain a given 'end-of-system' flow below the areas of major extraction (e.g. Namoi River, NSW). Another tactic, called a '**transparent**' dam release, requires all flows into the dam at certain times to be passed immediately downstream as though there was no dam present. This is intended to maintain natural flow variability for that part of the year when dam releases might otherwise be minimal (e.g. sections of the Murrumbidgee River, NSW). In contrast, a '**translucent**' dam release is when a proportion of the inflows at certain times is allowed to pass immediately downstream to try to restore the natural river flow variability associated with specific events such as minor floods (e.g. Lachlan River, NSW). Of course, these options are only possible on impounded rivers; in other systems, statutory regulation of the volumes extracted directly from the

Box 9.6 Dam re-operation for improved environmental outcomes

Large dams provide substantial socioeconomic benefits but have negative environmental impacts. We can partially restore river ecosystems downstream of dams by using 'dam re-operation' (Watts *et al.* 2011). For example, hydropower dams can incorporate re-regulating dams or off-channel storage. Coordinating the operation of a sequence of dams can restore components of the natural hydrograph, reducing impacts downstream. Improvements in the operation of water supply dams can be achieved by altering the pattern of water transfer between reservoirs (Watts *et al.* 2010), transferring water to groundwater aquifers at times that benefit the environment, or piggy-backing environmental flows on dam releases or inflows from unregulated tributaries. Sustainable operation of flood management dams should incorporate floodplain reconnection so that water released from dams during high flows can be conveyed within natural floodplain features or constructed bypasses. This reduces flood risks to communities, supports biodiversity and provides ecosystem services. Dam reoperation is complex; it can impact on water users, power production and society. Innovative case studies have demonstrated that the operation of dams can be altered to optimize environmental and socio-economic outcomes with multiple benefits for society and the environment.

Robyn Watts, Charles Sturt University

channel or connected groundwater is needed to achieve similar results.

Perhaps the most unusual tactic involves *reducing* water discharge to reinstate a period of drying in rivers and wetlands that were once temporary. This is termed a 'cease-to-flow event' when applied to rivers (Table 9.2, Rolls *et al.* 2012), or a 'drying event' when applied to wetlands, and is sometimes used where rivers or wetlands have become artificially permanent owing to their use as irrigation channels or water storages. The process involves re-establishing some of the natural variability at the low-flow end of the water regime (Reich *et al.* 2010). Although this approach has been used in several parts of Australia, its effects on biota and ecosystem processes have rarely been documented.

9.6 'BREAKING DOWN THE BARRIERS': FISHWAYS AND DAM REMOVAL

Figure 9.11 Fishway (right-hand side of photo) installed in the Goodga River, WA, to increase the area of breeding habitat available to a population of the western spotted galaxias *Galaxias truttaceus hesperius*, which is critically endangered. (Source: Stephen Beatty.)

The walls of impoundments are a barrier to the upstream and downstream movement of biota (Section 9.3), especially many native fishes. To overcome this problem, at least for some species, various types of **fishways** have been built on impoundments of different sizes. Early designs replicated those built for salmonid fishes in the Northern Hemisphere but few of our native fishes have the same capacity as salmon and trout to leap up stepped passages or swim against strong flows. More recently, fishways with quite shallow slopes and plenty of flow refuges (e.g. rocks, little backwaters) have proved more successful, especially for low-level barriers and impoundments up to about five metres high (Figure 9.11). More than a dozen vertical-slot fishways have been constructed on impoundments on the Murray River, and initial observations suggest that they have greatly improved fish movement along the river (Stuart *et al*. 2008), both for native species such as golden perch *Macquaria ambigua* and for invasive species like common carp *Cyprinus carpio*. For impoundments with higher walls, more imaginative solutions such as 'fish-lifts' are needed. If you have an interest in engineering, hydraulics and fish biology, then designing and building a better fishway could be the career you have been looking for.

Another point to remember is that even a shallow ford or seemingly insignificant weir can hamper the movement of biota at certain times of the year (Doehring *et al*. 2011). Furthermore, there are often multiple impoundments across streams and rivers, with only a single one needed to impede passage along the entire channel. To ensure effective passage, scientists and river managers must collaborate to ascertain the success of existing fishways (Box 9.7) and determine whether any bottlenecks occur where a single impoundment might be nullifying the effects of fishways upstream and downstream. This is a good example of the need for a large-scale perspective to ensure that the patterns of movement at catchment and landscape scales are preserved or restored.

In various parts of the world, restoration of flow regimes has progressed to the point of decommissioning some impoundments. Although removal of impoundment walls sounds like a positive step, it can have negative consequences unless carefully managed. For example, fine sediments may have accumulated for decades behind the wall (Doyle *et al.* 2005) and, if released all at once, may cause ecological problems downstream (Section 10.3).

Research overseas suggests that although some macroinvertebrates may recover relatively quickly following dam removal, other groups and riparian vegetation may take much longer (years to decades) to recover (Doyle *et al.* 2005). Monitoring the ecological and geomorphic responses after dam removal is providing major insights into recovery processes and the role of the flow regime in impounded rivers. In some parts of Australia, major programs have removed weirs along large stretches of rivers, but there has only been limited work done on the impacts of and recovery after weir removal. Removal of dams and weirs as a restoration option may become more frequent in the future as the cost of maintaining reservoirs exceeds the cost of their removal (Beatty *et al.* 2013, Box 9.8).

9.7 SYNTHESIS

Water regimes can be altered by changes to catchment runoff, groundwater recharge, the shape of the basin or channel, and regulatory structures in the waterbody itself. Most of these changes to water regime have been accompanied by changes to catchment, basin and channel shape (Chapter 10) and water quality

Box 9.7 Fish and microchips: tagging fish to assess fishway performance

Understanding fish behaviour helps us design fishways to mitigate the effects of impoundments and barriers on fish movement. Fishway success is commonly quantified using trapping or electronic tags to track fish movements (Baumgartner *et al.* 2010). In the Murray-Darling Basin, the 'Sea-to-Hume Dam' fish passage program aims to restore passage along 2225 km of the Murray River, necessitating fishways at 14 weirs and a series of tidal barrages. As part of the program, tens of thousands of fishes were implanted with passive integrated transponder (PIT) tags, analogous to the 'microchips' implanted in our pets. PIT tags contain no battery (they are energized by a capacitor), and therefore are small (9–23 mm), long-lived and inexpensive. Each tag transmits a unique code, enabling individual fish to be identified. Fishways along the river are fitted with electronic recording systems that energize and detect the tags, providing information on fish passage through fishways as well as large-scale movements between fishways. This helps us improve fishway design and provides new insights into the ecology of freshwater fishes (Leigh and Zampatti 2013).

Brenton Zampatti, South Australian Research and Development Institute

Box 9.8 Restoration of Lagoon of Islands: the potential of dam decommissioning

Lagoon of Islands, on the Central Plateau of Tasmania, was unique because it was dotted with 'islands' of woody vegetation, including *Callistemon* and *Leptospermum*, growing on a floating mat ('schwingmoor') of rhizomatous vegetation (Tyler 1976) where a rich birdlife also flourished. In 1964, Lagoon of Islands was dammed to supply irrigation water downstream and allowing more water to be used for electricity generation through nearby Poatina power station. A decade later, the unique vegetation community had died. By the late 1980s, the lagoon had an extensive bloom of the desmid alga *Staurastrum excavatum* (Sanger 1994). Poor water quality has plagued the lagoon ever since, rendering it unfit for use for drinking and irrigation. The cyanobacterium *Aphanothece* sp. formed massive blooms with densities of millions of cells per millilitre since December 2008, and it was clear that the costs outweighed the benefits of keeping the lagoon in Tasmania's hydro-electric system. Forty-nine years after the dam was commissioned, it was dismantled in April 2013, allowing the natural hydrology to recover and Lagoon of Islands to be rehabilitated. Will the system recover to its former glory?

Carolyn Maxwell, Hydro Tasmania

(Chapter 11), and invasive species have often capitalized on the changed conditions (Chapter 12). Restoration programs aim to recover water regimes as close as possible to natural patterns. In standing waters, changes in depth or related components such as the duration of inundation will be relevant to restoration of the water regime. In running waters, restoration of at least some components of the flow regime is usually the main focus. In groundwaters, restoration would seek to recover natural patterns in groundwater pressure, flux and residence times as well as recovering lost connections with surface water.

Restoring water regimes requires negotiation with other water-users. Ecological benefits must be weighed up against social and economic costs, and there is a need to demonstrate the success of strategies such as environmental water allocations, construction of fishways or decommissioning of dams. This calls for a clear explanation of the ecological mechanisms underlying each strategy as well as rigorously designed monitoring programs capable of detecting the success of the restoration. Monitoring also helps communities form realistic ideas of what restoration can do for aquatic ecosystems, and what it cannot.

We need to consider ways to limit our impacts on water regimes of standing and running waters so that they retain most of their natural character yet can be exploited sustainably. Management of water regimes requires a landscape-level perspective. Standing waters in a region must be managed as mosaics whose water regimes interact and whose biota move from place to place. Flow regimes in lotic environments must be considered at a catchment level, ensuring that they benefit channel and floodplain processes whenever possible and that impoundments do not prevent movements by fishes and other organisms. Groundwater regimes must take into account the interactions with their dependent ecosystems, and planned changes to water regimes in surface waters should always acknowledge the likelihood of lagged effects upon connected groundwaters and *vice versa*.

In Figure 9.1, we identified links between changes to three major aspects of water regime (timing, volume and duration) and the shape and structure of lentic and lotic waters (geomorphic features). In the next chapter, we explore these links more closely and see how human activities have affected the interactions between water regime and the physical features of catchments, basins and channels, particularly processes such as sedimentation. Our themes of the importance of a landscape-level perspective, the maintenance of natural variability, and the significance of linkages, especially across the land-water interface of fringing and riparian zones, emerge once more.

CHAPTER 10

Management issues: physical features

10.1 CHANGING PHYSICAL FEATURES, CHANGING PROCESSES

In the previous chapter, we explored how human changes to the water regime can have major effects on the water quality, organisms and ecological processes of standing and running waters. As we saw, many of these effects interact as multiple stressors resulting in complex ecological responses over time and at a variety of scales. These responses become even more complex when we take a broader landscape perspective and consider the effects of human activities on the physical environment. This physical environment encompasses the catchment as well as the shape and physical features of the waterbody (e.g. depth of basin or channel, shoreline profile, substratum particle size, etc.). In this chapter, we review management issues associated with anthropogenic changes to physical features of the waterbody and its catchment. Some of these changes have been **intentional** (e.g. dredging, channelization). Others, such as accelerated erosion and sedimentation, have been **unintentional** outcomes of agriculture and other land uses in the catchment and on the floodplain.

One theme in this book is the necessity to address causes rather than symptoms of environmental problems, where feasible. Many similar impacts arise from different land uses because the causes of the problems are similar or because of the collective effect of related land uses (Table 10.1). For example, poorly-managed land clearance for different human uses can result in sedimentation, salinization, eutrophication or a combination of these (Chapter 11). Furthermore, many of the problems that are primarily because of physical changes to the waterway or arise from poorly managed catchment land-uses are exacerbated by human alterations of the water regime (Chapter 9). Again, all these geomorphic changes may either be intended or unintended, although this seldom alters their ecological effects. Part of the challenge of managing these issues arises from their multiple causes and the complexity of interactions and feedback loops. On the positive side, well-planned restoration strategies such as sediment stabilization or catchment revegetation often have multiple positive effects, enhancing biodiversity (Chapter 12) and recovering ecological integrity and ecosystem services.

Another theme throughout this book has been the ecological significance of linkages at a range of scales. One of the most fundamental is the linkage between waters and their catchments (Section 1.5.2) because lentic and lotic waters act as ‘sinks’ for material washed in from the catchment or imported by groundwater. Volumes, composition and rates of transport of this material will be altered by physical changes to the catchment. At the land-water interface, fringing vegetation, the riparian zone and floodplains all play crucial roles in mediating this linkage. This chapter will review how humans have physically changed these important land-water interfaces, usually with severe impacts on aquatic ecosystems and their biota. After exploring the major problems caused by excessive inputs of sediments, the chapter discusses the role of fringing and riparian zones in mediating the effects of human activities in the catchment on the ecological processes in aquatic ecosystems, and concludes with

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Australian Freshwater Ecology: Processes and Management, Second Edition. Andrew J. Boulton, Margaret A. Brock,
Belinda J. Robson, Darren S. Ryder, Jane M. Chambers, and Jenny A. Davis.

Companion Website: www.wiley.com/go/boulton/freshwater

Table 10.1 Management issues arising from land-use change and other human activities: x = mild or temporary, xx = moderate and xxx = severe or persistent.

	Extensive clearing of native vegetation	Urbanization and industry	Grazing and feedlots	Cropping	Forestry and timber harvest	Mining and quarrying
Sedimentation	xxx	xx	xxx	xxx	xx	xx
Salinization	xxx	xx	xx	xxx	x	x
Eutrophication	xx	xxx	xxx	xxx	x	
Invasive species	xx	xx	xxx	xxx	xx	xx
Acidification	xx	xx	x	xx	x	xxx
Heavy metal inputs	x	xxx	x	xx		xxx
Toxic chemical inputs		xxx	xx	xx	xx	xxx
Thermal pollution	x	xxx	x	x	x	x

ways to manage land-water interfaces and recover lost natural physical complexity.

10.2 HUMAN ACTIVITIES AND THE PHYSICAL ENVIRONMENT

In Chapter 9, we saw how human activities have altered the water regimes of standing and flowing waters by direct extraction, drainage and irrigation, and the construction of impoundments. These changes to the water regime often happened at the same time as changes to the physical environment, and involved either direct geomorphic changes to the shape of the waterways, alteration of the physical structure of the catchment or both. The extent and types of these physical transformations mirror the historical changes in land use and human population density across Australia, especially since European settlement over two centuries ago.

10.2.1 Human changes to catchments

Before European settlement, burning of grasslands, shrublands and dry sclerophyll forests by indigenous Australians to improve their hunting of wildlife probably changed local water regimes and transport of materials by altering catchment vegetation and runoff. However, these activities over thousands of years never wrought such rapid and major changes to aquatic ecosystems as did the impacts of farming, forestry, mining and urban sprawl in the last two centuries. In many parts of the country, substantial incentives were provided to settlers to clear land almost completely of native vegetation and to establish farms and dwellings. Fertile floodplains attracted particular attention, and most of these arable habitats across the south were cropped, grazed or settled by the end of the nineteenth century.

Early on, forestry was a major industry, and particular species such as red cedar *Toona ciliata* and karri *Eucalyptus diversicolor* were eagerly sought. Much of the timber was exported as well as being used locally to build warehouses, bridges, jetties and houses. In the late 1800s, further demand arose for timber for railway sleepers and steam-engine fuel. Eucalypts were cut down on the floodplain to supply paddle-steamers along the Murray River. Early accounts indicate indiscriminate logging and considerable wastage. Overcutting of several prized riparian species (e.g. red cedar for furniture, Huon pine *Lagarostrobos franklinii* for ship-building) prompted some of the earliest legislation in Australia to protect single species from excessive exploitation.

Mining was another intensive industry that not only physically changed the landscape and channel forms (Section 10.2.2), but also required large amounts of wood as fuel to power pumps and mining machinery and as props for mine shafts. Many gold rushes in Australia occurred in dryland areas where native timber was systematically cleared over vast areas to provide wood for fuelling condensers to obtain drinking water. The landscape effects of this complete clearance of timber in parts of the semi-arid zone persist (e.g. goldfields of WA), along with the irretrievable loss of tonnes of scarce topsoil. Overall, Australia has lost almost 40% of its native forests and what remains is highly fragmented (review in Bradshaw 2012).

After both World Wars, soldier settlement schemes in southern Australia resulted in further extensive clearing of native vegetation while cities and towns began to sprawl into surrounding hinterlands, building houses on once-productive farmland and necessitating protection and construction of urban water supplies. In the 1950s through to the 1970s, hefty government incentives combined with recent technological advances and high post-war prices for crops such as wheat led to wide-scale clearing of thousands of hectares of sparsely wooded semi-arid vegetation. The area under winter grains soared (Henzell 2007, Figure 10.1a). Bumper crops were soon followed by inevitable droughts and loss of topsoil, invasion of exotic plants and, in many places, salinization (Section 11.4). Over the last 100 years or so, agricultural productivity across most of Australia has been driven more by international market demand and profitability than by good environmental management, leaving a legacy of numerous examples of severe degradation of standing and running waters (Figure 10.2).

Grazing by sheep, cattle and other introduced animals (e.g. rabbits, camels) has also substantially changed the physical landscape in Australia. Apart from several sharp dips caused by drought (e.g. 1895–1903, 1918–1920), sheep and cattle numbers have steadily increased since the 1860s, peaking in the early 1970s before declining again (Figure 10.1b,c). Grazing alters plant community composition, ground cover and surface microbial crusts, and, when poorly managed, can lead to serious erosion and loss of topsoil (which potentially then causes problems elsewhere when it deposits). There may also be severe compaction effects, especially in tracks leading to the water's edge (Figure 10.2), and these can rapidly become erosive gullies that funnel sediments into the waterway. Compacted soils hinder plant germination and growth as well as inhibiting burrowing by freshwater crayfishes (March and Robson 2006).

In recent decades, urban sprawl and the proliferation of the impervious surfaces associated with urbanization have affected the physical landscape in many parts of Australia. Most towns and cities commenced

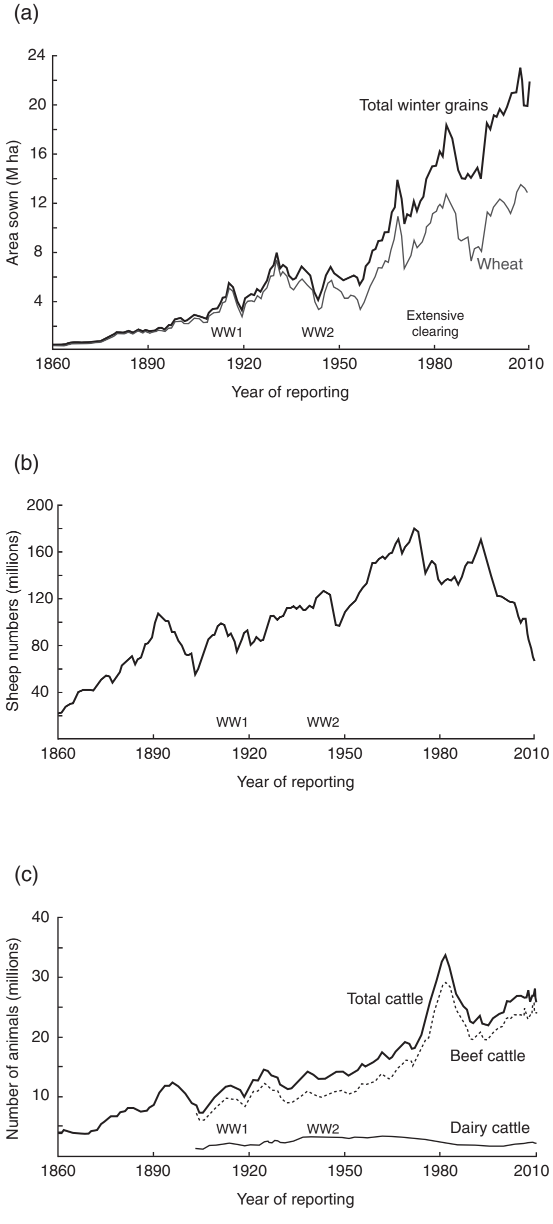

Figure 10.1 Area sown for wheat and total winter grains (a) and trends in numbers of sheep (b) and beef and dairy cattle (c) in Australia since 1860. (Source: Reproduced with permission from Department of Agriculture, Fisheries and Forestry, Australian Government.)

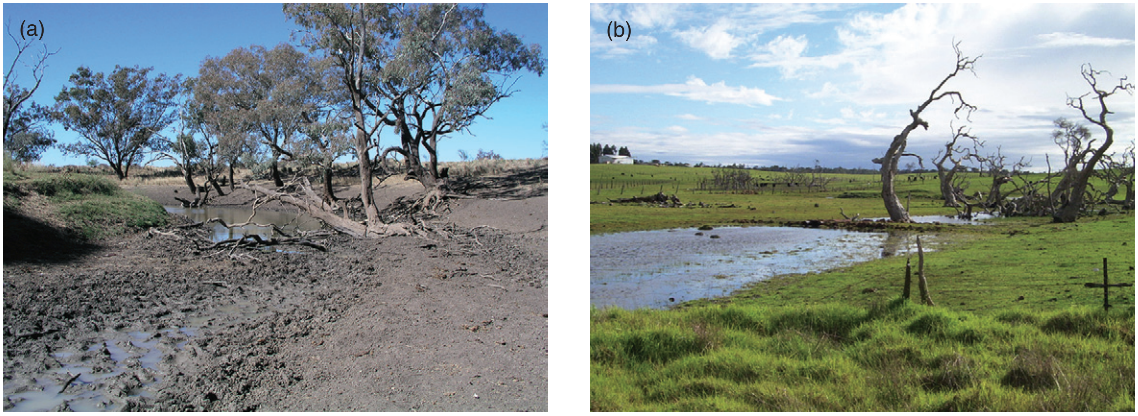

Figure 10.2 Much of the Australian rural landscape bears haunting evidence of the effects of poor land management: (a) unrestricted cattle access in Moomin Creek, Gwydir Valley, NSW; (b) headwaters of a dammed stream near Albany, WA, where waterlogging and salinity arising from land-clearing have killed the last few fringing native trees. (Source: (a) Darren Ryder; (b) Belinda Robson.)

on the banks of waterways for obvious reasons. With urban development and the increased ownership of motor vehicles since the mid-twentieth century came the demand for more roads, car parks and expressways, often at the expense of aesthetics or environmental values (Ashton 2006). Collectively, these developments substantially altered catchment drainage and infiltration patterns, resulting in flashier water regimes (Section 9.4.3). Despite tighter regulations to constrain the effects of the 'urban syndrome' (Walsh *et al.* 2005a), cities continue to expand in response to population growth.

10.2.2 Human changes to basins and channels

Since the early days of European settlement, many natural basins have been further excavated to increase the amount of water they can hold. 'Chain-of-ponds' wetlands (comprising a series of shallow basins linked by short channels, like beads on a string) were common in upland areas with low gradients, and they stabilized channels while acting as a 'sponge' to hold water in drier periods. Before their ecosystem services had been fully recognized, most of the shallow wetlands and low-lying wetter areas in much of southern Australia were drained or had channels cut through them to provide new pastures or croplands, improve access and to discourage pests such as mosquitoes and midges (Dale and Knight 2012). Shallow temporary lakes and swamps in some areas are still seen as a source of weeds and noxious odours, a harbour for feral and nuisance animals, and a contributing factor to waterlogging and soil salinity (Bennett and Whitten 2002).

Similarly, numerous natural stream and river channels have been deepened, straightened and widened either to convey water more rapidly to where it is needed for humans, stock and crops or to drain it away to prevent flooding and waterlogging. Thousands of kilometres of irrigation ditches and canals have been constructed, often severely disrupting surface and groundwater movements, altering floodplain drainage and affecting the water regime of nearby and receiving waters. Some of these irrigation canals are huge and can carry large volumes of water. For example, in 2011–2012, over 850 000 ML were diverted from the Murrumbidgee River to the Murrumbidgee Irrigation Area, delivered through a massive network of irrigation canals (Figure 10.3).

Irrigation canals and drains are often cut into shallow alluvial or even previously confined groundwater aquifers. This can accelerate groundwater pollution (e.g. nitrates from agriculture, Section 11.3) as well as changing the water regime of the aquifer. It also allows groundwater of poor quality (e.g. acidic or saline) to enter surface waters, as seen in parts of the WA wheatbelt, especially where groundwater tables

Figure 10.3 The Murrumbidgee Irrigation Area is fed by numerous canals capable of carrying huge volumes of water. The physical complexity of these canals is much less than that of natural river channels and aquatic biodiversity is often low. (Source: Darren Ryder.)

have risen because of changes in land cover (Robertson *et al*. 2010).

Physical changes to river channels typically occur through flow-induced incision when mean and peak discharges are increased by extensive clearing of catchment vegetation. Consistent trends of rapid incision, sedimentation and changes in channel shape have been reported across Australia following European settlement in temperate (e.g. Page *et al*. 2007), tropical (e.g. Bartley *et al*. 2008) and dryland (e.g. Stromsoe and Callow 2012) catchments. Most channel erosion occurs during large floods, and can be catastrophic (Rutherfurd 2000), with dramatic widening of channels, bank slumping and even channel avulsion (i.e. when the river rapidly forms a new channel).

A typical situation is that in the Hunter River near Singleton, NSW (Mika *et al*. 2010). Within several decades of European settlement and clearance of native vegetation, banks began to erode and the channel started to deepen and widen (Figure 10.4a,b). This was followed by an active phase of geomorphic adjustment, characterized by significant channel expansion and incision (Figure 10.4c), especially during the largest flood on record (February 1955). Low flows in the Hunter River at Singleton now meander within a broad channel of sediment bordered by a sparse riparian zone dominated by invasive willows *Salix* spp. (Figure 10.4d) – a vastly different channel profile from that of the river before European settlement.

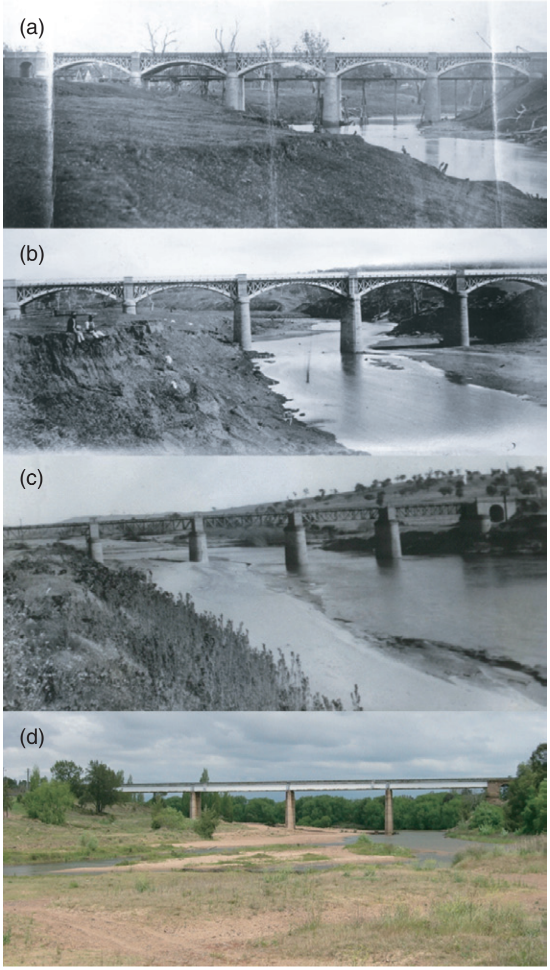

Figure 10.4 Human activities have dramatically changed the channel shape of the Hunter River at the Singleton rail bridge over time: (a) 1861, (b) 1866, (c) 1963 and (d) 2003. (Source: Mika *et al*. 2010. Reproduced with permission from Ecology and Society 2010. (a), (b) and (c) NSW Department of Environment, Climate Change and Water; (d) Nick Cook, NSW Department of Environment, Climate Change and Water.)

After the floods of the 1950s in the Hunter River, there was an era of 'river improvement' until the mid-1990s. This mainly involved engineering activities (e.g. adding concrete blocks, piles and grid mesh bays)

Box 10.1 Channel changes in response to impoundments

Two typical changes caused by impoundments to river channels have been reported worldwide. The first is the progressive accumulation of sediment behind large dams that trap most of the sediment from the catchment upstream. The second is the erosion of the channel downstream of the dam by 'hungry water' (Section 9.3). Australia has numerous dams, but interestingly, both these channel changes are quite rare. Sediment transport rates in southern temperate Australian rivers are usually low, and there are few examples of impoundments filling with substantial amounts of sediment. Instead, changes downstream of Australian impoundments fall into three types, depending on the modified flow regime. Type 1, the most common, is no measurable change. Type 2 occurs where flows are diverted out of the dam and away from the river (as in inter-basin transfers such as the Snowy River), and results in the channel width contracting and being invaded by vegetation. Type 3 is where the dam supplies irrigation water and high flow is concentrated into the drier months. These long months of high flow will armour the bed (Section 5.7.3) and erode the banks, substantially widening the channel.

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along with planting invasive species such as willows to stabilize banks (Spink *et al.* 2009). In many lowland rivers in Australia, 'improvement' activities aiming to control erosion, mitigate floods, increase discharge capacity and remove obstacles to river traffic were popular up until the late 1980s. Fallen trees and woody debris were routinely removed from the channel ('**de-snagging**') and trees adjacent to the channel were felled. The main intention was to improve channel capacity as woody debris was assumed to impede flow. However, subsequent studies have shown many of these de-snagging programs were counter-productive, even when assessed solely by engineering and hydrological criteria, because banks are destabilized, further erosion can occur and flooding problems may be transferred downstream (Smith 1998).

Other activities that physically alter river channels entail straightening channels, removing bars and islands, and constructing levee banks. Levees are often built to 'reclaim' floodplain land and protect property. However, in doing so, they alienate floodplain wetlands from inundation. Levee banks also increase channel incision or force floodwater to other parts of the floodplain, leading to incremental extensions of the built-up banks along the river and ultimately channelizing the entire system. Meanwhile, large areas of floodplain become starved of water except during accidental and catastrophic breaches of levees during large floods when water then remains on the floodplain for much longer than before. As channels become incised, so flows must be greater to overtop the banks and extend across the floodplain. Some 2145 km of levee banks were built between 1975 and 1998 on the Lowbidgee floodplain, the major wetland on the Murrumbidgee River in south-eastern Australia. This contributed to declines in waterbird numbers of up to 90% over 1983–2001 (Kingsford and Thomas 2004).

The presence of impoundments and weirs may have major effects on the shape of the channel although this is not always the case and depends on the degree of alteration of the water regime (Box 10.1). Upstream, wetted channel width typically increases as the impoundment fills and floods the valley behind it. Downstream, there may be little change or, depending on flows and bed structure, the channel may erode and widen or contract (Rutherfurd 2000). Frequently, this contraction is accompanied by the encroachment of bank-side vegetation. Exotic willows (Section 12.8.3) are especially successful at promoting channel constriction and they facilitate invasion by other introduced plants such as kikuyu grass *Pennisetum clandestinum* and African lovegrass *Eragrostis curvula* that further alter the physical shape of the river channel and beds.

Intentional **extraction of sediment** and other material from either within or the edges of standing and running waters obviously alters their physical shape. The most commonly extracted materials (other than water) from many rivers are sand and gravel. In some parts of Australia, immense volumes of sand and gravel have been removed. For example, during 1980–1981, some 730 000 tonnes of sand and gravel were taken from the Hunter River between Muswellbrook and Maitland (Erskine *et al.* 1985). River sand and gravel are an economically important resource, used in the construction industry, road building and landscaping. Although gravel extraction may also benefit navigation and create recreational areas, the detrimental effects are often severe. Excavation of large holes in river beds can lead to massive erosion upstream and downstream of the site, bank collapse, downcutting of tributaries where the main channel has been eroded or excavated, and a fall in alluvial water tables (Kondolf 1997). If sediments are removed from the neck of a meander or a floodplain channel, the river course may be diverted (Rutherfurd 2000). The most serious impacts occur when sections of the river that control erosion (e.g. subsurface cobble strata, armoured layers – Section 5.7.3) are removed and the bed becomes unstable. Where excessive sedimentation has filled large river pools, carefully managed sand and gravel extraction may be a viable option for restoration as long as the sources of sediment are also controlled and the effects of heavy machinery are restricted.

In some parts of Australia, such as southern NSW and south-western WA, **peat** has been extracted from swamps, shallow wetlands and, less commonly, stream headwaters for use as fuel or in horticulture. Alternatively, the extraction and subsequent channelization is aimed at draining the peat swamps to facilitate grazing and stock access. As well as obvious effects on physical form and water regime, this adversely affects the ecology of aquatic species restricted to these habitats where endemism is sometimes high.

When peat sediments become dry, they are prone to **wildfire**, followed by prolonged smouldering. To put fires out, chemical fire-retardants are sprayed on the peat, and flooding and trenching are often needed to contain the blaze because it is so difficult to extinguish (Horwitz and Sommer 2005). Applications of chemical fire-retardants increase nutrient concentrations in overlying waters when peatlands are reflooded (Blake *et al.* 2012). Fires also lower the bed of the wetland by combusting peat layers formed over thousands of years. This bed-lowering, combined with the trenching and flooding, changes the physical form of the wetland, impairing its interactions with connected shallow groundwater and altering its water chemistry.

Loss of vegetation (the source of organic matter for peat formation) and the increased rates of aerobic decomposition of the exposed and dry peats severely impair the peat-forming process. Consequently, restoration of peatlands requires time, patience and specialized techniques. For example, wildfires in the Australian Alps in 2003 burnt almost all the alpine, subalpine and montane bogs and fens, destroying many sphagnum hummocks and other peatland plants (Good *et al.* 2010). Successful restoration strategies targeted recovery of peat-forming processes. These strategies included returning shading and protection from ultraviolet light of remnant bog and fen plant populations, constructing barriers of straw bales across flowlines to promote surface water ponding, and inserting subsurface organic matter 'dams' to retard the flow of water from peat sediments.

Across much of the south-east, a history of hydraulic **mining** (using water under pressure to erode away banks to extract heavier ores) has left many streams and rivers with wide, shallow channels and pools choked with sand. Mobilized sand and gravels create immense '**sediment slugs**' that move downstream, smothering and removing the channel's natural complexity and leaving broad, homogenous and unstable beds, sometimes many metres thick. Sluicing for tin and gold in the late nineteenth century involved removal and washing of vast amounts of stream bank material, and Rutherfurd (2000) lists a number of examples of rivers whose channels have undergone major changes from hydraulic mining and sedimentation. The movement of sediment slugs is not always a simple downstream attenuation because tributaries can modify the process. Sediment in the main trunk stream can hold back sediments from the tributaries that are later released in pulses when levels of sediment fall in the main stream. Alternatively, sediment may move down a tributary and block the main channel, creating 'tributary junction plug wetlands' such as in the Glenelg River, Victoria (Lind *et al.* 2009). These complex sedimentation processes and channel changes can persist for decades after mining has ceased.

10.3 SEDIMENTATION: A PHYSICAL PROCESS WITH NEGATIVE FALLOUT

Almost all of the catchment land uses and waterway modifications described previously promote **sedimentation**, which becomes a serious environmental problem when the process of sediment input into receiving waters exceeds natural rates and amounts. As we saw in Chapters 2 and 5, sedimentation is a fundamental process in all lentic and lotic environments, both permanent and temporary. Standing waters gradually fill up with sediments while water flowing down headwater streams erodes their channels and carries mobilized sediments to settle out downstream in lowland reaches. In doing so, habitats are destroyed and created, and the dynamic processes of erosion and deposition help to maintain a diversity of ecological functions and biotic assemblages.

Erosion of soil is a natural process in the catchments of all standing and running waters. It may occur as slow removal by gentle sheet-flows or as rapid loss during torrential downpours or landslides (Chapters 2 and 5). However, catchments cleared of native vegetation, especially those on steep slopes in areas of high rainfall and dispersible soils, contribute increased loads of silt and sediments to the 'sinks' provided by waterways (Prosser *et al*. 2001). It is useful to review how different human activities have promoted excessive rates of sedimentation before we explore the ecological implications of this process and how best to manage it.

10.3.1 Human activities and sedimentation

Cropping agriculture usually alters or removes the original vegetation cover whose roots bound the soil particles, and which spread surface water flows, improved percolation into the soil, reduced wind erosion and sustained soil fauna that contributed further to the structure and cohesion of the sediments. Ploughing loosens the soil, rendering it more prone to being blown or washed away before a crop becomes established. This has been the cause of the irretrievable loss of much of Australia's precious topsoil since European settlement, especially during droughts and major dust storms.

Grazing removes vegetation cover and sometimes its roots as well. Compaction, through livestock trampling or the use of heavy farming machinery, decreases infiltration rates and increases overland flow, in turn accelerating sedimentation in receiving waters. Heavy rates of stocking with hard-hooved animals soon after European settlement led to immense sediment input into wetlands. For example, in 16 wetlands along the Murrumbidgee-Murray River, palaeolimnological studies indicate that sedimentation rates after European settlement accelerated by 2–80 times (Gell *et al*. 2009, Box 10.2). Rapid gully erosion in catchments such as the Mitchell River in northern Australia has been attributed to heavy grazing by cattle in the riparian zones during the dry season, which decreases the perennial vegetation along hollows and river banks (Caitcheon *et al*. 2012). Once this erosion cuts into dispersible sub-soils, gullies swiftly form and degrade the riparian zone (Shellberg *et al*. 2010).

In addition to gravel extraction and hydraulic mining, many other forms of **mining** have historically led to sedimentation. Problems have typically arisen either from poorly managed drainage around mine-works or from direct dumping of material into nearby streams. For example, in Tasmania, the Mount Lyell

Box 10.2 Sedimentation after European settlement

Sediments shift downslope but their passage may be delayed by temporary or permanent storage in fans or depressions. On floodplains, cut-off meanders and abandoned channels represent low points where sediments accumulate over centuries and even millennia. Special dating techniques applied to sediment cores across the landscape provide a timeline for this accumulation, and reveal rates as slow as one centimetre per century in upland bogs, to a centimetre per decade in lowland areas. One wetland in the lower Murray floodplain accumulated 14 m of sediment over 5000 years. These palaeolimnological techniques reveal widespread increases in sedimentation since European settlement, often as early as the mid-nineteenth century. In cores, the spike in sedimentation is illustrated by the replacement of benthic diatoms by phytoplankton, owing to the increased attenuation of light in the turbid waters. In basins associated with the Murray River, sedimentation has not slowed even though the river is now impounded. Indeed, the proliferation of cumbungi (*Typha*) since river regulation has accelerated sedimentation in channels and shallow wetlands. Sedimentation trajectories of most wetlands suggest a more terrestrial future, especially as flow regulation limits the prospects for renewal through flooding.

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copper mine discharged more than 95 million tonnes of fine sediment into the King and Queen Rivers, resulting in up to 5 m of sedimentation (Locher 1996) and causing a huge delta of toxic tailings in Macquarie Harbour. Discharge of tailings into waterways is now strictly controlled in Australia but the legacy of uncontrolled mining in the past will persist for centuries in many rivers and lake basins. Often this sediment is badly contaminated, further aggravating its impact (Section 11.6).

Urban areas are usually heavily paved and the flashy peaks of runoff from impervious surfaces (Section 9.4.3) accelerate sedimentation, especially down gutters and drainage ditches. These urban sediments often also carry toxicants and heavy metals. Poorly made roads crossing streams and rivers can act as substantial point sources of silt, although this can depend on traffic use. For example, in an experiment on sedimentation from a well-maintained but unpaved forest road across a Victorian stream, heavy truck traffic (defined as more than nine return passes per day) increased the median water-borne sediment yield from 269 to 725 mg L^{-1} (Sheridan *et al.* 2006).

Forestry activities, especially clear-felling with little or no vegetation being left along streams or drainage gullies, frequently contribute sediment to streams (review in Croke and Hairsine 2006). However, retention of even a narrow strip of vegetation can reduce these impacts (Thompson *et al.* 2009), especially in combination with carefully designed roads across streams. De-snagging waterways and removing trees along the channel edges typically promote local erosion and sediment inputs. Consequently, there are fewer roosting sites for waterbirds and a loss of cover and spawning habitats for many aquatic animals such as native fishes (Box 10.3).

The key points here are that firstly, numerous human activities contribute to changes in natural sedimentation processes, and secondly, almost all these contributions are detrimental. The main problems are the *rates* of sedimentation (usually an increase), the *types* of

Figure 10.5 Re-snagging with large logs along the banks of the Murray River has favoured populations of native fishes such as Murray cod (Box 10.3). (Source: Martin Casey).

Box 10.3 The importance of instream structural woody habitats to fishes

A key structural habitat for Australian native fishes is instream wood (snags), particularly in lowland rivers. Numerous studies show increased fish abundance and diversity associated with snags. For example, in the Murray River, over 90% of adult and juvenile Murray cod were found at woody sites (Koehn 2009). Other large, native fishes such as trout cod, Mary River cod and golden perch also shared such preferences. Instream wood creates habitat diversity (e.g. scour pools and a variety of water velocities) as well as suitable conditions for many prey. Fishes use snags as shelter, to hide from predators, to base territories around, or as feeding or spawning sites. Removal of wood has occurred in many Australian rivers, but restoration strategies now include its replacement. For example, in the Murray River between Albury and Yarrawonga, more than 5000 large red gum logs have been reintroduced (Figure 10.5) to provide additional structure and connection between habitat patches for native fishes. Such restored habitats are proving successful (Nicol *et al*. 2004) and illustrate the ecological importance of physical structure.

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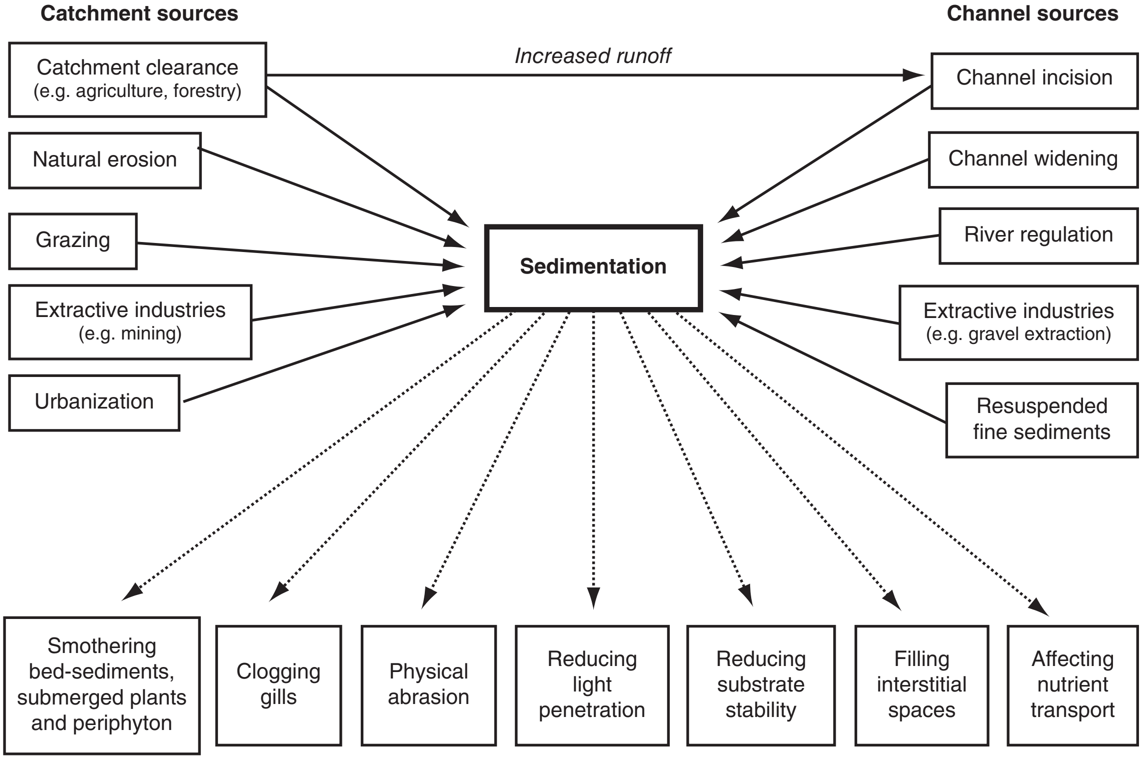

Figure 10.6 Sediments enter aquatic ecosystems from catchment sources and channel sources (solid arrows) and have many ecological effects (dotted arrows), explained in the text. (Source: Boulton and Brock 1999.)

sediment (especially when contaminated or fine enough to infiltrate and clog streambeds, Section 10.3.2), and the *locations* where the sediment settles out. When human activities alter natural sedimentation processes in standing and running waters, there are serious and often persistent ecological effects.

10.3.2 Ecological effects of sedimentation

In all aquatic ecosystems, the effects of sedimentation on **producers** have far-reaching consequences where periphyton and large aquatic plants form the basis of the food web (Henley *et al*. 2000). Turbidity from suspended sediment restricts primary production in the water column as well as in the littoral zone. Primary production is inhibited by reduction of light, physical damage to aquatic plants through abrasion, prevention of attachment of periphyton to substrata, and smothering of submerged plants and periphyton (Figure 10.6). There are often increases in nutrient transport and availability (leading to eutrophication, Section 11.3). Finally, in deep lentic environments, there are the physical effects of reduced light penetration on stratification depth and persistence (Chapter 2), with implications for water chemistry and biota (Chapters 3 and 4).

Benthic **macroinvertebrate** assemblages typically decline in abundance and taxonomic diversity in response to sedimentation (e.g. Campbell and Doeg 1989, Davies and Nelson 1994). In northern Queensland, mesocosm and field experiments adding silt to upland and lowland tropical streams revealed declines in densities and numbers of taxa, especially in the upland streams (Connolly and Pearson 2007). In lowland rivers, sedimentation affects recruitment of some aquatic invertebrates. For example, several species of gastropod and chironomid midge had reduced hatching from egg masses buried by sediments (Kefford *et al.* 2010). The influx of sediment into running waters often increases invertebrate drift (Section 7.7.1), presumably as an escape strategy. Suspended sediments impede feeding activities of many macroinvertebrates (Kefford *et al.* 2010) and smother their respiratory surfaces (Wood and Armitage 1997). Entry of fine sediments into the interstitial spaces of the hyporheic zone inhibits surface water-groundwater exchange (Section 8.2), reducing interstitial invertebrate abundance and diversity (Figure 10.6, Boulton *et al.* 2003) and smothering eggs laid in stream gravels by some species of fishes.

Marked declines in macroinvertebrate abundance occur during floods in sand-slugged streams such as the Creightons Creek system in north-central Victoria (O'Connor and Lake 1994). However, some groups such as chironomid midges that use silt to make their cases are favoured by sedimentation, and taxa associated with fine sediments (e.g. oligochaete worms, sphaeriid bivalves) may increase in number. Importantly, responses to sediment slugs are not always consistent across streams, even within a region. A subsequent study in the Creightons Creek system compared macroinvertebrates in several sand-slugged streams with those in unaffected clay-bed control sites; relative to controls, taxon richness and abundance in sand-slugged sections were lower in Creightons Creek, no different in nearby Castle Creek, and higher in Pranjip-Ninemile Creek (Downes *et al.* 2006).

Sedimentation has many adverse effects on **fishes** as well (reviews in Kemp *et al.* 2011, Lintermans 2012). Direct effects include reduction in growth rates, clogging of their gills, smothering of their eggs, increased stress and incidence of disease, reduction in available food (algae and invertebrates as described previously), and impairment of the efficiency of predation by visual hunters (Figure 10.6). Indirect effects include the loss of drought refuges such as pools when they become filled with sediment (Bond *et al.* 2008), damage or loss of spawning habitat, and modification of natural migration patterns.

Fundamental **ecosystem processes** such as respiration and photosynthesis can be substantially altered by sedimentation and sediment instability in sand-slugged rivers. For example, in Creightons Creek, an abrasive layer of sand now continuously moves downstream, severely inhibiting primary production by benthic algae in this unshaded clear stream with warm temperatures and sufficient nutrients (Atkinson *et al.* 2008). Enzyme activity by hyporheic microbes that regenerate nutrients in this stream is also affected by sedimentation, especially in unstable sand beds and bars during high flows. The combination of sedimentation and stream-bed instability in this sand-slugged creek largely governs rates and locations of benthic algal photosynthesis and microbial respiration (Atkinson *et al.* 2008), with obvious implications for the rest of the stream's food web.

10.3.3 Management of sedimentation

Effective management of sedimentation requires an understanding of the causes of the problem. Identifying where sediments originate is also critical because remedial actions differ depending upon whether most of the sediment originates from hillslopes or within the channel (Prosser *et al.* 2001). Models and sediment budgets have proved valuable tools for relating erosion processes to sediment yields and guiding effective management (e.g. Wilkinson *et al.* 2009) but site-specific assessments are essential to confirm model predictions. Sediments derived from erosion of the catchment can then be controlled by activities that reduce runoff rates, improve infiltration, and stabilize surface soils.

Revegetation is one obvious approach, and should be done with native species, preferably from the local area. Dense ground cover is usually planted to trap sediments and nutrients before they enter the waterbody. Planting trees and protecting vegetation on the banks and edges of waterways (Figure 10.7) serve to stabilize banks. This reduces channel erosion and is also a way for farmers to earn 'carbon credits' in keeping with government policy (in 2013) to combat climate change (Section 12.9).

There are several engineering approaches to remove sediment from standing and running waters. Dredging is expensive but in some waterways is necessary to reduce flooding risk and improve navigability of channels that have filled with silt. There are also various forms of silt traps used in urban streams; many of these also capture refuse and sediments high in heavy metals. The release of 'flushing flows' to scour sediments from channels and weir pools may cause temporary declines in macroinvertebrate and fish abundance (Doeg and Koehn 1994) but are usually successful in removing at least surface layers of silt (Thompson *et al.* 2007). Fine sediments deeper in the hyporheic zone are less readily removed and may need

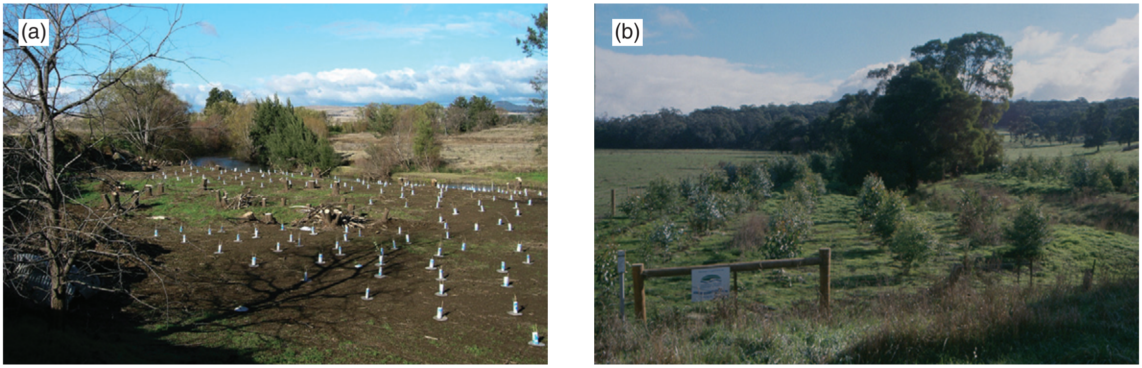

Figure 10.7 Riparian re-vegetation along (a) the banks of Whites Creek on the Hunter River, NSW, and (b) Boundary Creek in the Otway Ranges, Victoria. (Source: (a) Darren Ryder; (b) Belinda Robson.)

Box 10.4 Erosion in northern tropical Australian rivers

Considerable research now demonstrates that sediment supply in Australia's tropical rivers is dominated by sub-soil sources, caused mainly by channel and gully erosion (review in Olley *et al*. 2013). Initially, it was thought that sediment supply in these systems would be dominated by hillslope erosion. This was based on the assumptions that the open woodland vegetation that dominates the savannah, coupled with the intense tropical rainfall and seasonal burning regimes, would lead to high hillslope sediment yields, and that gully erosion was limited because the channel networks were at their fullest extent. Perhaps neglected in the original assumptions was that long-term slope evolution has meant that many of the steeper slopes are sediment-starved, and are either mantled by a cover of stones or stripped to bedrock. Hence, these slopes presently contribute very little sediment. Instead, much of the stored sediment that can potentially be mobilized in these landscapes is found in deposits at the base of slopes or in the extensive floodplains. The switch from indigenous management to cattle-grazing following European settlement often initiated or accelerated the erosion of these stored sediments, causing the erosion problems we see today.

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substantial bed-moving events. However, these short-term 'solutions' focus on the symptoms and are no substitute for channel and catchment management of sediment inputs.

In many cases, the dramatic changes in channel shape and sediment load soon after European settlement are beyond restoration to pre-European conditions. In these areas, new channel forms have often developed and management of sedimentation focuses on stabilizing the catchment and channels in these new configurations. Most areas where channel erosion commenced five or more decades earlier are now relatively stable whereas catchments cleared within the last 20–50 years may still be prone to major gully erosion (e.g. Shellberg *et al*. 2010, Box 10.4). High-risk areas are those where soils are exposed annually by traditional tillage techniques, rainfall is heavy and erosive, soils are dispersive or silty and hillslope gradients exceed 10%. In general, sediment management should focus on source streams and smaller tributaries before tackling the problem in major river channels downstream.

Other forms of restoration seek to add structure to streams adversely affected by sediment in an attempt to recover lost streambed complexity such as pools and riffles or to provide woody debris for habitat and spawning, especially in agricultural streams (Lester and Boulton 2008). In the sand-slugged Glenelg River, Victoria, restoration experiments removing sediment and replacing woody debris promoted spawning of the native flathead gudgeon *Philypnodon grandiceps* in restored runs but there were no clear positive effects on other fish species (Howson *et al*. 2010). Another restoration experiment adding wood to sand-slugged streams of the Granite Creeks complex, central Victoria, briefly increased the abundance of several native fish species but drought eventually eradicated fishes from both manipulated and unmanipulated sites (Bond and Lake 2005). Nonetheless, this study illustrated the potential for recovering streambed complexity in sediment-filled streams to re-create permanent pools that gave fishes refuge from drought.

Ultimately, the best approach for managing sedimentation is to restore near-natural rates of sediment inputs to the waterbody. Ideally, this would involve revegetation of catchments and restoration of lake and waterway geomorphology. However, because human uses of land for agricultural and urban purposes will continue, the reality is that only limited areas of the catchment can be revegetated and restored. Nonetheless, there is increasing interest in large-scale revegetation, especially as a means to mitigate carbon emissions (Mitchell *et al*. 2012), and perhaps there will be greater economic incentives to undertake large-scale control of sedimentation from erosive catchments using this approach. Again, these large-scale strategies require a landscape perspective that must effectively integrate the management of mosaics and networks of standing and running waters as well as their connected groundwaters and their land-water interfaces.

10.4 PHYSICAL PROCESSES AND LAND-WATER INTERFACES

In Australia, attention has focused on ways to manage sediment transfer across the land-water interface, especially where vegetation fringes standing and running waters. In Section 4.3, we saw how **fringing zones** are considered an integral part of all lentic waters because they are influenced by the presence of the water and mediate the transfer of energy, biota and organic matter and other materials between the aquatic ecosystem and the surrounding terrestrial landscape. In lotic environments, the **riparian zone** plays an equivalent ecological role (Section 7.2).

After reviewing the ecological roles of fringing and riparian zones, we then explore the human activities that threaten them and how best these might be managed. This section's emphasis is on the importance of preserving or recovering hydrological and ecological connectivity at multiple scales to ensure that fringing and riparian zones can function effectively.

10.4.1 Ecological roles of fringing and riparian zones

Most definitions of fringing and riparian zones based on landform or vegetation have practical limitations whereas legislative definitions for particular industries are often too restrictive, normally referring to a strip of set width. Consequently, ecologists prefer a **functional** definition such as that used for the riparian zone by the Australian National Land and Water Resources Audit (Sattler and Creighton 2002) that defines it as 'any land that adjoins, directly influences, or is influenced by a body of water.' This functional definition emphasizes the way that the riparian zone acts as an ecotone, sharing elements of the adjoining aquatic and terrestrial ecosystems but with its own special properties (Décamps 1993, Holmes *et al*. 2010). Being an ecotone, the riparian or fringing zone is vulnerable to threats from both aquatic and terrestrial directions, as we shall soon see.

These land-water interfaces have four main functions relevant to waterbodies: geomorphic influences, shading, litter inputs, and regulating nutrient and sediment fluxes (Cummins 1993, Naiman and Décamps 1997, Figure 10.8). To these a fifth one should be added – its ecological function as a habitat for a diverse biota whose activities influence the first four listed. These functions interact, and vary in importance depending upon the waterbody. For example, in a bedrock-controlled upland stream or lake, the geomorphic influence may be less than the effects of shading and input of leaf litter. In floodplain wetlands or lowland rivers where the riparian zone is harder to delineate, shading effects may be less significant than geomorphic influences or regulation of nutrient flux. In small streams with well-developed riparian zones, high litter input and shading imply that the ecosystem relies on allochthonous rather than autochthonous sources of energy (Section 7.4). Removing the vegetation of fringing or riparian zones is likely to change an aquatic ecosystem from one reliant for energy from

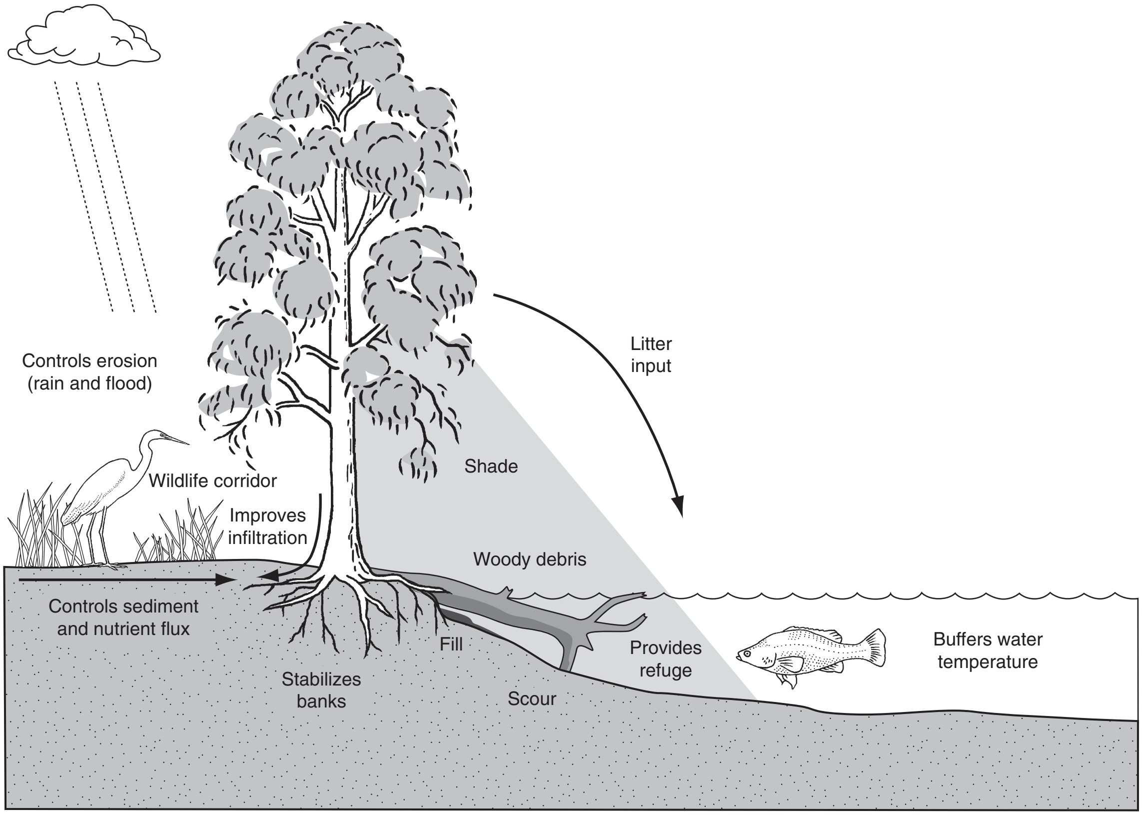

Figure 10.8 Main functional roles of fringing and riparian zones. (Source: Image drawn by Belinda Cale.)

detritus and terrestrial organic matter to one where autochthonous production supports the food web.

Logs and branches in the water retain leaf litter where it is broken down by microbes and invertebrates (Chapters 4 and 7), and the bank vegetation is a constant source of woody debris, both dead and living. This woody debris also provides habitat and spawning sites for native fishes (Box 10.3). Rooted vegetation stabilizes banks and undercut areas, creating refuges for many aquatic animals (Figure 10.8). In many streams in northern Australia, native fishes are threatened by degradation of the riparian zone that removes crucial habitat, alters food webs and favours invasion by non-native fishes (Pusey and Arthington 2003).

Riparian strips provide corridors for wildlife and, in arid areas, shelter and shade. For instance, common wombats (*Vombatus ursinus*) rely heavily on riparian zones in agricultural catchments in the south-east (Borchard *et al.* 2008). Fringing and riparian vegetation also protects the terrestrial stages of aquatic insects from extremes of weather and provides sites for egg deposition and for aquatic insect larvae to climb when they are ready to emerge as adults. Shading during the heat of the day is another crucial role, serving to buffer water temperature (Moore *et al.* 2005) and restrict evaporation. When shading is reduced by human activities, submerged plants and filamentous algae may flourish. In streams, this has been shown to alter in-stream carbon and nitrogen dynamics and the quality of food resources, with flow-on effects to aquatic invertebrates such as freshwater crayfishes (Giling *et al.* 2012).

Groundwater-surface water interactions (Chapter 8) strongly influence the functioning of fringing and riparian zones (Kalbus *et al.* 2006). One of the major processes involves denitrification (Section 3.9.2),

Box 10.5 Stream incision and riparian zone denitrification in Queensland streams

Denitrification in riparian zones can effectively remove nitrate from sub-surface water before it enters stream systems. This occurs when nitrate-laden water interacts with moist carbon-rich soil in the riparian zone, where conditions are ideal for denitrification. An assessment of riparian zones in the agricultural Maroochy Catchment of sub-tropical Queensland has revealed that incision of these streams has undermined the capacity of the riparian zone to act as a nutrient filter. This is of particular concern in these streams, which are naturally very low in nitrate. Stream incision, caused by a history of land clearing and agriculture, has lowered water levels in the stream and surrounding alluvial aquifers, causing water to travel though deeper carbon-poor soil layers where denitrification potential is much reduced. Incision also produces a drier aerobic soil column where nitrification can occur, building up a pool of nitrate during dry seasons. The reduced potential for denitrification, coupled with this potential build-up of nitrate in the soil profile, means that riparian zones of these incised streams have turned from a sink into a source of nitrate for these incised streams.

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the removal of nitrate from groundwater before it enters the waterway. However, erosion and channel incision can sometimes reverse this process and turn the riparian zone from a nitrate sink into a source (Box 10.5).

Grassed strips along streams filter sediments and nutrients extremely effectively because overland flow is slowed down by the grass, resulting in sediment deposition. For example, fencing and replanting the riparian zone of a 1.7-km section of an agricultural stream in south-western WA reduced sediment export from the catchment by an order of magnitude (McKergow *et al.* 2003). The presence of trees and other plants promotes water infiltration into the sediments (Dosskey *et al.* 2010) as well as supplying organic matter for microbial decomposition. In waterlogged soils, fringing vegetation also aerates the sediment, providing a fine film of aerobic soil around their roots (the rhizosphere). This fine-scale juxtaposition of aerobic and anaerobic conditions links crucial nutrient transformations such as nitrification and denitrification (Section 3.9.2). To be most effective, vegetated riparian zones need a combination of dense ground cover that acts as a filter and trees that stabilize banks and provide shade, wildlife refuges and organic matter.

10.4.2 Threats to land-water interfaces

Many human activities, exacerbated by the effects of climate change (Section 12.9), threaten the functions of land-water interfaces (Figure 10.9). Threats include levees and dams, point-source and diffuse-source pollution (Section 11.6), grazing and cropping to the water's edge, timber harvesting, water diversion, road construction, recreation and off-road vehicle use, mining and gravel extraction, groundwater pumping, invasive species, salinity and acidification, changes to burning regimes, insect attack and plant diseases, woody weed encroachment and removal of native vegetation, urbanization and fuel management (Richardson *et al.* 2007, Poff *et al.* 2011). These multiple stressors typically interact, and their interactive effects vary in importance at different locations along shores, among waterbodies, and across regions. Ecological responses are equally diverse and often system-specific.

Fringing vegetation is often cleared to improve access for stock, supply wood for fires and fencing, reduce local flooding by improving channel carrying capacity and, in populated areas, to 'beautify' urban wetlands and discourage flying-fox roosts, snakes and rats. Where rivers are straightened to facilitate run-off, channelization often inhibits regrowth of vegetation along the banks. Levee banks built to control and direct floods change the topography and vegetation while unrestricted grazing prevents re-establishment of many native species. For example, along the Murrumbidgee River in NSW, riparian condition declined with grazing intensity (Jansen and Robertson 2001). To maximize yields from the fertile land, cropping may extend almost to the water's edge, allowing nutrients,

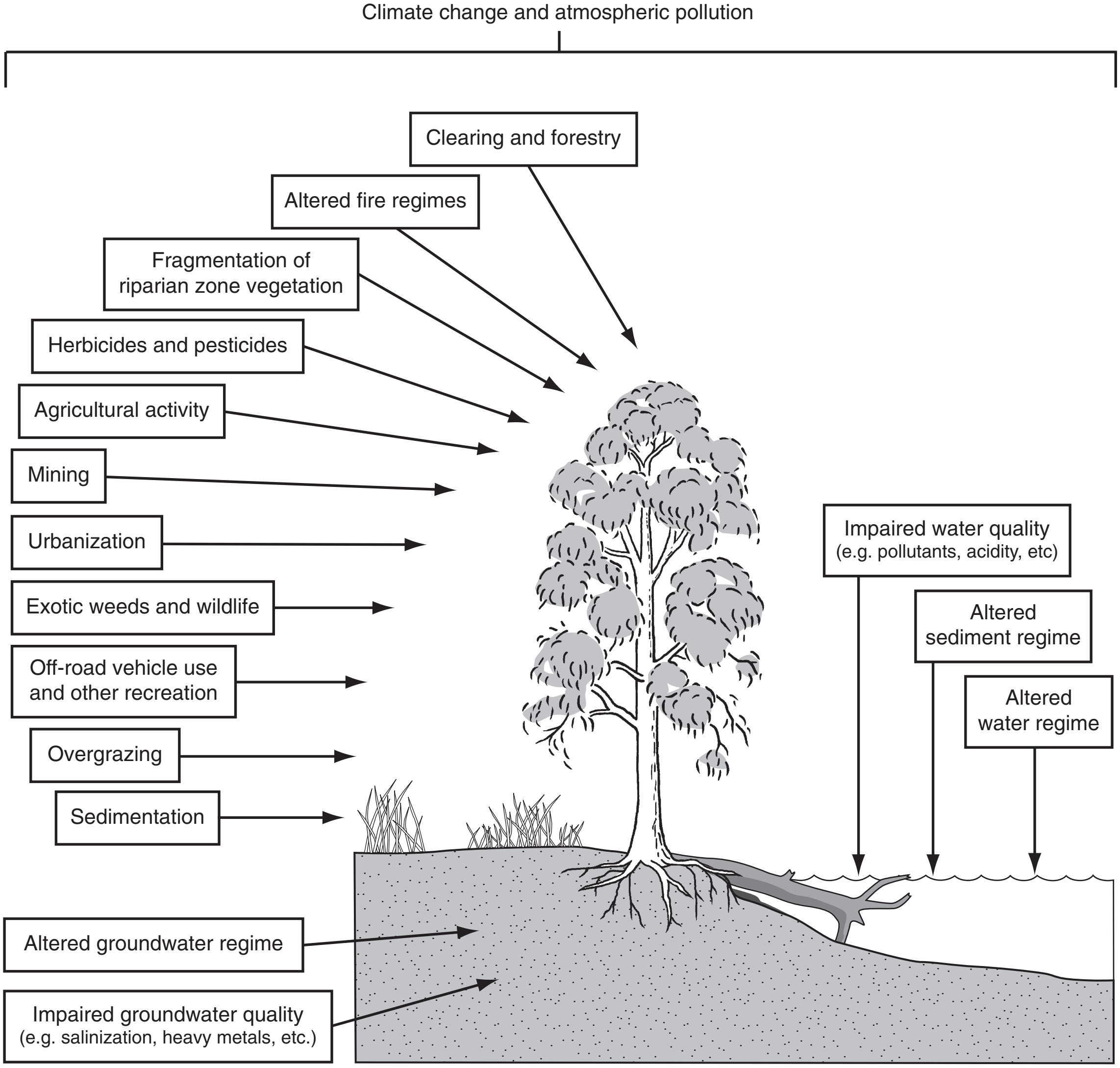

Figure 10.9 Numerous human activities threaten the ecological integrity and ecosystem services of functions of land-water interfaces. Because these zones are ecotones between land and water, threats arise from human changes to water regime as well as activities in the catchment. (Source: Image drawn by Belinda Cale.)

pesticides and herbicides to readily enter the waterway (Chapter 11).

Poorly managed logging threatens fringing and riparian vegetation, especially if the species being sought are typically found near water. Near town centres, standing waters and their fringing zones have often been used for rubbish dumps that have then been filled over using rubble and building waste. For example, between 1964 and 1974, the fringes of Lake Claremont, a groundwater-fed wetland on the Swan Coastal Plain, were used as a rubbish tip that was then converted to a golf course. This was closed in 2009 to restore the urban wetland although persistent effects of groundwater contamination from buried rubbish are likely. Natural regeneration of vegetation in these urban areas is often slow, especially when inhibited by leachates from historical domestic and industrial waste. The fringing zone and its vegetation are frequently damaged by multiple contaminants (Vidon 2010), including pesticides, heavy metals and acidic wastes from mining (Chapter 11), and saline seepage derived from water tables rising in response to land clearance.

Because of their ecotonal nature, fringing and riparian zones are especially prone to invasion by **exotic species** (Section 12.8). These create particularly severe management problems (Richardson *et al.* 2007). Invasive plants often smother and destroy natural vegetation or prevent it from becoming re-established once cleared. Most of the willow species in southern Australia are notorious examples. In northern Queensland, the rubber vine *Cryptostegia grandiflora* has invaded the riparian zones of many systems such as the 1700-km long Burdekin River (Lawes and Grice 2008). Other invasive woody species that are displacing riparian plants include pond apple *Annona glabra*, prickly acacia *Acacia nilotica*, Chinese elm *Celtis sinensis* and camphor laurel *Cinnamomum camphora*. The riparian zones of many small streams are infested with blackberry *Rubus* spp. that may grow across and shade the entire waterway. Introduced pasture grasses are also problematic in many fringing zones of rivers and wetlands, often outcompeting native grasses and sedges.

Fringing and riparian vegetation composition is greatly affected by **water regime**, particularly through changes in seed-set, germination and survival of recruits. In two contrasting WA rivers (the temperate Blackwood River and the subtropical Ord River), riparian vegetation assemblage composition and structure were strongly correlated with flooding frequency (Pettit *et al.* 2001). When natural water and sediment regimes are modified (Chapter 9), bank erosion and changes in base flow and patterns of flooding threaten native riparian vegetation. Altered water regimes often favour invasive species. For example, a survey of 24 riparian wetlands along the Murray River indicated that exotic plant cover was highest and native non-weed cover lowest in wetlands that had experienced the greatest change in hydrology from river regulation (Catford *et al.* 2011). Changes in inundation frequency often kill native fringing vegetation through flooding and drowning or excessive drying, opening up areas for tolerant invasive plants to become established.

Figure 10.10 After wildfire burnt the riparian zone of this Victorian stream in 2003, excessive sediment was washed into the channel, filling pools and smothering riffles. Note the dense epicormic regrowth from the trunks of some of the burnt riparian eucalypt trees. (Source: Andrew Boulton.)

Most of our native vegetation is subject to **wildfires**, and prescribed burning is common in many regions to protect homes, farms and other infrastructure. Experiments on burning regimes in the Australian tropical savannah indicate that although much of the terrestrial biota is resilient to fire, riparian vegetation and its associated biota are notable exceptions (Andersen *et al.* 2005). Wildfires in the south-eastern alpine areas in 2003 led to large sediment slugs extending down several hundred kilometres of stream channel (Figure 10.10), reducing fish abundances by 95–100% at some sites (Lyon and O'Connor 2008). It is likely that fire-related reduction of the riparian zone also removed habitat structure, organic matter and shading, further impeding post-fire recovery.

10.4.3 Management of land-water interfaces

The ideal situation is when the natural fringing and riparian zones are intact, and only vigilance is required to protect them. More commonly, they have been cleared of vegetation for decades and some form of revegetation is necessary. However, before vegetation can be reintroduced, the shore or bank usually needs to be stabilized and sources of sedimentation must be

Box 10.6 Seed banks and restoration of riparian vegetation

Riparian soils usually contain many seeds from a range of plant species. These 'soil seed banks' allow species to persist during unfavourable periods, sometimes for decades or more. Given suitable conditions (e.g. wetting), many of these seeds will germinate, enabling species to re-establish. Since only a proportion of seeds germinate at any time, riparian seed banks contribute to the long-term resilience of riparian vegetation (Capon and Brock 2006). Seed banks can play a role in riparian revegetation where disturbances have ceased or are managed (e.g. exclusion of grazing). As trees and shrubs rarely maintain persistent seed banks, riparian soil seed banks are particularly important for regeneration of species-rich herbaceous understoreys. Perennial herbs that usually rely on vegetative reproduction may also regenerate from seed banks after extreme disturbances (Reid and Capon 2011). Riparian seed banks themselves are affected by disturbances, especially clearing, which opens the area to outside seed sources, including those of invasive species. Therefore, passive restoration of riparian vegetation from seed banks may promote establishment of invasive species whereas actively restoring canopy vegetation will allow native seed banks to restore themselves over time.

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controlled (Section 10.3.3). Strict legislation now controls human activity in the fringing or riparian zone, and even if the intent is **restoration**, these legal requirements must be addressed before any revegetation or other works commence.

The success of programs to rehabilitate riparian vegetation has varied widely across regions, depending upon local environmental conditions, the severity of the impacts and the type of restoration used. Where restoration has failed, it is often because unexpected geomorphological processes have occurred (usually associated with severe floods), disease or herbivore outbreaks have impaired vegetation growth, or altered water regimes have affected re-establishment from the seed bank. Uncontrolled infestations of willow, blackberry and other invasive species prevent native plants from recovering, and maintenance of the restored riparian zone must continue long after the initial ground preparation and planting. Monitoring the success of restoration programs is essential to determine the success or otherwise of restoration programs (Mika *et al*. 2010). Often, well-planned and long-term experiments are needed (e.g. The Riparian Restoration Experiment, Box 13.6). Even when strategies fail, the results provide insights into how the system functions or what to do better in future (Section 13.3).

In southern Australia, willows used to be popular choices for riparian zone revegetation programs but they are now recognized as noxious weeds (Section 12.8). Instead, most land managers recommend that native species, preferably of local provenance, should be reintroduced. The long-stem planting method has been especially successful. Seedlings are grown in pots for 10–18 months until they develop long woody stems. They are then planted with three-quarters of the stem below ground. This buried stem develops a robust root network, greatly enhancing plant survival and stabilizing riparian sediments. Revegetation of riparian and fringing zones can be supplemented using material from local seed banks (Box 10.6). However, sometimes these seed banks contain propagules of invasive species as well and will help restore only some components of the riparian assemblage (Williams *et al*. 2008). It is usually necessary to fence areas where restoration is occurring, at least until the vegetation becomes established, because of the effects of livestock grazing and trampling (Burger *et al*. 2010).

In arid and semi-arid zones, fringing and riparian vegetation is naturally sparse around many waterbodies, and extensive replanting programs may not be warranted. Many streams in these areas are prone to flash floods that remove shallow-rooted riparian vegetation and substantially rework the stream channel, creating large gravel bars while scouring deep channels in other braids of the stream-bed. Water flowing through this gravel in the hyporheic zone undergoes substantial chemical transformations. Although riparian vegetation may be naturally lacking, the gravel beds probably serve as an equally important trap for sediments and nutrients. In other streams, especially those draining urban areas, riparian revegetation may be limited by constraints on available land as well as effects of the flashy hydrograph typified by high flows from impervious surfaces soon after rain (Walsh and Breen 1999, Groffman *et al*. 2003).

Another dilemma is determining the ideal **width** of an effective fringing and riparian vegetation. This is of considerable relevance to land-owners who set aside land that may be currently productive, necessitating a trade-off between the short-term profits from farming this land versus the long-term improvement in water quality and ecological condition. Although various widths (typically scaled to size of waterbody or stream order) have been proposed in guidelines for catchment activities such as logging, the substantial natural variation in the widths of these vegetated zones among sites (e.g. Mac Nally *et al*. 2008) implies that their delineation for protection or to guide restoration efforts should be established on a site-by-site basis. Both terrestrial and aquatic species must be considered and there are various biological criteria (e.g. Semlitsch and Bodie 2003) that guide this conservation process.

Often the focus is on establishing trees and shrubs but herbs, forbs and ground cover are also crucial. Similarly, aquatic vegetation at the 'blurred boundary' of the land-water interface must also be considered, especially in terms of the **water regime**. As we saw in Chapter 9, human changes to the season, duration, frequency, depth and variability of flooding have altered aquatic vegetation along the edges of land-water interfaces and on the floodplain. Manipulation of one or more of these components of the water regime components may help restore this vegetation by stimulating germination of the natural seed bank (Brock *et al*. 2000). The potential of this approach was explored in a large-scale experiment that simulated different frequencies, durations and extents of flooding in a purpose-built set of wetlands supplied with the same initial seed bank. Different water regimes allowed different species to germinate and establish (Brock and Crosslé 2002). Stable water levels (i.e. more permanently either flooded or dry) reduced available habitat, and rapidly raising or lowering water levels (as seen in many farm dams) did not allow time for aquatic vegetation to establish. Instead, slower fluctuations created a mosaic of habitats for a species-rich biota and demonstrate elegantly the link between water regime, species ecology, and vegetation dynamics at the land-water interface.

Finally, it is essential to realize that all management and restoration of fringing and riparian zones must be done in a landscape context, guided by appropriate models and empirical data. One theme throughout this book has been the importance of linkages at multiple scales, and we have seen how these govern physical, chemical and biological processes in standing and running waters at the landscape scale. Therefore, to be fully effective, restoration and management of ecotones such as the fringing and riparian zones that mediate these linkages must also be at the landscape scale (Sheldon *et al*. 2012, Box 10.7).

Box 10.7 Spatial scales of land use, riparian zones and river health

Stream ecosystem health, measured by a range of indicators from water quality to fish diversity, is strongly influenced by adjacent land-use. Some of these indicators respond to riparian factors while others are influenced by the cumulative effects of land use in the upstream catchment. To explore this further, we quantified the degree of influence of land use at nested spatial scales (catchment, reach and site) on 14 common indicators of stream health measured from over 120 sites in south-eastern Queensland between 2002 and 2008. Forest density close to the survey site and in the hydrologically active near-stream areas of the catchment, urbanization in the riparian buffer and tree cover at the reach scale were all significant in explaining ecosystem health, suggesting an over-riding influence of forest cover close to the stream. We used models generated from this analysis to predict that good ecosystem health can be maintained in catchments where 80% of hydrologically active areas close to the stream have mid-dense forest cover. Moderate health can be obtained with 60% cover. These restoration targets can now be used for riparian restoration within the south-eastern Queensland region.

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10.5 RECOVERING NATURAL PHYSICAL COMPLEXITY

In this chapter, we have seen how the natural physical complexity of many waterways has been severely reduced by sedimentation and various human activities such as de-snagging and engineering for access, water supply or flood control. This natural physical complexity, occurring across multiple spatial scales (Chapters 2 and 5), supports a diverse array of ecological processes and organisms (Chapters 4 and 7). However, simply restoring physical complexity or habitat heterogeneity is seldom adequate in a restoration program (Palmer *et al.* 2010), and must be supplemented by other strategies such as the recovery of near-natural water regimes, control of sedimentation, improvement of water quality and the reintroduction of native species. Furthermore, the spatial scale of this restoration of natural complexity is crucial to the success of the process, and should be as extensive as possible to have the most benefit.

Most restoration of natural physical complexity occurs at the reach scale or, in standing waters, at particular sites. One popular approach has been the reintroduction of woody debris, usually as engineered log jams (Figure 10.11) within the waterway (e.g. Bond and Lake 2005, Lester and Boulton 2008, Howell *et al.* 2012). In some rivers, these engineered log jams have been very successful in recovering streambed complexity. For example, Brooks *et al.* (2004) monitored the effects of 20 log jams installed in a 1.1-km reach of the Williams River, NSW, that had previously been de-snagged and had most of its riparian vegetation removed. After several large floods, there was a new pool-riffle sequence and an increase in pool depth, pool and riffle area and spatial complexity of the bed-material distribution compared to the control reach. Fish species richness and abundance also increased in the restored reach.

Figure 10.11 A newly built engineered log jam, upstream of Munni Bridge on the Williams River, NSW. These promote physical complexity of the channel and provide refuges from high flow. (Source: Sarah Mika.)

Frequently, new standing waters are constructed to fulfil purposes such as water storage, nutrient treatment or drainage control. Although the intention is seldom to enhance native aquatic biodiversity, this seems a missed opportunity. For example, many impoundments such as farm dams and reservoirs for water supply conventionally have steep and linear banks. However, habitat complexity can be readily engineered into the design to provide a variety of depths and sinuous shorelines. Shallows can be vegetated, islands added to provide waterbirds with refuge from foxes and other terrestrial predators, and flooded trees retained for roosting birds. Unfortunately, the ecological success of these efforts to restore natural complexity is seldom assessed formally. Although there are community education programs that promote the benefits of wetland restoration (Tennant-Wood 2004), few of these involve the public in gathering ecological data on the success of such efforts.

Efforts to restore natural physical complexity at a landscape or sub-catchment scale are rare in Australia, largely constrained by cost and opportunity. One impressive example is the channel restoration in the lower LaTrobe River, Victoria, where meanders have been reinstated in a section of river that had been straightened and heavily modified over the preceding century (Box 10.8). More of these sorts of projects are likely in Australia as it becomes evident that they are cost-effective, self-sustaining and ecologically successful.

All of these strategies to recover natural complexity must include efforts to control processes that would compromise the restoration. These processes include sedimentation, inputs of poor-quality water, altered water regimes, invasion by exotic species, and the presence of barriers to fish migration. Measuring the success of the restoration is essential, including monitoring appropriate control and reference sites (Box 11.7) and incorporating social, political and economic aspects into the program at the outset (Section 13.3).

Box 10.8 Large-scale river restoration of the lower LaTrobe River, Victoria

From 1880, the LaTrobe River catchment was cleared and the channel was straightened, removing some 74 natural meanders so that by 1980, the lower river was 25% shorter. This increased channel capacity by 67% and reduced the duration of overbank flow three-fold (Reinfelds *et al*. 1995). The ecological consequences of this river engineering, combined with de-snagging, vegetation removal and water extraction, were severe, prompting calls for restoration. Since the 1980s, fencing and revegetation of riparian zones have occurred along much of the lower LaTrobe River. Eight meanders have been fully or partly reinstated, and further works are planned. Focus is especially on cut-off meanders that have extensive remnant vegetation and where there is potential to improve access to other high-quality habitats. Meander reinstatements are seen as making best use of the available environmental flows because they can increase compliance with flow targets such as frequency of overbank flooding. Although the cost of reinstatement is high (~$250 000 per meander), this is substantially less than purchasing more water to achieve equivalent benefits (Hillemacher *et al*. 2012).

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The visual effect of restoration of physical complexity can be a powerful motivation for local communities to protect natural complexity and appreciate the importance of habitat heterogeneity in aquatic ecosystems.

Recovery of natural complexity to promote biodiversity presupposes that ecological connectivity is present and that the desired species can recruit to the restored basins and channels. This requires landscape-scale planning to protect or restore refuges and dispersal corridors, depending on the modes of recolonization by the biota (Chapters 4 and 7). All too often, restoring natural complexity at a fine scale is thwarted by lack of appreciation of broad-scale patterns of hydrological and ecological connectivity. Not only does this jeopardize successful ecological restoration, it also limits the commitment of adequate resources to restoration and creates unrealistic public expectations about rates of recovery (Williams *et al*. 2011). However, with improved technology for landscape-scale assessments of waterways and greater appreciation of the need for this broader context, there is scope for better planning to restore physical complexity of degraded standing and running waters across multiple spatial scales.

10.6 SYNTHESIS

Many aquatic management issues arise from the interaction of altered water regimes with anthropogenic physical changes to waterbodies and their catchments. Fringing and riparian zones at the interface of land and water usually bear the brunt of human activities in both these environments. Although these interfaces are among the most ecologically valuable on the planet (Strayer and Findlay 2010), they suffer numerous pressures that impair their ecological integrity and biodiversity. Removing or reducing these pressures and restoring damaged ecological processes require an understanding of the interactions between water regime, physical complexity and ecological connectivity at a range of spatial and temporal scales. Causes rather than symptoms must be addressed.

One of the main threats to natural physical complexity in waterbodies is sedimentation. Although strategies such as dredging or the release of flushing flows can be used to remove sediments, restoring near-natural processes of sedimentation is a better management approach because it addresses the cause rather than the symptoms. Seldom will restoration of physical complexity and processes be enough. Aquatic ecosystems experience multiple stressors, and management approaches must address these complex and interacting stressors. Frequently, alterations of water regime and the physical environment by human activities cause serious management problems associated with poor water quality, such as salinization, eutrophication and acidification. In the next chapter, we explore these water quality issues, including the many links back to processes and ecological effects covered in this chapter and in Chapter 9.

CHAPTER 11

Management issues: water quality

11.1 WHAT IS WATER QUALITY?

So far in this book, we have used the term **water quality** to collectively mean the physical, chemical and sometimes biological conditions in surface waters and groundwaters. Occasionally, we have referred to it as being 'poor' or 'good', implying some scale of value but without being specific. In a management context, water quality is commonly defined as a measure of the physical, chemical and biological characteristics of water necessary to sustain a **desired water use**. For example, water quality that might be considered to be 'poor' for human consumption may be classed as 'good' when found in a natural salt lake. Thus, water quality is assessed against criteria that define whether it is appropriate for a particular use, such as drinking water for humans or the ecological requirements of an aquatic ecosystem. This assessment usually entails comparisons with guidelines or threshold values, reviewed later in this chapter.

Many human activities alter water quality in lentic and lotic environments, either intentionally (e.g. diluting discharged waste) or as unintended (but not unexpected) consequences of modifications of water regime (Chapter 9) and physical features of basins, channels and catchments (Chapter 10). There is usually some 'detective work' needed to unravel the drivers of the changes in water quality. For example, a rise in salinity may be caused by a combination of land-clearing, changes in groundwater levels and diversion of freshwater inflows. To manage the causes of the problems, we need a good understanding of the mechanisms of cause-and-effect as well as how they interact.

After introducing a framework for assessing and managing mechanisms (causes, effects and ecological and management responses), we apply it to four major water quality problems in aquatic ecosystems in Australia and overseas: eutrophication, salinization, acidification and various forms of pollution. We then review the use of water quality guidelines and ecological risk assessments, approaches to sampling and biomonitoring, and finally, the complex interactions of multiple stressors affecting water quality in aquatic ecosystems.

11.2 MANAGING WATER QUALITY

One widely used approach to manage water quality involves a framework that explicitly includes assessment of the cause and mechanisms of the problem, their ecological effects and the ways in which management strategies might address these. This logical cycle (Figure 11.1) begins by identifying the human activities that are the **driver** or main cause of the problem, which generates a **stressor** (e.g. salt, nutrients) causing particular **ecological impacts**. These impacts may include death of vulnerable biota or blooms of nuisance algae, and usually result in a loss of **ecosystem services** such as provision of drinking water or the recreational benefit of a waterbody. Ideally, this loss provokes a **management response** to address the problem, and Figure 11.1 indicates one or more points where intervention will produce the best outcome. Monitoring the effectiveness of these different management responses is essential and feeds back into our

Australian Freshwater Ecology: Processes and Management, Second Edition. Andrew J. Boulton, Margaret A. Brock, Belinda J. Robson, Darren S. Ryder, Jane M. Chambers, and Jenny A. Davis.

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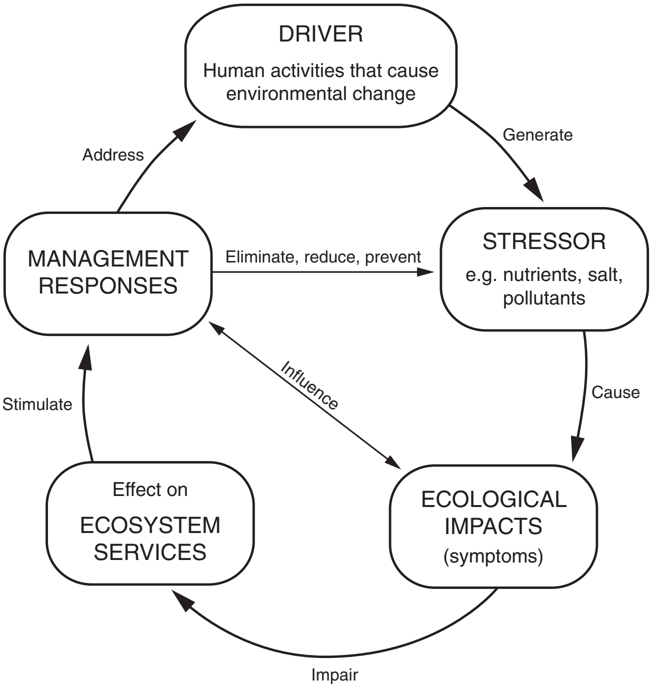

Figure 11.1 A management framework that shows how human activities (driver) generate a particular stressor that has ecological impacts affecting ecosystem services and eliciting management responses. These responses can intervene at different steps in the cycle, and their effectiveness is assessed by monitoring and evaluation.

understanding of the drivers, ecological impacts and benefits of various management strategies (i.e. **strategic adaptive management**, Section 13.3). Resources for environmental management are always finite and we must use them as effectively as possible. Therefore, we must continually monitor our success in managing issues and allocating resources.

Potential solutions in the short to medium term are usually aimed at quickly alleviating the symptoms to avert economic or other hardship. However, sometimes a long-term solution can be achieved rapidly (e.g. prevention of the release of pollutants from industry). Note that the speed at which we solve the problem is different from whether the solution is short- or long-term. Nonetheless, many long-term solutions entail ecological restoration to recover lost or impaired ecosystem services, often taking many years (e.g. re-establishment of native vegetation in the riparian zone, Section 10.4.3).

A key point about the management framework in Figure 11.1 is that there are multiple places for management intervention. Several strategies can be applied at once. A logical framework like this one helps us to identify and distinguish the drivers, stressors and ecological impacts so that we have a better understanding of the problem and therefore can design the most effective management approaches to restore and protect the ecosystem and its services. This is the same way we used conceptual models in Chapters 1–8; diagrams that represent very complex situations but help us see likely links and are always open for testing and refinement.

The framework can be supplemented by tabulating aspects of each water quality issue (Table 11.1) to reveal where drivers and ecological responses might interact, what sorts of effects on different ecosystem services might be expected, and what short- and long-term management options exist. Of course, all these

Table 11.1 Summary of the main drivers, stressors, major ecological impacts and effects on ecosystem services and some examples of management responses for the four water quality issues reviewed in this chapter.

	Driver	Stressor	Major ecological impacts	Major effects on ecosystem services	Examples of management responses	
					Short–medium term	**Long term**
Eutrophication						
	Human activities that increase nutrient inputs to waterways	Excess nutrients (mainly compounds of nitrogen and phosphorus)	Increased plant growth resulting in accumulation of organic matter, and often hypoxia	Loss or impairment of provisioning (e.g. drinking water, fisheries), supporting (e.g. nutrient cycling), and cultural services (e.g. recreation, aesthetic appeal)	Remove algal blooms; dredge sediments; aerate water; add chemical agents to bind nutrients	Improve land management; remediate sediments; use slow-release fertilizers; restore riparian vegetation
Salinization						
	Human activities that cause saline water tables to rise (e.g. land clearing, irrigation of crops) or that modify water regime to favour salinization	Increased salinity	Death or decline in abundance of salt-intolerant freshwater biota; increase in salt-tolerant species	Loss or impairment of provisioning (e.g. drinking water, fisheries), supporting (e.g. nutrient cycling), and cultural services (e.g. recreation, aesthetic appeal); damage to infrastructure; loss of biodiversity	Divert saline runoff from entering freshwaters; release flushing flows to dilute saline water; draw down saline groundwater levels through pumping or deep drainage	Replant deep-rooted vegetation in catchment to reduce groundwater levels through increased evapotranspiration; adopt different irrigation methods to conserve water
Acidification						
	Human activities that expose acid sulfate soils, release acidic groundwater or acid mine drainage, or produce acid rain	Decreased pH	Harm to biota; reduction in nutrient availability; increased solubility and toxicity of metals	Loss or impairment of provisioning (e.g. drinking water, fisheries), supporting (e.g. nutrient cycling), and cultural services (e.g. recreation, aesthetic appeal); damage to infrastructure; loss of biodiversity	Treat with lime or other alkaline material; restore reducing conditions by adding organic matter	Avoid exposure of acid sulfate soils; regulate storage and runoff from mines and tailings; control industrial emissions
Pollution						
	Human activities that release contaminants (listed in Table 11.2) into waterbodies	Presence of contaminants (listed in Table 11.2)	Lethal or sublethal impacts (listed in Table 11.2) on aquatic biota and ecosystem functions	Loss or impairment of provisioning (e.g. drinking water, fisheries), supporting (e.g. nutrient cycling), and cultural services (e.g. recreation, aesthetic appeal)	Filter and chemically treat water to remove some contaminants; contain and seal off contaminated water	Identify and control sources of contaminants; educate public and industry to reduce pollution and inputs to drains and waterways

ecological processes are closely interwoven and linked in space and time at different scales. Managing these processes is not easy, and individual components often cannot be teased apart. Table 11.1 can be used to help us investigate how aquatic ecosystems respond to four common stressors caused by human activities, and explore how best to use our ecological understanding of aquatic ecosystems (Chapters 1–8) to identify feasible and effective management responses.

11.3 EUTROPHICATION

Eutrophication is the process of **nutrient enrichment** in waterbodies that causes excessive plant growth and accumulation of organic matter. The effects on ecosystem services in standing and running waters are usually undesirable and attract public attention. Eutrophication occurs naturally but when human activities accelerate the process, management intervention is needed.

11.3.1 Natural and anthropogenic eutrophication

Natural eutrophication is fuelled by nutrients from sources including the atmosphere, groundwater and the catchment (Section 3.9). Nutrients adsorbed on sediments or dissolved in the water accumulate in lentic and lotic waters, and are taken up by aquatic plants (Figure 11.2) and animals. Over thousands of years, most basins fill with organic material and sediment, and eventually become terrestrial ecosystems. Relative to the surrounding landscape, excessive nutrients have accumulated in these basins and natural long-term eutrophication has occurred.

Figure 11.2 A wetland rich in organic matter on the nutrient-poor sands of the Swan Coastal Plain near Harvey, WA. Shallow waterbodies may be relatively nutrient-rich but most of the nutrients are bound in living (fringing vegetation) and dead (detritus) organic matter. (Source: Jane Chambers.)

Human activities accelerate the natural process of eutrophication by adding nutrients to the water. This anthropogenic eutrophication is seldom intentional, and often arises as a result of the release of effluent from sewage treatment plants, nutrient-rich runoff from fertilized crops and urban lawns, or inputs from various industries. Managers focus on anthropogenic eutrophication, and need a good idea of the drivers, stressors and processes so that they can intervene appropriately to control the problem. Of course, the most obvious response is to curtail nutrient inputs, but for pragmatic (not necessarily scientific) reasons, that option may not be practical.

11.3.2 Drivers, stressors and processes of eutrophication

Eutrophication is primarily caused by increased concentrations of various compounds of nitrogen and phosphorus (the **stressors**), as these are the two nutrients usually in the most limited supply in waterbodies (Section 3.9). Management often focuses on phosphorus (P) because it is often limiting and exists in fewer chemical forms, whereas nitrogen (N) occurs in many chemical forms and can be fixed from atmospheric sources, primarily by cyanobacteria. For example, in 2010, an N:P ratio <5 promoted the growth of the nitrogen-fixing cyanobacterium *Nodularia spumigena* in Lake King in Gippsland, Victoria (Holland *et al.* 2012). Initially, diatoms dominated the phytoplankton. However, over time, the cyanobacteria were able to use all the available P while fixing their own N, outcompeting the diatoms. This cyanobacterial bloom caused a greater problem than the diatoms because it was denser and potentially toxic to fishes and other biota. Although N and P are the usual causes, eutrophication can be driven by an excess of any nutrient that limits growth. Diatoms require not only N and P but sufficient dissolved silica for their outer shell (Section 3.6.2). Consequently, enrichment with silica can fuel diatom blooms provided other factors such as flow or turbidity do not limit their growth.

Many people associate eutrophication just with algal blooms but we must keep in mind that all aquatic plants can flourish when supplied with extra nutrients (and assuming there are no other constraints on their growth). For example, high concentrations of nutrients cause outbreaks of floating plants such as duckweeds and the water fern *Azolla* (Section 3.9.2) as well as invasive plants such as alligator weed *Alternanthera philoxeroides* and water hyacinth *Eichhornia crassipes*, often shading and killing submerged plants and causing other ecological problems (e.g. in the wet tropics in Queensland, Tsatsaros *et al*. 2013). In addition to ecological impacts (Section 11.3.3), blooms of these plants impair recreational use of the water and clog filters on offtake pipes.

Nutrients such as nitrate (NO_3^-), ammonium (NH_4^+) and phosphate (PO_4^{3-}) are taken up by aquatic plants during growth (Figure 11.3). When the plants

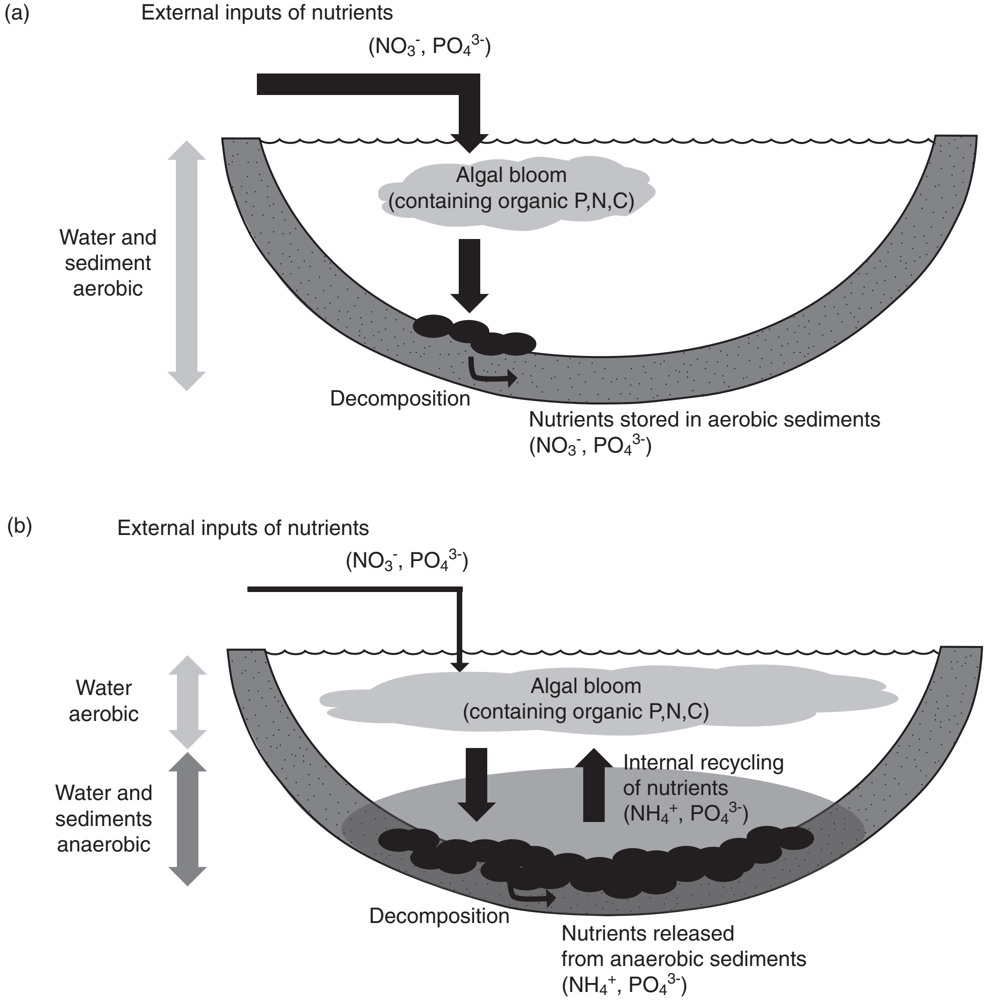

Figure 11.3 Two stages in the process of eutrophication. (a) Initially, external inputs of nutrients cause a bloom of aquatic plants (in this case, algae). When the bloom collapses, organic matter settles at the bottom and is decomposed without severely depleting dissolved oxygen. During this process, mineralized nutrients are stored in the aerobic sediments. (b) Later, with further and larger blooms, excessive organic matter accumulates on the bottom. The increased microbial decomposition consumes all the dissolved oxygen in the sediment and overlying water (shaded oval). Under these anaerobic conditions, ammonium and phosphate are released into the water. This internal recycling provides another source of nutrients to fuel further algal blooms that may persist even if external inputs of nutrients decline.

die, they are decomposed by microbes, releasing ammonium and phosphate to the water column. These nutrients 'recycled' from the decomposing organic matter constitute an **internal nutrient load**. When excessive organic matter accumulates, oxygen in the sediment and water column is soon consumed by aerobic microbial respiration. After the oxygen is gone, anaerobes use other electron acceptors such as iron for respiration (Section 3.7), which releases phosphate bound to the iron and other metals, further promoting the internal recycling of nutrients. Thus, although the input of nutrients from the catchment is the driver that initiates eutrophication, once sufficient organic matter and nutrients have accumulated in the sediment, internal recycling can maintain excessive plant growth without further external inputs. These internal nutrient loads can be huge. For example, in a water supply reservoir near Orange, NSW, during anoxic periods in summer, internal loads of inorganic phosphate and ammonium were 365 and 338% of their external annual loads (Al Bakri and Chowdhury 2006).

Although nutrient enrichment is the primary cause of eutrophication, other factors can affect whether excessive plant growth will occur. Therefore, managers may be able to use these other factors to solve problems associated with eutrophication, such as blooms of potentially toxic cyanobacteria (Box 11.1). Factors such as flow, water residence time, turbidity and stratification may all influence when blooms will occur in Australian rivers (review in Davis and Koop 2006). This also means that predicting when a bloom will occur is seldom easy because it is not always triggered simply by an influx of large amounts of nutrients.

The main **driver** of eutrophication is human activities that export nutrients from catchments into waterways, including sewage inputs. Much of Australia is highly weathered and nutrient-deficient. In this landscape, fertilizers are necessary for economic agricultural production, and eventually dissolved and particulate nutrients enter surface and groundwaters. Clearing land (Chapters 9 and 10) often causes erosion, promoting the input of sediment-bound nutrients.

Nutrients enter waterways from **point** or **diffuse** sources. Point sources such as dairy sheds or sewage treatment plants discharge from one or more pipes and are relatively easily managed. Diffuse sources (i.e. when inputs occur across broad areas) are much more difficult to manage. Of increasing concern is the pollution of groundwater with nutrients, particularly nitrate in agricultural areas (Drewry *et al*. 2006). When surface inflows are low, groundwater contributions of nutrients into surface waters may be substantial. For example, in the Swan River, WA, during the dry summer months when warm, still conditions promote algal blooms, groundwater delivers 55% of the flow and about 10% of the total nitrogen load (Linderfelt and Turner 2001). Groundwater can hold

Box 11.1 Managing cyanobacterial blooms in lowland rivers by understanding interactions with flow

Blooms of cyanobacteria are common in the lowland rivers of the Murray-Darling Basin. *Anabaena circinalis* is one species of particular concern because it can produce saxitoxin, a potent neurotoxin. Low flows can lead to persistent thermal stratification, which can contribute to the formation of *Anabaena* blooms during the hotter months. Under these conditions, *Anabaena* uses buoyancy mechanisms to remain in the well-lit surface waters, allowing it to compete successfully for light with other phytoplankton. Blooms can occur within two weeks under these conditions. The onset of persistent stratification is related to flow velocity, and a velocity $>0.03\,\mathrm{m\,s^{-1}}$ is generally sufficient to prevent persistent stratification. As *Anabaena* growth is related to flow, flow-management strategies can be used to prevent blooms. Knowing the channel area of a river section, managers can calculate the discharge that corresponds to that velocity. They can then protect flows (through limits on water extraction) or release water from impoundments (e.g. environmental flow allocations) to keep flow levels above these critical thresholds for bloom development and so prevent these problematic cyanobacterial blooms.

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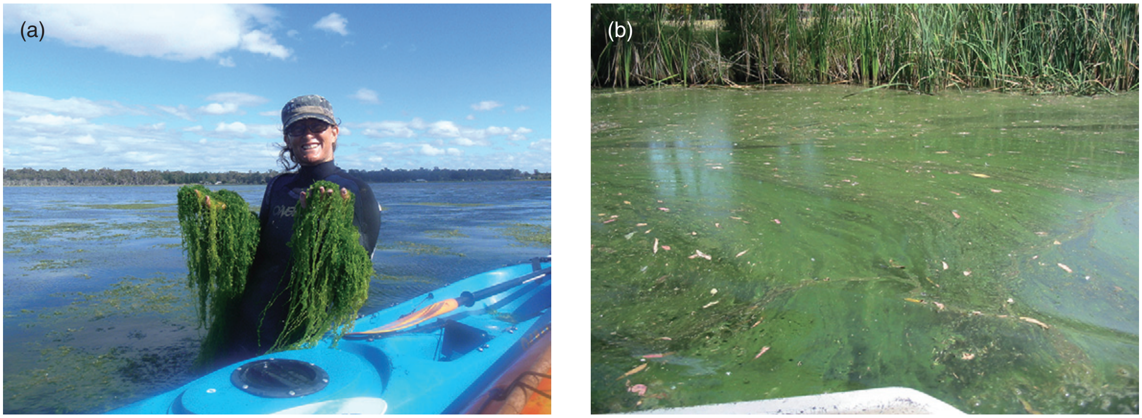


Figure 11.4 (a) Macroalgae in the Vasse-Wonnerup Wetlands, WA, and (b) a cyanobacterial (*Microcystis* sp.) bloom in the Canning River, WA. (Source: (a) Jane Chambers; (b) Peter Novak.)

significant stores of nutrients that move slowly but inexorably towards lakes and rivers. Fertilizers applied 50 or more years earlier can eventually cause eutrophication in a wetland or river receiving this time-lagged nutrient-rich groundwater.

11.3.3 Ecological impacts and effects on ecosystem services

The most obvious ecological **impact** of eutrophication is excessive plant growth. Most of us have seen (and smelt) accumulations of aquatic plants (Figure 11.4) washed up on the shore or that turn water bright green, red or brown, depending on the blooming species. Anthropogenic eutrophication typically enriches the water column with dissolved nutrients, favouring algae that acquire their nutrients from the water column over rooted aquatic plants that gain most of their nutrients from the sediments. With increasing nutrient enrichment, there is usually a progressive change in dominance from submerged rooted aquatic plants to algae. At very high nutrient concentrations (especially of phosphorus), cyanobacteria often dominate, helped by their capacity to fix atmospheric nitrogen.

Although the increased plant growth creates food for grazers, their feeding pressure is rarely sufficient to reduce the bloom because the excess nutrients allow such rapid plant growth. This rapid growth eventually depletes available nutrients in the water and the bloom collapses, blanketing the sediment with dead cells and other detritus. These build up to form a flocculent layer that can often be re-suspended by wind, waves or flow, increasing the turbidity of the water and releasing nutrients back into the water column. Sometimes, this promotes fresh algal blooms, and the process may persist for months.

Microbial decomposition of the organic matter derived from the dead bloom can deoxygenate the water column, usually killing aerobes such as fishes (Figure 11.5). Their rotting corpses provide further detritus for microbial decay. Some of these microbes cause other ecological problems. For example, the bacterium *Clostridium botulinum* (type C) produces a toxin when water temperatures exceed 25°C and can poison waterbirds foraging in the sediments. This poisoning, known as botulism, sometimes kills large numbers of waterbirds in eutrophic waterbodies during summer (Galvin *et al*. 1985).

The increased turbidity, reduced light and oxygen (Figure 11.5), and the presence of algal blooms impair many **ecosystem services**, especially the provisioning, supporting and cultural ones. Cyanobacteria cause taste and odour problems in water supplies and compromise aesthetic values. Some cyanobacteria release toxins when they decompose. Several species of *Microcystis* and *Oscillatoria* produce hepatotoxins that can kill domestic and farm animals and cause liver damage in humans, and species of *Anabaena* produce a

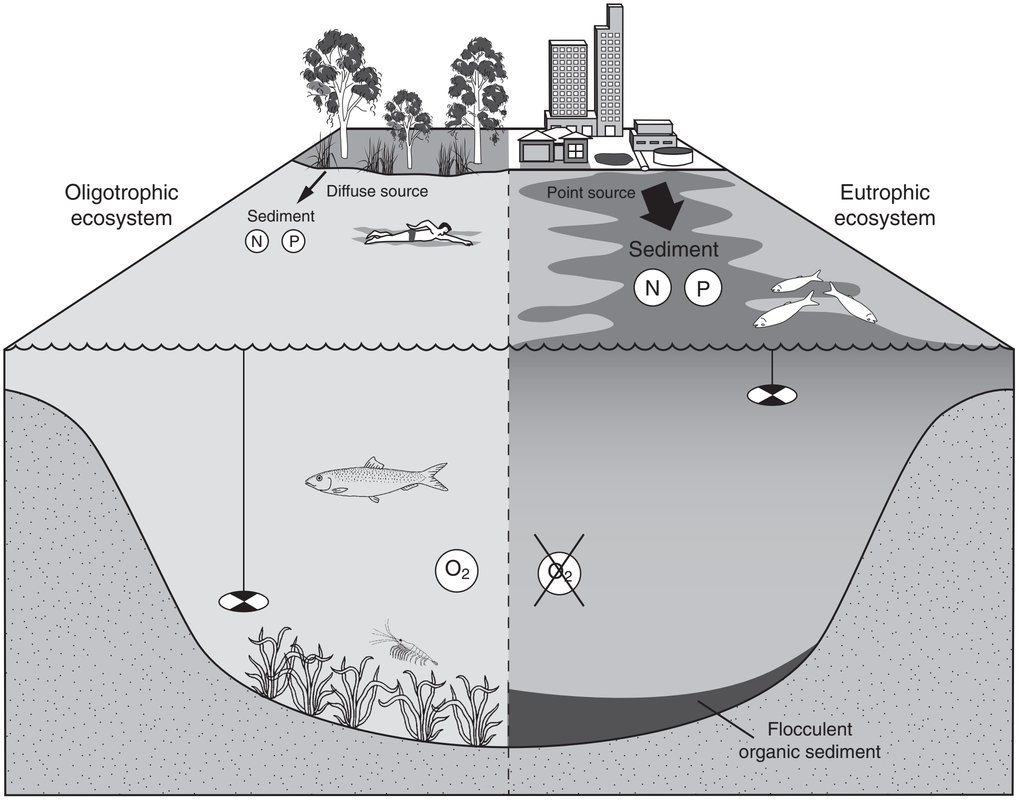


Figure 11.5 Ecological effects of eutrophication. In the left hand panel, nutrient inputs and sediment loads from diffuse sources are low, the system is oligotrophic with low biogenic turbidity (high Secchi depth), oxygen concentrations are high, aquatic biota flourish and the water is safe for swimming. In the right hand panel, a sewage treatment plant emits nutrients from a point source and the system is eutrophic. Sediment loads and turbidity are high, oxygen concentrations are low or near zero, and dying plant material accumulates as flocculent organic sediment. Aerobic organisms such as fishes die and many ecosystem services are impaired. (Source: Bricker *et al.* 2007. Modified and reproduced with permission of National Centers for Coastal Ocean Science. Image drawn by Belinda Cale.)

neurotoxin that may also be fatal to livestock. However, there are no Australian cases of human deaths from either group of toxins (Stewart *et al.* 2006). Recreational activities that involve body contact with water such as swimming and boating may be banned in eutrophic waters for many months and the negative effects of this on public confidence and tourism can be serious. A single cyanobacterial bloom in Lake Hume reduced the estimated recreational value of $3 million per annum by one-third (Crase and Gillespie 2008).

Diversity of native species declines and the lack of submerged plants further reduces the habitat complexity of the waterbody. Fisheries may collapse and supporting services carried out by key ecological processes (e.g. nutrient cycling, denitrification) are usually impaired. The rich stores of benthic detritus support immense populations of larval chironomid midges (bloodworms). People living near eutrophic urban wetlands complain about the huge swarms of emerging adult midges attracted to house lights at dusk. Nuisance insects that flourish in eutrophic waters can affect quality of life, health and economic value in affected areas (e.g. parts of Hervey Bay, Queensland: Ratnayake *et al.* 2006).

11.3.4 Management of eutrophication

The most effective management seeks to address the cause of the problem, in this case, reducing the input of nutrients using strategies such as changing land use, reducing fertilizer use and using slow-release fertilizers, amending soils to improve nutrient retention, controlling erosion and restoring riparian vegetation. However, stopping the input of nutrients will not immediately reduce their concentrations in a waterbody because nutrients may continue to enter from the catchment and groundwater for decades. Therefore, while reduction of nutrient inputs addresses the ultimate cause, more immediate measures are usually needed to treat the symptoms and quell public concern.

Short- to medium-term management usually involves treating the symptoms of eutrophication by removing blooms physically (e.g. using machinery to remove algal biomass) or chemically by 'bombing' blooms with copper sulfate or spraying a phosphorus-binding agent (Figure 11.6). Other short-term options involve modifying physical, chemical or biological processes in a waterbody. Physical modifications include destratifying standing waters (Box 2.3) or flushing nutrients from them (Box 11.1) using environmental water allocations (Section 9.5). Engineering options sometimes involve cutting channels as in the case of the eutrophic Peel-Harvey Estuary to improve tidal flushing (Wildsmith *et al*. 2009) or constructing retention basins that are planted with vegetation to remove nutrients. These 'constructed wetlands' need careful management to ensure nutrient uptake processes are maintained and that they are not overwhelmed by inputs of nutrients or associated pollutants.

Figure 11.6 One management option for reducing eutrophication is to spray a phosphorus-binding agent into rivers. (Source: GeoCatch WA.)

Chemical modifications often attempt to prevent nutrient release from the sediment by increasing the redox potential of the sediment either through aeration or by adding nitrate. It may seem counterintuitive to add nitrogen to reduce eutrophication but as phosphorus is often the limiting nutrient, adding nitrate can prevent the release of phosphorus bound to iron ions because the nitrate increases the redox potential (Section 3.7). In severe cases, drastic measures are needed, such as dredging the nutrient-rich sediments or chemically treating the water to precipitate out phosphorus with alum (aluminium sulfate) or other compounds.

Long-term solutions often take advantage of natural ecological processes. Earlier in this book, we saw how shallow waterbodies provide excellent conditions for denitrification, sedimentation and nutrient uptake. Managers take advantage of these conditions to reduce nutrient export from the catchment, by either protecting natural wetlands whose vegetation will temporarily intercept nutrient-rich water or by restoring riparian vegetation along drains and waterways. One challenge in controlling eutrophication is that so little nutrient is needed to promote blooms. Soils typically contain 200–500 mg L^{-1} of P whereas the minimum threshold for algal blooms to occur is 0.02–0.05 mg L^{-1} (Wasson *et al*. 1996). Consequently, it may not be possible in an agricultural or urban catchment to reduce nutrient inputs to the level required to prevent algal blooms.

Long-term management of eutrophication is also a social issue. Figure 11.1 shows the sequence of linked effects of a stressor on the aquatic ecosystem and the various points at which management intervention is possible. This underpins the 'treatment train' approach (Australian Government 2002), which has a major social component requiring changes in public behaviour and attitude to, in this case, nutrient inputs. A typical treatment train from nutrient source to sink might include land-use planning, eco-efficiencies such as reducing wastes and promoting recycling in industry, agriculture and the home, water-sensitive urban design, source control (including education to promote environmental awareness), best practice in drainage design, and management and effective treatment, reuse and disposal of wastes. Unless there is a public and political willingness to adopt long-term management measures, symptoms will continue to be treated in a costly and temporary way.

11.4 SALINIZATION

Salinization of inland waters is the process that increases their concentrations of dissolved salts (Williams 1987). In areas where evaporation exceeds rainfall, salts readily accumulate in soils. In these dryland areas, comprising nearly a third of the world's land area, salinization poses a serious threat to many ecosystem services including drinking water quality, agricultural production, fisheries and even the foundations of buildings. Many human activities accelerate salinization, and it is rated by the Millennium Ecosystem Assessment (2005) as one of the major stressors of freshwater ecosystems.

11.4.1 Natural and anthropogenic salinization

Salinity is a natural part of much of the Australian landscape. Salt, mainly sodium chloride, accumulates across the huge areas of the continent with low rainfall, high evaporation rates and often internal or no coordinated drainage (Section 1.5.4). This salt primarily comes from either ancient deposits of marine sediments or from the ocean carried by wind and rain. It accumulates near the surface, carried by capillary rise through the soil profile, where it is concentrated by evaporation. Salt concentrations in waterbodies can exceed that of seawater ($35\,\mathrm{g\,L^{-1}}$) up to the maximum solubility of sodium chloride ($\sim 360\,\mathrm{g\,L^{-1}}$), especially while salt lakes are drying out.

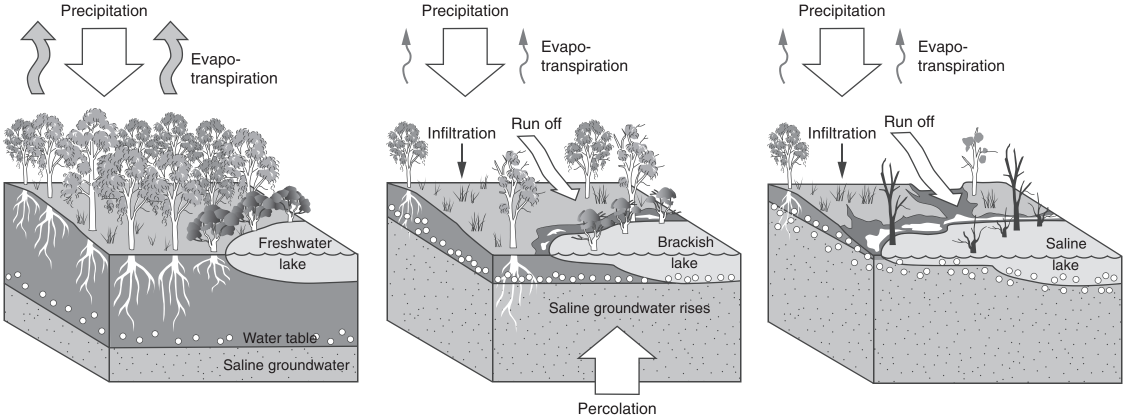
Natural salinization, termed **primary salinization**, has occurred for millennia (e.g. the wheatbelt region of south-western WA for 2.8 million years, George *et al.* 2008) and naturally saline standing and running waters are common across most of Australia (Timms 2007). Not surprisingly, many native aquatic species can tolerate high concentrations of salt (Chapters 4 and 7). Anthropogenic salinization, often called **secondary salinization**, arises from diverse human activities such as land clearing and irrigation that raise groundwater tables, mining and other industries, and even effluent from sewage treatment plants (review in Cañedo-Argüelles *et al.* 2013).

11.4.2 Drivers, stressors and processes of salinization

The primary **driver** of secondary salinization in Australia is human activity that causes saline water tables to rise (e.g. land clearing and irrigation of farms) or that so modifies the water regime of a waterbody that its dissolved salts increase. Secondary salinization is particularly common in dryland areas where there is sufficient rainfall to support agriculture or where rainfall is supplemented by irrigation. The process is usually mediated by groundwater, and the distribution of salinized land in Australia closely corresponds with the presence of groundwater tables within two metres of the surface or where groundwater levels are rising owing to clearing or irrigated agriculture. Salinization occurs at a regional scale and is a diffuse-source rather than point-source issue.

Salt is the primary **stressor** on freshwater biota through its effect on the osmotic potential of water. Organisms can either regulate their internal salt concentrations or tolerate some variation (Section 4.8) but eventually, increasing salinity exceeds their ability to do so. This stresses and ultimately kills most freshwater plants and animals as salt concentrations exceed physiological thresholds. Sometimes, even quite small changes in salinity can have major effects on community composition (Kefford *et al.* 2011).

Across much of Australia, **dryland salinization** results from land clearance. Replacement of deep-rooted native trees with shallow-rooted crops reduces the amount of evapotranspiration (Figure 11.7). Rainfall inputs exceed evapotranspiration, leading to a rise in the groundwater that carries salt previously stored in the soil up to the surface. As the groundwater approaches the surface, evaporation concentrates the salts in the shallow groundwater, which often emerges from saline seeps, affecting soils, terrestrial vegetation and surface waters. Saline seeps may be only small areas of the total catchment yet contribute most of the salt. For example, almost all salt exported by streamflow from an ephemeral, non-irrigated catchment in the central Murray-Darling Basin came from saline seeps that occupied <2% of the catchment area (Hughes *et al.* 2007). Where saline seeps emerge, salt crusts or **scalds** often form. These are evident as patches almost devoid of vegetation, often with precipitated salt spreading slowly out from the edges.



Before clearing

Most water is used where it falls. The system is in balance. Freshwater lake supports diverse biota.

After clearing

Saline groundwater rises and is concentrated at the surface by evaporation. Lake becomes brackish, water levels rise, and freshwater biota decline.

Later

Accumulation of salt at the surface and along lake shore. Erosion of denuded catchment. Lake now saline with reduced biodiversity.

Figure 11.7 Secondary salinization caused by clearing deep-rooted vegetation that allows saline groundwater to rise. Catchment vegetation dies, erosion and waterlogging occur, and freshwater lakes become saline, reducing aquatic biodiversity. (Source: Modified and reproduced with permission of Department of Agriculture and Rural Affairs © State of Victoria, Department of Environment and Primary Industries 1980. Victorian Resources Online, www.dpi.vic.gov.au/vro. Image drawn by Belinda Cale.)

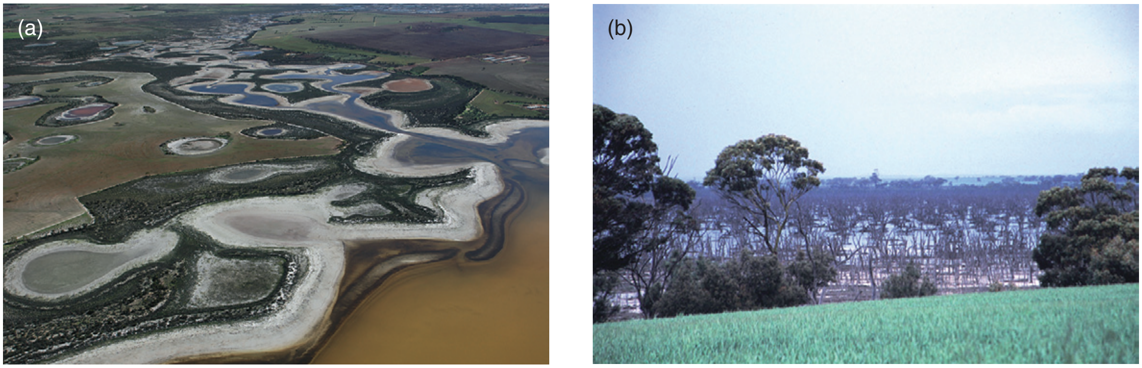


Figure 11.8 (a) Waterlogging and salt dominate the lower parts of the landscape in this aerial photo of secondary saline lakes near Wongan Hills, WA. (b) A wheat field thrives only a few centimetres higher in elevation than the salinized Lake Taarblin in the WA wheatbelt. (Source: Jenny Davis.)

Wetlands and rivers are usually the first areas to be salinized by rising groundwater, either because of direct hydrological connections or because these surface waters lie in the lowest part of the landscape (Figure 11.8a). In agricultural areas, salinization of these low-lying areas is exacerbated when water is diverted, drained or pumped into them from agricultural land to protect crops from rising saline groundwater; sometimes crops lie merely centimetres above saline lakes and seeps (Figure 11.8b). In extreme cases, most plant cover is lost, leaving the topsoil exposed to the erosive forces of wind and rain.

Poorly managed land use can also cause salinization. **Irrigation salinity** arises when irrigated water exceeds the requirements (or evapotranspiration) of the crop and groundwater is recharged, raising the water table and causing waterlogging. Inefficient and excessive water use, irrigating land with poor drainage or unsuitable soils, poor drainage practices (e.g. inefficient drains or ponding of water on the land) and seepage from irrigation channels and water storages all raise groundwater. The good news is that efficient irrigation practice can significantly reduce the rate of salinization and makes economic sense in the long term. Another cause of irrigation salinity is the application of slightly saline water to farmland, usually because there are no other sources of water. In the Murray-Darling Basin where approximately 75% of Australia's irrigation water is used, secondary salinization of rivers is partly caused by floodplain irrigation (Hughes *et al.* 2008) and partly caused by dryland salinization in the upper catchment (Jolly *et al.* 2001). Thus, these two processes can contribute to salinity problems simultaneously, but may need different management approaches according to land use and the cause of the salinization.

Many industries produce saline water as a by-product. This water often also contains other contaminants (Section 11.6) and the salinity is not always sodium-chloride dominated. Saline waste water from coal-mining and coal seam gas extraction (Section 8.6) typically differs in ionic composition and dominant salts from those of natural saline lakes and dryland and irrigation salinity. Therefore, information on the effects of sodium-chloride salinity is of limited use when uncritically applied to predicting the ecological responses to saline waters from these industries.

Finally, although most salinization is groundwater-mediated, it may also occur through surface-water evaporation. This is a natural process in most inland waters in dryland areas of Australia but can be accelerated by human activities. Sometimes, the acceleration is intentional, such as when salt is being harvested from evaporation ponds or naturally saline waters are being managed for this purpose. However, more commonly, the cause is unintentional change to drainage or erosion that mobilizes salts and imports them to surface waters where evaporation concentrates the residues.

11.4.3 Ecological impacts and effects on ecosystem services

The ecological **impacts** of salinization on aquatic ecosystems depend on the capacity of resident species to cope with changes in salinity. Many freshwater plants and animals become stressed when salinities exceed $1\,\mathrm{g\,L^{-1}}$ and few freshwater biota persist at salinities above $10\,\mathrm{g\,L^{-1}}$ (Figure 11.9, Nielsen and Brock 2009). In general, biodiversity decreases as salinity increases. Salinization leads to permanent changes in flora and fauna, and affects the rates of many ecological processes such as organic matter decomposition and nutrient cycling (Schäfer *et al.* 2012).

Highly saline water is often clear because salt ions interact with the ionic surface of clay particles causing them to attract rather than repel each other. The particles aggregate and settle out. Dissolved organic carbon is removed from the water in a similar process, increasing water clarity and also altering nutrient cycling pathways (Section 3.9). Light penetrates to the bottom of many shallow saline waters, promoting the growth of tolerant producers in benthic mats.

Salinization affects most provisioning, supporting and cultural **ecosystem services** of freshwaters, and indirectly influences regulating services (e.g. reduction in vegetation cover hastens erosion). The impairment or loss of drinking water and, depending on the degree of salinization, water for most provisioning and supporting services is the main concern. Economic costs of the loss of these services are huge. In Australia in 2005, salinity affected 30% of the land surface and 16% of agricultural land (Rengasamy 2006) at an estimated annual cost of $3.5 billion. Medical problems also arise. For example, salinization can promote the spread and establishment of populations of salt-tolerant mosquitoes (e.g. *Aedes camptorhynchus*) that can be vectors of diseases such as Ross River fever (Jardine *et al.* 2011).

Many supporting services mediated by freshwater biota are adversely affected by salinization. Regulating services associated with natural water purification and waste treatment will be impaired as salinity increases, as will indirect effects on erosion regulation and land cover. The loss of cultural services such as 'sense of place' and heritage values is potentially immense. Many people despair when they see secondarily salinized landscapes and this is especially acute for landowners forced off their property by salinization. Health problems and high suicide rates are not unusual in

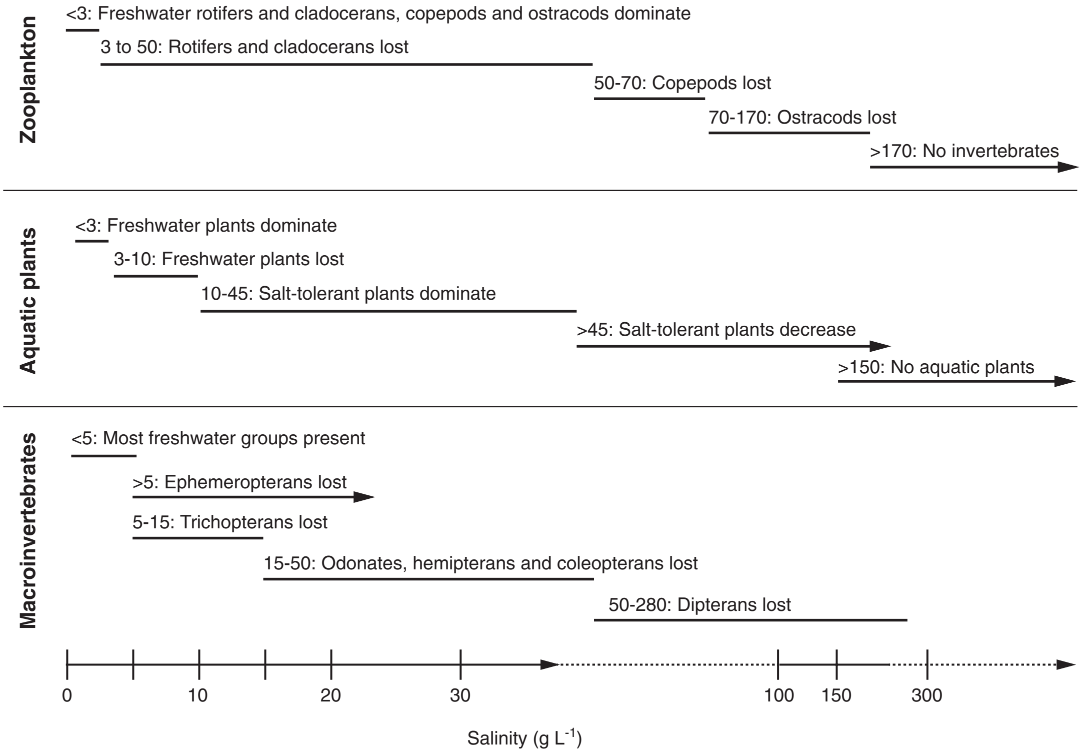


Figure 11.9 Change in assemblage composition of zooplankton, aquatic plants and macroinvertebrates along a gradient of salinity of different inland waters. Note the variations in scale along the horizontal axis. (Source: Nielsen and Brock 2009. Reproduced with permission of Springer Science and Business Media.)

these communities. Often, there is a close correlation between human health and ecosystem health, in this case, dryland salinity in south-western WA (Jardine *et al.* 2006).

11.4.4 Management of salinization

Secondary salinization is a landscape-scale long-term issue. There are no ‘quick fixes’. Nonetheless, to tackle it effectively, we need to identify the primary cause and how the balance between salt inputs (I) and outputs (O) has been altered when we change the water balance (Figure 11.7). Progress of salinization can be monitored against the ratio of salt outputs to inputs (O/I, Jolly *et al.* 2001). Before salinization, the salt balance is considered equal and $O/I = 1$. Salinity rises in surface waters until it reaches a new equilibrium based on the new water balance. This then yields salt O/I ratios that can be compared regionally. Salt O/I ratios in the Murray-Darling Basin range between 0 and 5.6, and may be as high as 8 in SA, 13 in northern Victoria, and 20 in south-western WA (Jolly *et al.* 2001). Strategies to manage salt aim to reduce the O/I ratio, and this ratio is closely monitored as a measure of the effectiveness of the management actions.

The choice of management options depends upon whether the primary cause is dryland or irrigation salinity. Choices also depend on aquifer depth and salinity, geomorphology, present land use, and economic and social issues. In some cases, there may be no effective solutions and we must learn to ‘live with salt’ (Macumber 1990).

Short-term management of salinization aims to remove or reduce the stressor, salt. Efforts to remove salt usually involve flushing it, potentially moving the problem elsewhere. Often, this approach is not feasible. Salinized areas are usually in dryland regions and

Box 11.2 Toolibin Lake: a case study in salinity management

Toolibin Lake is listed as a Wetland of International Importance under the Ramsar Convention and has the highest recorded waterbird diversity for the inland south-west of Australia. Within this zone, it is also the last wetland that retains comparatively extensive areas of mixed woodland (*Casuarina obesa* and *Melaleuca strobophylla*) across its floor. Efforts to conserve and recover the lake from salinization and related threats have continued for over 30 years, entailing surface water diversion, groundwater pumping and revegetation. Decline in lake-floor vegetation has now largely stabilized, and some sites are recovering. Conservation is an iterative process of research combined with operational application. In turn, this has depended on continuous support for the project at executive and middle management levels within the Department of Environment and Conservation. Such support is critical for projects, such as that at Toolibin Lake, where the probability of success is uncertain and which require long-term (decades) management. Ongoing monitoring, including critical scientific re-evaluation, is crucial to optimizing management while recognizing the challenge of monitoring and gathering adequate data over long time periods.

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there is little freshwater available for flushing. Instead, options tend to focus on preventing salt entering the surface waterbody, typically entailing physical diversion structures at the inflow and pumping to reduce groundwater inputs (Box 11.2). Pumping water into evaporation basins or 'sacrificial wetlands' temporarily delays salinization of parts of the catchment but obviously at the expense of the receiving wetlands.

Deep drains have also been dug to reduce groundwater levels but sometimes these intercept acid groundwater. In parts of the Western Australian wheatbelt, these drains may carry water three times the salinity of seawater and with a pH <3 (Stewart *et al*. 2009). These groundwater drains bypass soil processes that might neutralize the water, resulting in acidic, saline water entering downstream aquatic ecosystems (Degens *et al*. 2012).

Short-term options often involve disposal of saline water, usually into rivers to flush them into estuaries where the effects are expected to be less severe. Releases may either be continuous, only during high flows, or pulsed at various times of the year. The ecological effects of releases seem to depend on the timing and duration and salinity of releases and on the biotic group. Marshall and Bailey (2004) found that pulsed salinity reduced macroinvertebrates, whereas Nielsen *et al*. (2007) experimentally showed that zooplankton and aquatic plant communities emerging from seed and egg banks subjected to brief pulses of saline water ($5\,\mathrm{g\,L^{-1}}$) were more species-rich than those emerging under continuous exposure to the same salinity. Further work is needed, especially as larval stages or young seedlings are typically less tolerant of salinity than eggs, seeds and adults.

Long-term management of salinization must encompass entire catchments and often surrounding regions. To manage dryland salinization, deep-rooted vegetation must be restored to lower the water table. However, as most areas suffering from dryland salinization are significant agricultural areas, large-scale revegetation is rare. Instead, bans on further clearing are imposed. Salt-tolerant deep-rooted vegetation is being planted in some salt-affected areas along with the use of perennial deeper-rooted pasture crops. In the Murray-Darling Basin, revegetation in areas to reduce baseflow that is delivering salt has been much more beneficial than planting vegetation to simply optimize biodiversity (Cheng *et al*. 2013).

Increasing the efficiency of irrigation techniques is a long-term management strategy to tackle irrigation salinity, and has economic as well as environmental benefits. Schemes have to be planned at a catchment-wide scale to maximize their effectiveness, and must also consider groundwater flow paths and interactions with connected surface waters. Often, these are done in conjunction with other industries so that all sources are managed under the same scheme. Multiple strategies and points for intervention occur (Figure 11.1), depending on whether the sources are diffuse or point ones. The Hunter River Salinity Trading Scheme in

NSW seeks to minimize the impact of saline wastewater discharges from point sources such as coal mines and power stations on downstream water users while also managing groundwater inputs and other diffuse sources. Salinity in the Hunter River has increased because of industrial releases as well as increased groundwater intrusion caused by rising water tables associated with land clearing, irrigation and saline wastewater discharges (Muschal 2006). The Scheme schedules releases during high and flood flows to maximize dilution effects, and salinity limits are set so that discharges during high flows are managed on a catchment and sub-catchment scale.

11.5 ACIDIFICATION

Acidification is a reduction in the pH of water. The term encompasses the effects of the loss of ions such as calcium, magnesium and potassium via leaching as well as the direct effects of acidity on aquatic biota. Many inland waters have pyritic sediments and are naturally acidic, especially in the pH range 4–6. However, the issue becomes a management problem when human activities increase acidity, and this is the sense in which we use the term 'acidification' in much of the text to follow.

11.5.1 Natural and anthropogenic acidification

The low pH naturally found in many waterbodies in Australia is primarily caused by chemical weathering of the underlying soil type or by humic acids leached from organic matter (Section 3.2.3). Generally, the biota of these acidic waters can tolerate the low pH and there may be quite specialized assemblages of acidophilic (acid-loving) plants and animals that would be threatened by an increase in pH.

The rest of this section will deal with anthropogenic acidification. This is caused by human activities that either promote the oxidation of particular ions such as sulfide and various metals or that increase atmospheric inputs of sulfur dioxide or nitrogen oxide to form sulfuric and nitric acids that fall as 'acid rain'. Regional differences in these forms of acidification reflect geology, water regime, industrial activity and climate. Indeed, anthropogenic acidification is a perfect example of a management issue that encompasses nearly all physical, chemical and biological processes covered in Part I of this book.

11.5.2 Drivers, stressors and processes of acidification

In Australia, the primary **drivers** of acidification are exposure of acid sulfate soils, leachates from mines and their tailings, industrial emissions causing acid rain and, in some agricultural areas, the release of naturally acidic groundwater through the creation of deep drains. Most of these drivers are seldom intentional but the **stressor**, low pH, causes widespread and sometimes chemically complex changes to aquatic ecosystems that may be hard to reverse.

Acid sulfate soils are naturally occurring sediments, usually of marine origin, that contain high concentrations of iron sulfides. The **process** of acidification involves the oxidation of the sulfides in this soft, black and sticky or gel-like mud. When inundated, the sediments are anoxic, the iron sulfides are stable, and pH is almost neutral (Figure 11.10a). However, when the water is drained and the soils are exposed to air, the iron sulfides are oxidized, releasing sulfate (Figure 11.10b). The high level of organic carbon in sediments often results in the process being accelerated by bacteria (Sections 3.6.1 and 8.4). On reflooding, acid is mobilized into the overlying water (Figure 11.10c), and potentially into groundwater and nearby connected waters, including estuaries.

Potential acid sulfate soils are ones that will become acidic on exposure. They are widespread across Australia (Figure 11.11a) and, contrary to popular belief, not just restricted to coastal areas. Where they do occur coastally, this tends to be in northern Australia (Figure 11.11b). Acid sulfate soils are common in and near waterbodies. Therefore, activities such as the construction of residential canal estates on rivers and estuaries, dewatering for land development, mining or agriculture, drainage of wetlands, digging drains through acid sulfate soils and dredging are all likely to cause acidification by exposing potential acid sulfate soils to the air.

Drought can also expose these soils. During the 'Millennium Drought' (1997–2010), Bottle Bend Lagoon on the Murray River (Box 11.3, Figure 11.12) was one of the earliest to show signs of acidification as water levels fell. Other sites soon followed, and the presence of acid sulfate soils in the Lower Lakes of the

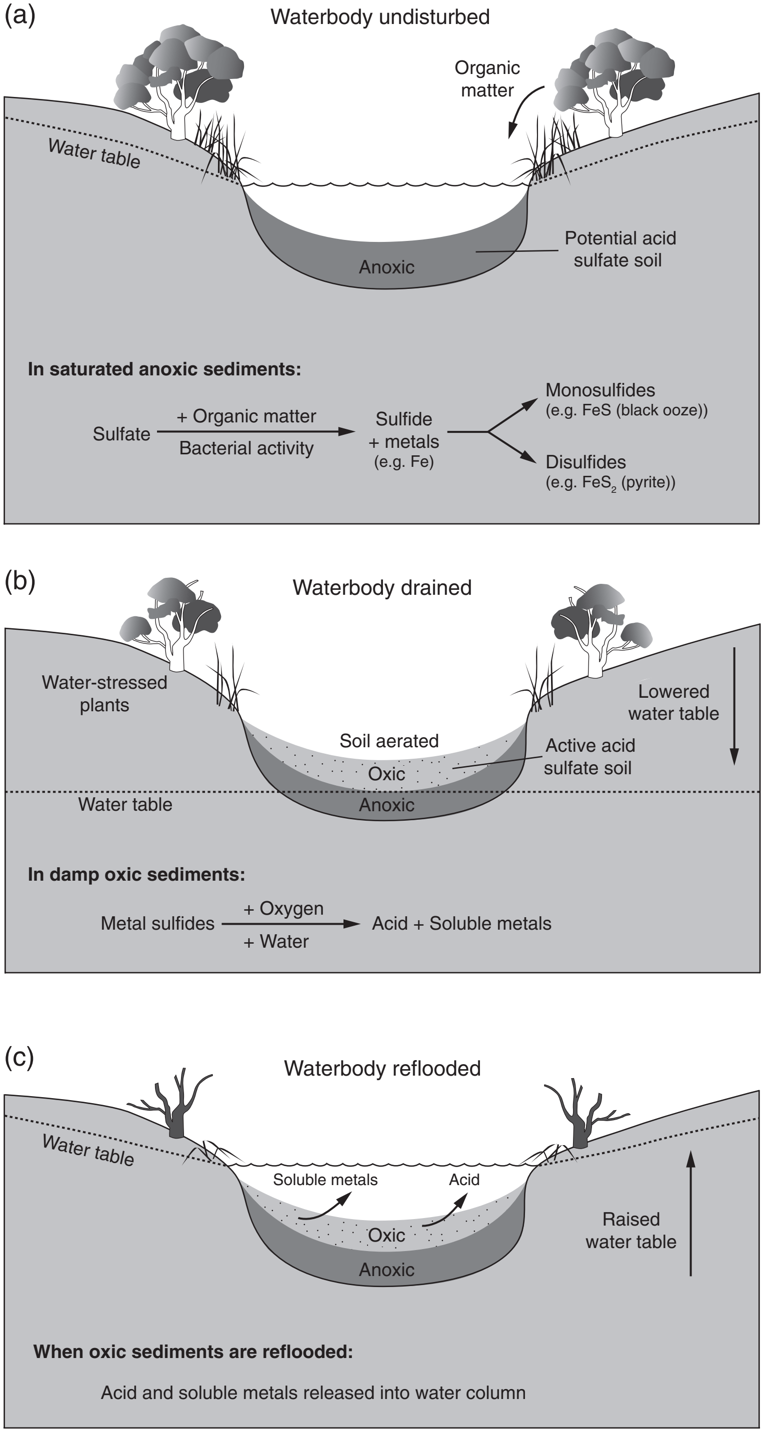

Figure 11.10 Conceptual model of the formation and acidification of acid sulfate soil in a waterbody during drying and wetting. (a) Potential acid sulfate soils form in anoxic layers during inundated conditions. Sulfate is reduced to sulfide by bacteria, and may combine with metals to form monosulfides and disulfides. Left undisturbed, they cause no harm. However, if exposed to air (b), sulfides oxidise to produce acid and the oxic sediments become active acid sulfate soils. (c) When rewetted, acid and soluble metals can be released into the water column. (Source: Modified and reproduced with permission from Environment Protection and Heritage Council and Natural Resource Management Ministerial Council 2011. Image drawn by Belinda Cale.)

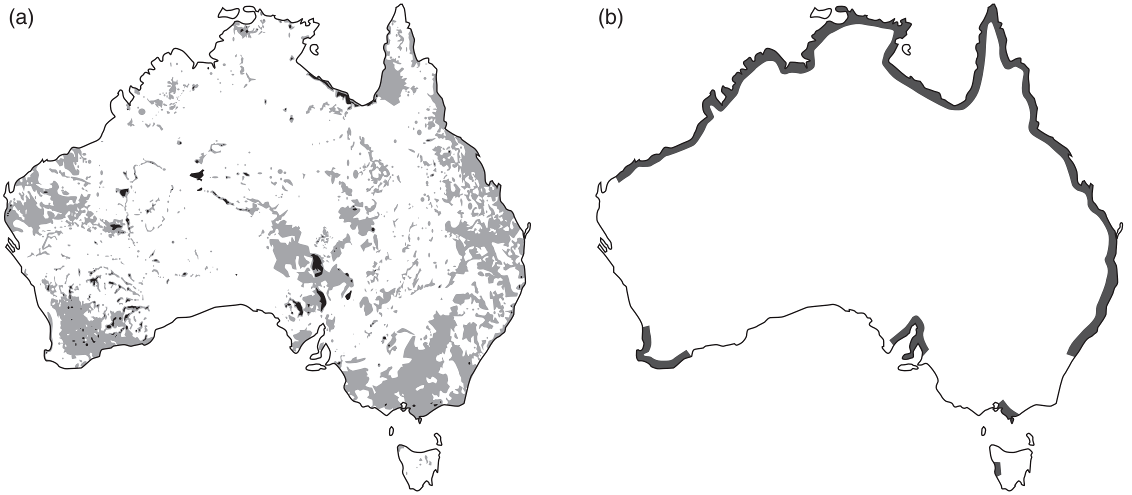

Figure 11.11 Distribution of potential acid sulfate soils (a) within Australia (www.asris.csiro.au/) and (b) around the coast. (Source: (a) Maps created from http://www.asris.csiro.au/. Reproduced with permission of CSIRO; (b) Maps created from White *et al.* 2007 and reproduced with permission from Elsevier.)

Box 11.3 Acidification, salinization and fish kills in an inland wetland in south-eastern Australia following partial drying

The acidification of Bottle Bend Lagoon, over 300 km inland from the south-eastern Australian coast, highlighted that acid sulfate soils are not only a feature of coastal regions. The source of the sulfate in this Murray River wetland was highly saline groundwater seeping from the elevated water table next to a weir pool. After low flows in 2002 disconnected the wetland from the river, it mostly dried out, oxidizing the sediments and generating sulfuric acid. As it refilled, its acid-neutralizing capacity was overwhelmed, and pH decreased from 7.24 (May 2002) to 2.93 (August 2002). Toxic metals such as aluminium and manganese were liberated in high concentrations and, with high salinities ($>30\,000\,\mu S\,cm^{-1}$) and low pH, contributed to widespread fish kills (McCarthy *et al*. 2006). High river flows when the drought broke flushed the wetland and water quality improved. In April 2013, the pH was 7.69 and salinity $2660\,\mu S\,cm^{-1}$. However, future acidification could arise from drying and rewetting the remaining acid sulfate soils.

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Murray-Darling system in South Australia raised further fears for the integrity of this embattled Ramsar site. There is now a much greater awareness of the effects of changes in water regime on potential acid sulfate soils associated with inland waterbodies, especially in light of the drying climate projected for much of southern Australia (Section 12.9).

Several human activities promote acidification. Mining for coal or metal ores causes **acid mine drainage** that leaches from tailings. These materials are usually associated with metal sulfides, especially pyrite (FeS_2). When exposed to air, these sulfides oxidize as we saw for acid sulfate soils. Acid mine drainage often mobilizes other metals (Box 3.3) that become soluble at low pH, reaching concentrations toxic to most biota. In some areas, natural acidification within the soil arises from oxidation of various metals (e.g. iron, aluminium). This process releases

Figure 11.12 Bottle Bend Lagoon in the Murray-Darling system, NSW. This once-vegetated aquatic ecosystem was a victim of acidification when acid sulfate soils, exposed by low water levels during the 'Millennium Drought', were re-flooded. (Source: Paula D'Santos.)

hydrogen ions, and these soils and their groundwaters can become highly acidic (pH <3). When drains are dug into the **acidic groundwater**, for example to combat salinization in agricultural areas (Section 11.4.4), the resulting acidic and saline water causes serious impacts when it enters waterways (Degens *et al.* 2012).

Another source of acid is **acid rain**, caused by the oxidation of emissions of sulfur dioxide and nitrogen oxides (e.g. from motor vehicles, coal-fired power plants). Acids enter waterbodies as rain or dry deposition. Acid rain is prevalent in highly industrialized areas where it causes major concern. However, across most of Australia, it is seldom seen as a serious issue because of the lower degree of industrialization. One exception is the Mount Lyell Mine near Queenstown, Tasmania, where 70 years of sulfur dioxide emissions from the copper smelters caused acid rain which, together with acid mine drainage, led to acidification of the King and Queen Rivers.

11.5.3 Ecological impacts and effects on ecosystem services

Irrespective of its cause, a reduction in pH has the same ecological **impacts** on aquatic processes and biota. Few species are able to tolerate very low pH because it interferes with enzyme function necessary for basic metabolism. Furthermore, low pH increases solubility of iron, aluminium, manganese and other heavy metals, rendering them toxic to most plants and animals. Aluminium toxicity causes gill damage in fishes while acidic water directly damages the skin and gills of fishes and other aquatic animals. Damage to gills reduces their capacity to take up oxygen or regulate intake of salts and water. Skin damage increases the susceptibility of fishes to fungal infections such as epizootic ulcerative syndrome, also known as 'red spot disease' (Lintermans 2007).

Sometimes, the chemical effects of a decline in pH are revealed by colourful changes. For example, water may become orange (caused by iron floc and associated bacteria), milky (forms of aluminium at pH 5–6) or blue-green (aluminium floc at pH 4–5). These flocs smother plants and restrict their photosynthesis, reduce the complexity of natural microhabitats in the sediments, and clog interstitial spaces, restricting exchanges of surface and groundwater. Primary producers may be eliminated or severely stressed by acidification. Acidity can reduce the bioavailability of essential nutrients such as phosphorus, calcium, magnesium and molybdenum. When the pH falls below 4, aluminium and manganese toxicity are the main elements causing plant death. As pH declines, there is a change in plant species composition, with acid-tolerant species such as water lily (*Nymphaea*) and spike rush (*Eleocharis*) becoming more dominant (Sammut *et al.* 1996). There may also be sequential loss of crustaceans, molluscs and other organisms requiring calcification for shell formation.

Acid sulfate soils also deoxygenate overlying water. One of the most notorious forms is **monosulfidic black ooze**, organic materials that contain one of the iron sulfides (monosulfide) responsible for acid sulfate soils. These black oozes (Figure 11.13) accumulate in drains and creeks, sometimes to a depth of several metres. When they become suspended, even in concentrations as low as $1\,\mathrm{mg\,L^{-1}}$, they can deoxygenate the water in a few minutes. Floods often suspend these oozes and cause major fish kills. For example, a 1-in-20 year flood in February 2001 down the Richmond River, NSW, deoxygenated some 23 km of the waterway in an unprecedented fish kill (Bush *et al.* 2004).

As we saw for salinization, acidification affects almost all the provisioning, supporting and cultural **ecosystem services** associated with inland waters. Some

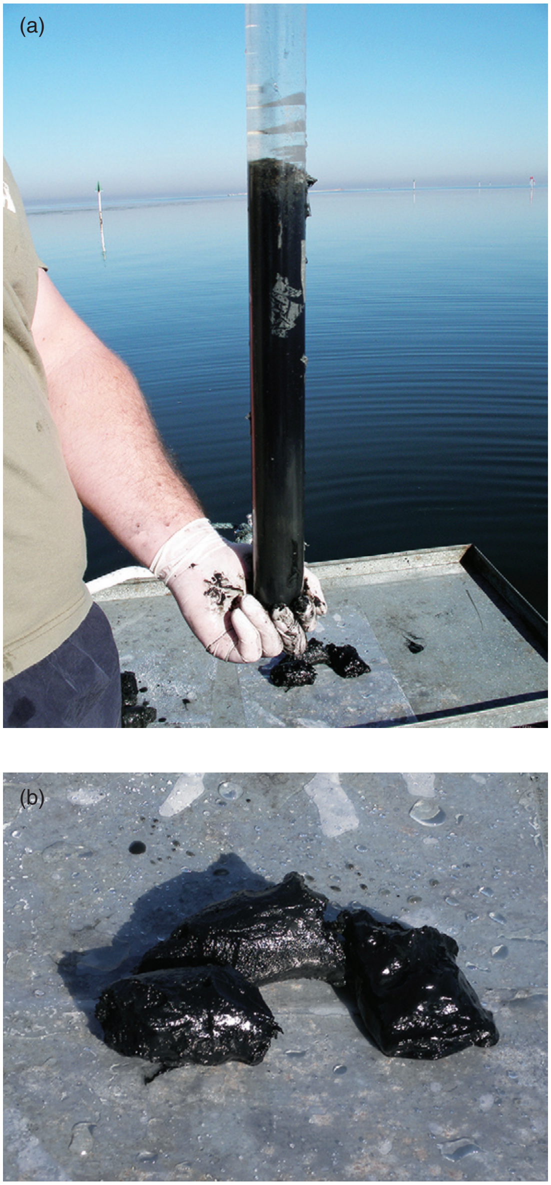

Figure 11.13 Monosulfidic black ooze in a benthic core (a) from a canal estate on the Peel-Harvey Estuary, WA, is black and gel-like (b). (Source: Leigh Sullivan.)

regulating services are also indirectly impaired. Drinking water can be rendered corrosive and toxic, and often unsuitable for other uses too. For example, disturbance of peat soils in wetlands near Perth led to groundwater with a pH as low as 1.9 entering the wells and bores used by residents. Mobilized metals (e.g. arsenic up to 7 mg L^{-1}, aluminium up to 290 mg L^{-1} and iron up to 1300 mg L^{-1}) and low pH killed plants in suburban gardens irrigated from the groundwater bores and provoked concerns about human health (Appleyard *et al.* 2004).

Acidic water corrodes concrete and metal, damaging bridge foundations, water pipes and other structures. In surface waters and groundwaters, there are reductions in biodiversity and rates of nutrient cycling and other ecological processes that underpin provisioning and supporting ecosystem services. Fisheries often suffer sporadic fish kills, and rotting corpses detract from aesthetic and recreational values. Direct effects of acidification can limit recreation that involves body contact with water. Almost all of these issues attract public attention and prompt management action to treat the symptoms or remove the causes.

11.5.4 Management of acidification

After acidification has occurred, it can be difficult to restore the original aquatic ecosystem in the **short term**. One common approach is to add alkaline materials, such as agricultural lime (calcium carbonate, $CaCO_3$), to neutralize the acid. Hydrated lime (calcium hydroxide $Ca(OH)_2$) is more soluble and effective but its high pH (~12) can harm biota and the environment if too much is applied too rapidly. To avoid this, it is often added as a slurry to ponded acidic water. Another short-term solution is to use hydraulic separation to sluice sulfide material from sediments that contain <20% clay and have a low organic matter content. This sulfide material can then be neutralized or reburied under water where anaerobic conditions will render it safe from acidification (Dear *et al.* 2002).

The best **long-term** management option for acidification is prevention. The production of detailed regional maps of potential acid sulfate soils, coupled with stringent regulations controlling land development and dewatering, have greatly reduced the frequency of unintentional exposure of acid sulfate soils. The need to keep acid sulfate soils flooded is now recognized as a good reason for maintaining natural water regimes in permanent waterbodies and providing sustained environmental flows in permanent rivers to prevent the bed from drying out. Where acid sulfate soils must be disturbed, impacts can be minimized by avoiding areas with high concentrations of sulfides, designing drains to be shallow and wide rather than deep and narrow, and minimizing groundwater drawdown caused by dewatering, deep drainage or extraction bores in areas of potential acid sulfate soils.

Oxidation is the prime driver of acidification, and so reducing the redox of the sediment by providing a source of organic material can alleviate the problem (Gilbert *et al.* 2004). In Collinsville, Queensland, water from a pit lake receiving acid mine drainage from coal mining operations was dosed with green waste and treated sewage. This increased the pH from 2.4 to 5.5 in only 145 days, primarily through microbially mediated sulfate reduction (McCullough and Lund 2011). Controlling acid mine drainage involves minimizing oxidation and transport of oxidation products, reducing the loads of contaminants and treating any acidic waste-water to allow its reuse or safe discharge. Finally, control of acid rain and dry deposition is achieved by regulating industrial and domestic emissions (State of the Environment 2011).

11.6 POLLUTION

Any anthropogenic physical, biological, or chemical change in water quality that has an adverse effect on the biota is considered **pollution**. Note the emphasis on human causes. Although natural processes often alter water quality with adverse effects on biota, this is not considered pollution. However, when human activities introduce naturally occurring substances such as heavy metals, salt or nutrients into waterbodies at concentrations far exceeding normal levels, we consider these substances as pollutants. Pollutants also include synthetic chemicals that do not occur naturally, and are created by various industries (Table 11.2).

Pollutants can be classified as biotic, chemical (organic and inorganic) and physical (Table 11.2), and span a diverse array of materials with an equally diverse array of impacts on aquatic ecosystems. Despite this diversity, there are some common themes and Table 11.2 helps illustrate these for a few of the major groups of pollutants in our inland waters.

11.6.1 Drivers, stressors and processes of pollution

As we said earlier, pollution is, by definition, an anthropogenic process, and any human activity that causes the process is the **driver**. Rapid advances in technology have led to our daily use of an increasing array of chemicals ranging from personal care products to pesticides. Hundreds of thousands of compounds, most of them organic, are now unintentionally released into the environment and ultimately enter our surface and groundwaters as **contaminants**, our collective term for these **stressors**. These contaminants include the nutrients, salt and acids discussed already, and in this section, we shall explore the diverse array of other contaminants.

One factor affecting processes of pollution is whether the source is point, diffuse or both (Section 11.3.2). Point sources include effluent discharges such as from sewage treatment plants, industrial sites, agricultural and aquaculture feedlots, power stations and many accidental waste spills. Diffuse sources are more difficult to control and include atmospheric sources and runoff from urban, industrial and agricultural land.

Another factor is the contaminant's solubility in water and its potential for biological uptake. We have seen already how changes in environmental conditions (e.g. pH) can affect the bioavailability of contaminants. Often, we need a good grasp of chemistry and of the ecological conditions of particular waterbodies to understand how pollution is likely to occur, its likely ecological impacts, and the probable persistence of the contaminant in the aquatic environment. Although controls on the release of pollution from human activities in Australia are stricter than in the past, many of these contaminants are long-lived and persist in sediments, groundwaters and the water column for decades or longer. Decades after human activity has ceased, seepage and runoff from waste dumps, landfill and the shafts and tailings of derelict mines continue to contribute toxic heavy metals and other pollutants into inland waters, along with vast amounts of contaminated sediments (Figure 11.14). Particularly concerning are persistent organic pollutants and heavy metals because many of these resist degradation by chemical, biological or photolytic processes (Petrovic *et al.* 2013).

Physical pollution occurs mainly through raised or lowered water temperature. For example, many industries use water to cool machinery and the

Table 11.2 Types of aquatic pollution, common sources and their impacts on aquatic ecosystems. Physical pollution by sedimentation is discussed in Section 10.3.

	Stressor	Examples	Typical sources	Principal impacts on aquatic ecosystems
Physical				
	Extremes of water temperature	Hot or cold water exceeding temperatures in receiving waters	Coolant from power stations and other industries; released water from deep in large impoundments; unshaded waters where overhanging vegetation has been removed	Alters rates of productivity and metabolism; changes reproductive cues; kills riparian and fringing vegetation; warming reduces dissolved oxygen solubility; eliminates species sensitive to increased temperature
Chemical: Organic				
	Pesticides	Organochlorides and organophosphates	Agricultural, silvicultural and urban uses	Kills or impairs non-target species; bioaccumulates in predators; acts as endocrine-disruptor (see below)
	Hydrocarbons	Petroleum products (e.g. polycyclic aromatic hydrocarbons)	Oil, gas, coal and other fuels; rubber tyres	Creates black ooze (anaerobic sediments fuelled by carbon); induces cancers and mutations; is readily absorbed into fatty tissues; affects permeability of membranes and gills
	Oxygen-demanding substances	Carbon wastes with high biological or chemical oxygen demand, food wastes such as fats, manure	Sewage; runoff from agriculture, paper mills, food processing, etc.	Causes deoxygenation of water column, adversely affecting aerobes and altering redox conditions
	Endocrine-disrupting chemicals	Synthetic and natural chemicals that interfere with the synthesis, secretion, transport, binding or action of hormones	Industrial, agricultural and sewage effluents; personal care products; medicines and pharmaceuticals	Disrupts sex ratios, growth and reproduction in fishes and other organisms; interferes with endocrine function
	Surfactants	Detergents	Household and industrial uses; fuel additives	Reduces surface tension of water; toxic to aquatic biota may contain nutrients
	Organic solvents, volatile organic compounds	Polychlorinated biphenyls (PCBs), chlorofluorocarbons, formaldehyde, pesticides such as DDT and methoxychlor	Industrial applications, paints, refrigeration, solvents, fuel, additives	Disrupts hormonal processes; absorbed into fatty tissues; induces cancers and mutations; toxic to aquatic biota
Chemical: Inorganic				
	Heavy metals	Mercury, cadmium, lead, chromium, zinc, arsenic	Mineral processing, electroplating and acid mine drainage	Toxic; accumulates in organisms and up food chains
	Inorganic solvents	Acids, caustic agents, salts	Industrial effluents, household cleaners	Toxic; alters water chemistry and pH
	Radioactive substances	Uranium, thorium, iodine	Mining and processing of ores, power plants, electronic waste	Induces cancers and mutations
Biological				
	Pathogens	Bacteria, viruses and some parasites (e.g. *Giardia*)	Untreated human and animal sewage	Causes illness or death; modifies behaviour

Figure 11.14 Contaminated sediments washed from mine tailings into the King River, Tasmania, form a huge delta extending into Macquarie Harbour. (Source: Jenny Davis.)

resultant warmer water may be released into nearby surface waters and groundwaters. In rivers spanned by large dam walls, water released downstream often comes from the cooler depths of the impoundment. Both these types of thermal pollution change the natural regime of water temperature in the receiving system, sometimes over hundreds of kilometres (Section 11.6.2). Clearing shading riparian and fringing vegetation usually increases water temperature (Box 12.8) and is another form of thermal pollution.

Chemical pollution involves a wide range of organic and inorganic contaminants (Table 11.2). Inevitably, surface waters and groundwater act as 'sinks' for most of these contaminants. These contaminants enter through direct release into the water, deposition from the atmosphere either in precipitation or as drift (e.g. aerial pesticide application), catchment runoff carrying the chemicals in dissolved forms or attached to sediments or organic matter, and importation by mobile organisms. Sometimes, the process is subtle. For example, medical advances yield an increasing list of pharmaceuticals for human and veterinary use, various hormone and health supplements, and personal care products including perfumes, soaps, sunscreens and cosmetics. Most of these are organic compounds that are bioavailable and biologically active (e.g. oestrogen). Ultimately, these compounds are excreted and, despite technological advances in sewage treatment, many retain their biological activity when they enter aquatic ecosystems (Campbell *et al.* 2006). Another source is insect repellents or sun blocks on our skin that are washed off when we enter inland waters. This under-researched pathway of chemical pollution may be significant in waterbodies where tourist pressure is heavy.

Pathogens are the primary form of **biological pollution** and include bacteria, viruses and some protistan parasites such as *Giardia*. Pathogens are microorganisms that are detrimental to the health of humans, animals or other biota, and they usually enter surface waters and groundwater from untreated human sewage or animal wastes from feedlots, dairies and other livestock industries. Pathogens and invasive organisms are also spread by humans and their vehicles moving between waterbodies or over wet ground. Some of these include the fungal pathogen *Batrachochytrium dendrobatidis* causing the global pandemic of chytridiomycosis that is killing off the world's frogs (Section 12.7), root-rot fungus *Phytophthora cinnamomi*, and the colourfully named freshwater alga, rock-snot *Didymosphenia geminata*.

11.6.2 Ecological impacts and effects on ecosystem services

The ecological **impacts** of pollutants may be acute (short term) or chronic (longer term). An **acute** impact is one that develops rapidly, usually quickly causing sublethal or lethal responses. Often the link between the pollution event and the response is evident. Conversely, **chronic** ecological impacts occur much more gradually and this delayed response often makes it more difficult to determine the contaminant or combination of contaminants that caused it. Again, responses may be lethal or sublethal.

As we have seen in earlier sections, the ecological impacts of these pollutants depend on their sources, concentrations, chemical forms, and their interactions with other contaminants. Some pollutants may have greater ecological impacts when they co-occur than when alone, and this complexity of interaction can hamper prediction of ecological impacts in natural waterbodies. Furthermore, different stages of the life-cycles of plants and animals typically differ in their susceptibility. Seedlings and larvae are often at greater risk from many contaminants than adult plants and animals. Finally, environmental conditions affect the ecological impacts of most pollutants. These conditions may include seasonal changes in water temperature whose extremes may provide extra stress on organisms already subject to other pollutants, the effects of variations in water regime that may affect the concentrations of dissolved contaminants, and redox conditions that affect chemical bioavailability.

The ecological impacts of physical or **thermal pollution** depend on the extent to which the water temperature is altered from background levels of variability and whether it is warmer or cooler. Warmer water can promote algal growth and accelerate the rate of development of many organisms as long as it does not exceed thermal limits of particular life stages. Rates of many ecological processes may also increase, especially those that are microbially mediated. However, warmer water contains less dissolved oxygen, affecting organisms such as fishes and other aerobes (Chapters 4 and 7). Changes in water temperature may also interfere with environmental cues for reproduction and other behavioural traits.

Water discharged into rivers from the hypolimnion of stratified storages is often much cooler than the surrounding river, and the cold-water pollution may persist for hundreds of kilometres downstream of the dam (Figure 11.15). Although this cold water may favour some invasive salmonid species, it adversely affects most native fishes. For example, downstream of Dartmouth Dam in Victoria, daily water temperatures in the Mitta Mitta River are sometimes 10–12°C below normal, and modelled spring-summer water temperatures have fallen from 14–20°C pre-impoundment to 10–15°C (Todd *et al.* 2005). Eggs and larvae of native Murray cod cannot survive below 13°C, and the impact of these cold-water releases on post-spawning survival poses a significant threat to the viability of this species downstream of the dam (Todd *et al.* 2005).

The ecological impacts of **chemical pollution** are diverse, and depend on the types of contaminants (Table 11.2). Few ecological processes are not impaired by one or more of these chemical pollutants. However, in Australia, there is little empirical information on the specific effects of most contaminants on native biota. The few data we have indicate that taxon-specific responses are complicated, variable and depend on life-history traits as well as physiology (Box 11.4). This means we must be cautious about relying heavily on the results of simple dose-response experiments where the survival of organisms is monitored under standard conditions when subjected to different concentrations of a given contaminant. The situation is further complicated because contaminants usually exist as ‘cocktails’ of different mixtures whose effects are modified by environmental conditions.

Many contaminants **bioaccumulate** within an organism over time, sometimes in different body organs. The rate of bioaccumulation is a complex function of multiple factors, including the amount of contaminant ingested or absorbed, its persistence within the organism, the frequency with which it is taken up and whether the contaminant is chemically trans-

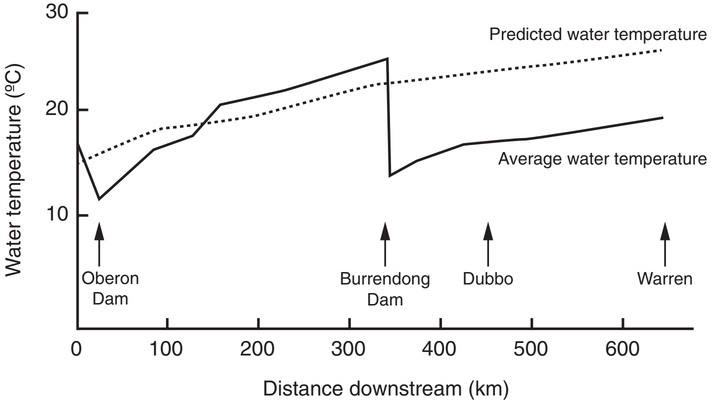

Figure 11.15 Cold-water pollution of the Macquarie River, NSW, downstream of Oberon and Burrendong Dams. Average surface water temperatures (solid line) were measured at 13 sites along the river and deviated from predicted pre-impoundment water temperatures (dotted line) for over 300 km downstream. (Source: Modified and reproduced with permission from Harris 1997.)

Box 11.4 Pesticide impacts on macroinvertebrate communities in running waters

Pesticides are difficult pollutants to measure. Biologically relevant concentrations can be as low as parts per billion. Contamination in running waters typically occurs episodically, associated with spray drift or rainfall. Therefore, regular monitoring may underestimate pesticide exposure, and methods that can detect peak concentrations should ideally be used. Although most studies assess physiological responses, life-history traits are also relevant. For example, densities of some short-lived chironomid species are reduced by experimental pesticide exposure but their populations recovered within weeks (Beketov *et al*. 2008). However, macroinvertebrate taxa with longer life-cycles recovered far more slowly. Field surveys in Australia (Schäfer *et al*. 2011) and Europe show that the stream macroinvertebrates most at risk from pesticide exposure are taxa that are both physiologically sensitive to organic toxicants and have life-cycles that limit their ability to recover after a disturbance. A meta-analysis of world studies revealed that pesticide concentrations previously considered environmentally safe are, in fact, reducing the abundance of physiologically sensitive and long-lived macroinvertebrate taxa (Schäfer *et al*. 2012). These findings imply that pesticides are having a greater impact on stream macroinvertebrate communities than is generally acknowledged.

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formed within the organism. When an organism from a higher trophic level consumes one from the level below, part or all of the contaminant is usually absorbed into the higher consumer where it, too, may bioaccumulate. Typically, the concentrations of the contaminant increase with trophic level in a process termed **biomagnification**. This is seldom a simple cumulative process. Instead, different contaminants have different rates of biomagnification, and the rates may vary across environments and years, depending on food-web changes and demographic processes. For example, although mercury is known to be biomagnified in some aquatic food webs in southern waters, Jardine *et al*. (2012b) found only very limited mercury accumulation in food webs of the Queensland wet-dry tropics, and barramundi (*Lates calcarifer*), a large predatory fish of commercial, recreational and cultural importance, had concentrations below human consumption guidelines. However, fish foraging on the floodplain had higher mercury concentrations than those feeding at sea (Jardine *et al*. 2012b).

There are two main ecological impacts associated with biomagnification. The first is that impacts can apply to diverse taxonomic groups of consumers at multiple trophic levels. For example, in a review of the effects of endocrine-disrupting chemicals, Burkhardt-Holm (2010) reported changes in sex hormones and sex differentiation resulting in feminization and masculinization of invertebrates, fishes, amphibians, reptiles and fish-eating birds at several trophic levels of consumers. The second impact is that top carnivores are usually the most seriously affected, and may be the first trophic level to go locally extinct. In 'top-down' systems (Section 4.6.7), this may have major implications for the rest of the food web.

The effects on the different types of **ecosystem services** closely resemble those for the previous three water quality issues. Water contaminated by various pollutants may not be drinkable or useable for other provisioning services. When pollutants impair biodiversity and ecological processes such as nutrient cycling and natural chemical filtration of water, many supporting and regulating services are lost. Finally, various cultural services of waterbodies are compromised when contaminants prevent recreational pursuits or ruin the aesthetic appeal.

11.6.3 Management of pollution

Management of pollutants is seldom easy. Most contaminants are in low concentrations and are frequently adsorbed onto sediments (Box 6.6) or retained in the fats and oils in aquatic organisms. Once pollutants have entered a wetland, it is seldom practicable to physically remove them. Fortunately, many contaminants are degraded by natural microbial processes or are diluted or modified over time. For example, microorganisms can decompose organic chemicals such as hydrocarbons to obtain energy. Wetland plants such as sedges can bioaccumulate some metals in their tissues without apparent harm, although these metals are likely to be released when the plant dies. 'Constructed wetlands' (Section 11.3.4) exploit these ecosystem services to strip pollutants from stormwater; however, much of the contaminated material accumulates in the wetlands and must be harvested or managed appropriately.

Obviously, prevention is better than cure. Management options that restrict the release of contaminants or that use chemical treatment to detoxify or bind the pollutants into a non-toxic form are preferred over attempts to clean up polluted waters or decontaminate sediments. Depending on the pollutant, **short-term** management of contaminated waters or sediments may involve sealing off toxic mine wastes and other sources of trace metals by enclosing pits, waste dumps and tailings ponds in impervious membranes or chemical sealants. If only a small volume of water is contaminated, chemical treatment or filtration may be feasible, and is a usual procedure for drinking water in many areas. These solutions are invariably expensive and typically require specialized equipment and constant monitoring.

Long-term management of contaminants is sometimes impossible. For example, persistent contaminants such as DDT are beyond our control and although these substances have been banned for many years, we will live with their legacy for decades to come. This problem usually applies to diffuse-source pollutants. For point-source ones, there are frequently controls on industries that oblige them to either contain the contaminant, chemically neutralize it or release it in tightly regulated amounts. In many cases, successful control relies on education programs. For example, simple awareness programs (Figure 11.16) help educate the public about how dumping waste down a drain affects local wetlands and rivers.

11.7 WATER QUALITY GUIDELINES

What is the best way to assess the possibility that one or more stressors might be affecting water quality in a particular aquatic ecosystem? How can we predict when a problem may be starting so that we can prevent it instead of having to clean up the mess? To assist managers to tackle these two pressing questions in Australia, **water quality guidelines** have been developed that indicate appropriate water quality for freshwater and estuarine waterbodies (e.g. www.environment.gov.au/water/policy-programs/nwqms/). These guidelines take into consideration the diversity of landscapes, climates and types of aquatic ecosystems, and the intended use of the water. To use the guidelines, a manager first defines the primary management aims. This step involves identifying the environmental values of a given waterbody and likely environmental concerns, deciding what level of protection is needed and then agreeing on appropriate management goals. Armed with this, the manager can now determine the appropriate water quality guideline and this largely determines the **water quality objectives**. A water quality guideline is a number (concentration limit), range or descriptive statement of conditions recommended for a designated water use, whereas water quality objectives are specific targets that indicate management performance. The next steps are to establish a monitoring and assessment program (Section 11.8), initiate the planned management strategies and then track them to see if they achieve the objectives.

Figure 11.16 Simple awareness campaigns such as messages stencilled next to roadside drains can help prevent inappropriate dumping of wastes down urban drains. (Source: Swan River Trust, WA.)

This approach is fine in theory but becomes problematic when we wish to use it to determine the water quality to protect aquatic ecosystems and their ecological processes. The main drawback is the assumption that thresholds and factors controlling ecological processes can be identified precisely and then managed at

Box 11.5 Two examples of Ecological Risk Assessment (ERA)

Seeing examples of ERA in action helps illustrate its power. The first example is a quantitative ERA for the Magela Creek (Northern Territory) floodplain that combines risks from a point source (Ranger uranium mine) with diffuse non-mining landscape-scale risks (Bayliss *et al*. 2012). A high level of protection for the biodiversity of aquatic ecosystems was used as the assessment endpoint. Mining risks were assessed for four mine-associated solutes (uranium, manganese, magnesium, sulfate) and non-mining risks were assessed for weeds, feral pig damage, wild-fire and saltwater intrusion associated with climate change. Results showed that non-mining risks currently exceed risks from mine water contaminants by several orders of magnitude. The second example is a probabilistic ERA to assess the current and future (in 100 years) risks associated with salinity in the Goulburn-Broken River system, Victoria (Hart *et al*. 2003). Salt concentrations that would protect a given percentage of species were assessed against the predicted (modelled) salinity in each river. Exceeding the capacity of the most sensitive 5% of species was taken as the measure of risk, and was small (median around 2%).

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these levels to prevent problems. Water quality guidelines in Australia acknowledge that the relationships between ecological processes and their components are complex, variable and seldom can be determined precisely. Therefore, a **risk-based approach** is commonly employed. Risk assessment is a protocol that applies in areas of uncertainty and, in the absence of ‘hard data’, offers a way forward but not necessarily a solution.

Risk is the probability that an adverse effect will occur when a target is exposed to a particular level of a stressor. This probability is quantified as the probability of the **likelihood** of the event (i.e. exposure) multiplied by the probability of the **consequences** or effects of the event. This is best illustrated by two examples (Box 11.5) of Ecological Risk Assessment (ERA) that assess the risks to plants, animals and ecosystems of ecological value (Hart *et al*. 2006, 2007). These risks may be physical (e.g. drought), chemical (e.g. contaminants) or biological (e.g. invasive species). The key point is that ERA and related approaches allow managers to quantify the risks associated with particular scenarios of single or multiple stressors in a given ecosystem over a given time period. Coupled with techniques for comparing scenarios and estimating uncertainty (e.g. Bayesian network models, Chan *et al*. 2012), water quality guidelines can be integrated with data and expert judgments of species’ tolerances, ecological processes and contaminant pathways to help managers decide on a suitable strategy for tackling complex problems associated with various forms of pollution.

11.8 MONITORING AND ASSESSING WATER QUALITY

Effective management of water quality depends on being able to measure it accurately and to assess whether differences in it are meaningful over time and among places. A detailed account of all the requirements of a good monitoring program is beyond this book’s scope but Downes *et al*. (2002) is an excellent starting place for interested readers. However, it is useful to briefly explain the different approaches to monitoring and present a few ‘pointers’ for a well-designed study.

11.8.1 Condition monitoring

Condition or **surveillance monitoring** aims to assess the status or trends in ecological condition, and is usually done at large spatial and temporal scales (e.g. multiple catchments over multiple years). Large-scale condition monitoring does not attempt to assess effects of individual management or other interventions, but to quantify the change in condition over time. Well-designed surveillance monitoring programs (Box 11.6) should be able to detect physical, chemical and biological changes in response to one or more stressors, distinguishing the effects of these from long-term trends (e.g. changes in climate) or seasonal variation.

To monitor the ecological condition of a waterbody, sometimes termed its **environmental health**, we

Box 11.6 Surveillance monitoring to assess trends in ecological condition

Surveillance monitoring programs, tailored to answer specific questions about changes in ecological condition over time, should be well-designed and, ideally, have guaranteed long-term funding.

Some handy design hints include:

Representative sampling: Use a probabilistic sampling method (e.g. simple random sampling) and avoid using existing sites based on 'expert opinion' or without knowing how they were selected.

Stratified sampling: Keep it simple. Use only a few sampling levels (e.g. pools vs riffles) and confirm they are all needed.

Assess where variation lies: Document spatial and temporal variation early in the program and review sampling design accordingly.

Adequate replication at appropriate levels: Determine desired precision to detect a change at the level of interest. Consider the benefits of taking more samples but less intensively for some variables, especially in temporary systems.

Existing data: Unless designed for your purpose, treat these as pilot data to inform an improved sampling design.

Site alignment: Do not try to align sampling sites from different components (e.g. macroinvertebrates and riparian vegetation) at the expense of representativeness.

Scale: Rather than subsampling within sampling locations, focus on replicating samples across the spatial and temporal scales for reporting.

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can measure a wide variety of variables. We usually choose ones that can be reliably (and often easily) measured, unambiguously indicate the specific problems of concern (e.g. salinization, acidification), are well known and for which there are guidelines or reference conditions, and whose responses to natural variation can be readily interpreted. Often, we measure a suite of physical, chemical and biological variables at the same time, sometimes including ones that may be of special interest to stakeholders (e.g. fishes, frogs). Many of these variables have been described in Chapters 1–8, and often include collective measures of biodiversity or certain ecological processes (e.g. ratios of photosynthesis to respiration). For example, we could measure the organic load in the sediment of a waterbody that might be affected by eutrophication. This load integrates the effects of nutrient enrichment over time, illustrating the degree of eutrophication and the ecological condition of the ecosystem. The organic load can be determined by measuring carbon dioxide flux, denitrification rate or the P/R ratio of the sediment (Section 11.3).

Monitoring of ecological condition or environmental health often relies on rapid bioassessment based on aquatic macroinvertebrates. Macroinvertebrates are diverse, mediate or reflect many ecological processes in standing and running waters, and vary in their tolerance to different impacts and disturbances. They may live up to several years within a waterbody, implying that their abundance reflects the environmental conditions in the weeks and months preceding their collection. Like many countries, Australia has national environmental monitoring programs that use rapid bioassessment of invertebrates to assess the condition of rivers and wetlands. Some of these methods are refinements of the Australian River Assessment System (AUSRIVAS, described in Simpson and Norris 2000), and involve sweep-netting (Sections 4.3 and 7.2) macroinvertebrates from several habitats such as pools, riffles and edges. Invertebrate identification is often to family level only (e.g. Chessman 1995, 2003), and data are compared with various models that predict the families that should be present in natural waterbodies.

Other indicators of ecological condition include abundance and composition of diatoms (Chessman *et al.* 2007), which have been used in various national audits of river condition (e.g. Davies *et al.* 2010), supplementing other measures such as fish and invertebrate community composition as well as the physical features of the channels and adjacent land. Increasingly, ecosystem processes such as benthic photosynthesis and respiration, measured using specially designed chambers (Figure 11.17), are being included in assessments of ecological condition to complement

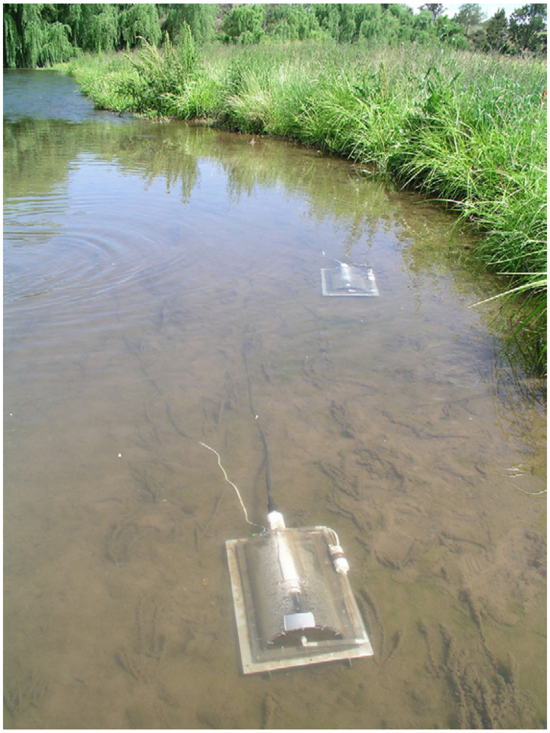

Figure 11.17 These two perspex chambers, equipped with electronic probes and data loggers to measure changes in dissolved oxygen in the enclosed water of the Hunter River, NSW, provide estimates of benthic photosynthesis and respiration. Excluding the light and measuring dissolved oxygen consumption provides an estimate of respiration alone and enables calculation of P : R as a potential index of river condition. (Source: Darren Ryder.)

the more traditional sampling of biological components such as diatoms, invertebrates and fishes.

11.8.2 Detecting environmental impacts

Often, we wish to detect the environmental impact of particular human activities on aquatic ecosystems. The impact may be a pulse disturbance (Section 7.7), such as a spill of contaminants, or a press or ramp disturbance associated with salinization or acidification. Alternatively, we might want to know whether a certain management intervention is successful – in which case, we hope the 'impact' is a beneficial one.

Detecting an impact typically requires two pieces of evidence: evidence that shows that the impacted site differs from unimpacted sites that are otherwise similar, and evidence that this difference is due specifically to the impact and not to chance differences or the effects of processes unrelated to the impact. To obtain these two pieces of evidence, three types of sites are needed: **impact** sites and unimpacted **control** and **reference** sites. If there is more than one location experiencing the impact, we may be able to detect spatial variation in the effects of the impact. Ideally, there should be more than one control site, so that natural variation among sites can be estimated and distinguished from impacts. Control sites are ones that ecologically resemble the impact sites but have not experienced the impact. Reference sites represent what we predict would resemble unimpacted sites in good condition, and they usually have desirable attributes. Reference sites are useful especially when assessing restoration success because they can show whether the restored 'impact' sites are becoming more like the reference sites (Box 11.7), which would indicate that their condition is improving. However, in the real world, pristine reference sites are rare because almost all sites in a catchment are degraded to some extent by human activities. In these situations, developing a monitoring design becomes far more difficult and assistance from a scientist experienced in monitoring design should be sought.

11.9 MULTIPLE STRESSORS AND MODELS OF ECOSYSTEM CHANGE

Stressors such as nutrients, salt or pollutants seldom occur in isolation. When two or more stressors interact with an ecosystem, it can be difficult to predict the ecological responses. Developing and testing conceptual models of the impact of **multiple stressors** on aquatic ecosystems is an excellent way to identify potential cause-effect mechanisms and predict changes. Such models need to incorporate the possibility of non-linear responses; in other words, there might be thresholds or synergistic effects that cause 'ecological surprises' or 'catastrophic regime shifts' (Scheffer *et al*. 2001, Gordon *et al*. 2008). Using models to describe the types of reaction to one or more stressors provides opportunities to develop appropriate management strategies, set water quality targets based on thresholds, guide risk assessment and determine the likelihood of success of particular interventions.

Box 11.7 Detecting environmental impacts

Designs to detect specific human activities in freshwater ecosystems should follow basic principles of experimental design, including controls and replication at the appropriate scale. One family of designs commonly used is termed Before-After-Control-Impact (BACI), which relies on having a spatial control (a comparable site unaffected by the human activity) and being able to collect relevant data before the activity commences. To improve generality of conclusions, multiple control sites (and, rarely, multiple impact sites) can be included although such designs are more costly. For planned developments such as new agricultural infrastructure, 'before data' may be feasible. However, for assessing pre-existing activities, only 'after data' are available, limiting the design to a spatial control-versus-impact situation. Some human activities occur at a scale that makes replication impossible (e.g. flow modification on large rivers) so we can use causal criteria, sometimes called levels of evidence, to further support the link between the human activity and the response of interest. Finally, assessments of restoration activities such as riparian re-vegetation not only require control and impact (i.e. restoration) sites but should include reference sites that represent a directional target for the restoration activity.

Gerry Quinn, Deakin University

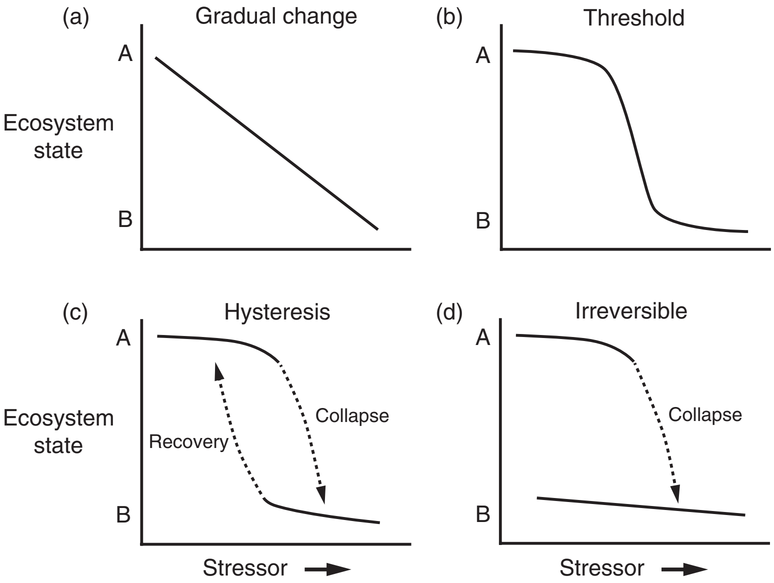

Figure 11.18 Four models (a–d) of possible pathways of ecosystem response and recovery to changes in the intensity of a stressor. Ecosystem A is the 'desired' state, B is a 'degraded' ecosystem. (Source: Davis *et al.* 2010. Reproduced with permission of John Wiley & Sons.)

Let's look at four models that describe possible trajectories of ecosystem responses to one or more stressors and, after management intervention, the possible recovery pathway (Figure 11.18, Davis *et al.* 2010). Assume that we are interested in the changes between a 'desirable' or 'undisturbed' state A to a degraded state B, and that there is only a single stressor causing the change. The simplest model (Figure 11.18a) is of *gradual change*. The change in state from A to B follows a linear pathway as the stressor intensifies. This implies that if we reduce the intensity of stressor, the ecosystem recovers towards state A.

More commonly, responses are non-linear. The *threshold* model (Figure 11.18b) is when the ecosystem response to an intensifying stressor is gradual up to a point, then sharply changes before becoming gradual again. If recovery follows the same pathway, a manager would want to try to reduce the stressor intensity over that small range to restore the ecosystem back towards the desirable state A, and then perhaps control the stressor intensity below that threshold.

What if the recovery trajectory is different from the initial response pathway? In the *hysteresis* model (Figure 11.18c), ecosystem response to an intensifying stressor is gradual up to a point before the ecosystem 'collapses' and becomes a very different one. We saw this in the alternative states model (Section 4.5.5), when addition of nutrients to a clear-water lake dominated by aquatic plants caused a sudden collapse into a turbid, phytoplankton-dominated state. In the hysteresis model, recovery does not follow the same pathway as the response (Figure 11.18c) and to restore the ecosystem to the desired state A, a manager must reduce the stressor intensity to a threshold below that initiating the collapse.

Of course, this assumes recovery is possible. The fourth model (Figure 11.18d) describes an *irreversible* change when the ecosystem cannot be returned to the desired state A by simply reducing the intensity of the stressor, and will persist in the degraded state B. Outcomes of all three of the non-linear models potentially represent 'ecological surprises' but the last model of irreversible change is the one most likely to result in a catastrophic loss of a particular aquatic ecosystem state. Shifts in ecosystem state become irreversible when the ecological processes that maintain the prior state vanish from the landscape (Gordon *et al*. 2008). This may have occurred in the WA wheatbelt where salinization has occurred over huge spatial scales, and in some regions for a very long time (>100 years). The seed banks fundamental to the development of plant-dominated, seasonally drying systems may have disappeared from waterbodies now dominated by benthic microbial communities (Davis *et al*. 2010). Further research is needed to determine the longevity of seed banks and the potential for recovery if changing climatic conditions result in more frequent rainfall events and a return to fresher conditions.

Therefore, knowing how an ecosystem is likely to respond to intensifying stressors is one of the most valuable insights that a manager can have. The situation becomes more complicated when there are multiple stressors because then we may get multiple thresholds. Some stressors acting together have much greater effects than being simply additive (**synergistic** effects) whereas other stressors cancel each other out so that when combined, they have a lesser effect (**antagonistic**). Human activities such as agriculture and urbanization alter the water regime (Chapter 9) and change the physical form of the landscape and waterbodies (Chapter 10) as well as their water quality (this chapter). All these changes, combined with diversity of waterbodies and landscapes across Australia, generate a variety of possible responses and recovery pathways that challenges aquatic ecologists and managers to reliably predict the outcomes of management strategies. Models like those described earlier help us seek patterns in responses in aquatic ecosystems to changes in water quality.

11.10 SYNTHESIS

Eutrophication, salinization, acidification and water pollution are four water quality management issues that have severe ecological impacts. All of them impair ecosystem services, especially those associated with provisioning, supporting and cultural services. People are sometimes alarmed by visible evidence of these impacts, such as corpses of fishes floating after a fish kill or the white expanse of a salinized wetland that was once fresh. Public alarm prompts management actions, often short-term 'fixes' to treat the symptoms. However, to adequately address the problem, we must understand the cause and the ecological mechanisms.

When we do this, we see that most water quality problems are caused by multiple stressors. The effects of these stressors are not always predictable, and responses are typically modified by environmental conditions associated with water regime (Chapter 9) and the physical structure of the catchment and waterbody (Chapter 10). We can use conceptual models supported by empirical data to generate various scenarios of potential outcomes from one or more stressors. The desirability of these different scenarios can be assessed by using water quality guidelines and ecological risk analysis to predict the responses to certain management strategies. We can then devise an appropriate monitoring program to track the environmental impacts and ecological responses to our management interventions at different points in the framework shown in Figure 11.1. If successful, we will recover lost or impaired ecosystem services while learning more about the complexity of aquatic ecosystems.

However, even if we successfully address all the major problems with water regime (Chapter 9), physical features (Chapter 10) and water quality (this chapter), there are other stressors to consider. These include the effects of invasive species, and in the next chapter, we look at these new stressors in the context of biodiversity conservation and climate change in Australian aquatic ecosystems.

CHAPTER 12

Management issues: biodiversity conservation and climate change

12.1 WHAT IS BIODIVERSITY AND WHY DOES IT NEED CONSERVATION?

Biodiversity is the variety of living organisms from all sources, including terrestrial, marine and aquatic ecosystems, and the ecological complexes of which they are part (IUCN www.iucn.org/iyb/about/). It includes genetic diversity within species, diversity among species and diversity of ecosystems. Conservation aims to maintain taxa and their interactions as communities within sustainably functioning ecosystems, and to protect each taxon's genetic diversity, an attribute vital to its on-going evolution.

We need to conserve biodiversity for both ethical and utilitarian reasons. Ethically, none of us has a right to cause extinction of any species, and we should avoid any actions that might do so. From a utilitarian perspective, biodiversity helps aquatic ecosystems withstand or recover from the effects of multiple stressors and, therefore, continue to provide the ecosystem goods and services on which we rely as a species. Put bluntly, sustained losses of biodiversity will lead ultimately to human extinction. As freshwater ecosystems and their biodiversity are among the most threatened on the planet (Dudgeon *et al*. 2006), it is imperative that we conserve what remains.

The previous three chapters described how human activities that change water regimes, physical features and water quality threaten biodiversity. These threats, largely driven by growth in human populations and associated with anthropogenic climate change, include the issues covered in Chapters 9–11 as well as other threats such as adverse effects of invasive species, changes in fire regimes, intentional harvesting and habitat fragmentation (reviewed by Steffen *et al*. 2009). Most of these threats interact to affect biodiversity of aquatic ecosystems (Figure 12.1), and their effective management must integrate many of the threads and linkages described in the previous 11 chapters.

12.1.1 Setting priorities in biodiversity conservation

In the years since Europeans settled Australia, most aquatic ecosystems have been profoundly altered and freshwater species extinctions have occurred. For example, the gastric brooding frog *Rheobatrachus silus* has not been seen in the wild since 1981 (Williams and Hero 1998) and is listed as 'presumed extinct' under the Environmental Protection and Biodiversity Conservation Act (1999) (EPBC Act). Management attempts to manage our impacts and to conserve what biodiversity remains, and this calls for much ecological knowledge – about taxa and their distributions and genetics, ecosystem processes, and the multiple threats to taxa and communities. It also requires prioritization, planning and implementation of both short- and long-term management strategies, often working within a tight budget.

Setting priorities is helped by two kinds of tools. The first is a **set of criteria** (e.g. IUCN 2001) by which to judge how threatened a taxon is (i.e. the relative risk that it will soon go extinct). Judgment is based on the taxon's abundance and range area, how rapidly either

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Australian Freshwater Ecology: Processes and Management, Second Edition. Andrew J. Boulton, Margaret A. Brock, Belinda J. Robson, Darren S. Ryder, Jane M. Chambers, and Jenny A. Davis.

Companion Website: www.wiley.com/go/boulton/freshwater

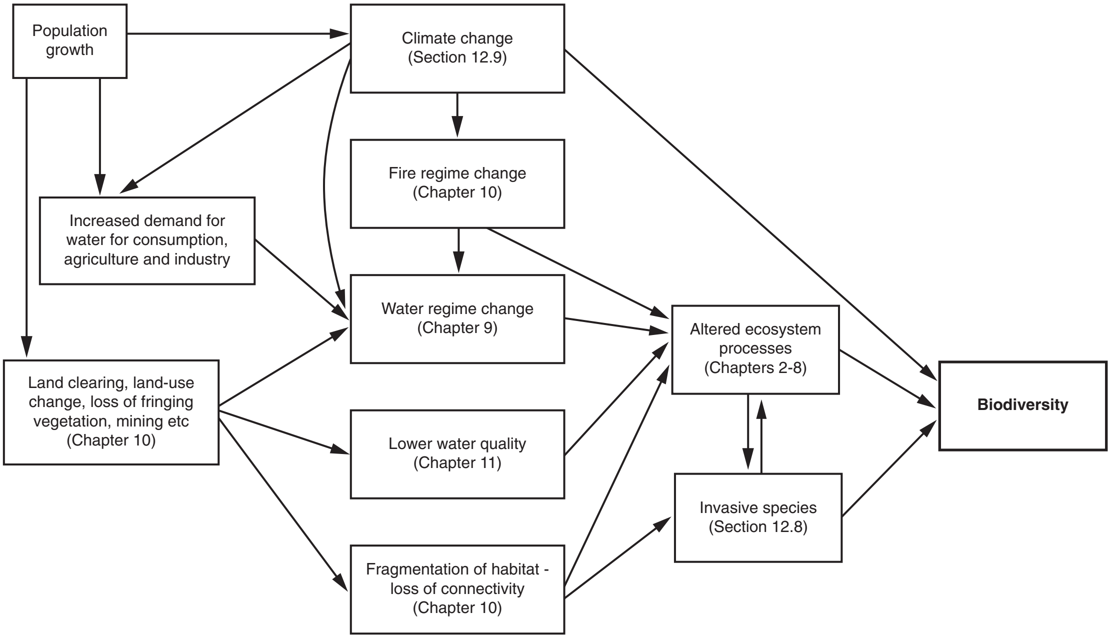

Figure 12.1 Main processes threatening biodiversity in Australian aquatic ecosystems. Arrows indicate direction of effects.

is declining, and the extent of fragmentation of its populations. Using such criteria, Federal and State governments in Australia assess a taxon as being anywhere from 'secure' to 'extinct', and list taxa by degree of threat. Those taxa deemed most threatened may then get special conservation attention, depending on social and economic considerations. Trade-offs are typically unavoidable and there are various generic frameworks (e.g. Wilson *et al.* 2009) to decide where, how and when to invest conservation resources because budgets are nearly always finite.

The second tool consists of **conservation laws** to protect native species so they do not become threatened. These partly reflect how much society values biodiversity when its conservation conflicts with other interests. In Australia, attitudes have changed over time. Early laws protected individuals of a few species: firstly, those valued for hunting (including non-native trout), and then a few other useful or charismatic species. Gradually, from the 1960s onwards, laws expanded to cover most native plants and vertebrates (Jarman and Brock 2004). However, taxa continued to become threatened and since 1995, laws have allowed nearly all native vertebrates and invertebrates, plants and fungi (and even genetically defined sub-populations of any of these) to potentially be listed as threatened, thus supporting protection for their populations and, importantly, their habitats.

Ecological communities can also be listed as threatened to gain conservation attention, and processes that threaten taxa and communities (Key Threatening Processes) may be listed to trigger action to abate their impacts. Australian States, Territories and the Commonwealth all have complementary conservation legislation but how well are aquatic species and ecological communities protected by this system? This depends on the taxonomic group and where they live. Typically, vertebrates are more likely to be recognized and listed than invertebrates or plants, and no unicellular organisms are yet listed (2013). Individual taxa are more likely to be listed than ecological communities, although some aquatic communities have been listed (Section 12.7).

Where ecosystems remain relatively intact, a longstanding conservation approach has been to declare an area containing a target ecosystem as protected.

Ideally, we would conserve an adequate number of sites representing the full range of Australia's ecosystems. In this chapter, we describe why this approach seems particularly ill-suited to aquatic systems. We then review conservation challenges posed by some traits of dispersal and life-history that are common among aquatic organisms. Finally, we assess threats arising from many of the human activities described in Chapters 8–11, as well as additional ones such as altered fire regimes, invasive biota and climate change.

12.2 AQUATIC LANDSCAPES: NETWORKS AND MOSAICS OF HABITATS

The ecological and hydrological linkages among surface waters and between them and groundwater (Section 1.5.2) are being incorporated into landscape-scale management of surface and groundwaters as connected systems. Sometimes, this management revolves around catchments or sub-catchments, especially where the focus is on river channels and their associated standing waters. Other times, management focuses on natural landscape features that contain a variety of aquatic habitats. One example of an **aquatic landscape** is the rivers and floodplain wetlands (Figure 12.2) that lie between the East Alligator and Mary Rivers, much of which is in Kakadu National Park in the NT. The landscape is spatially complex, with interconnected lotic and lentic waters providing habitats that vary from fresh to hypersaline and harbour diverse plant communities. It is also temporally complex because the aquatic habitat expands during the wet season and contracts during the dry season, some habitats seasonally changing in salinity. In addition to their biodiversity, the Kakadu wetlands have great cultural value and provide recreational experiences and livelihoods for many Australians.

Figure 12.2 Diverse ecosystems in an aquatic landscape: open water with floating and submerged aquatic plants, and a *Melaleuca* swamp in the background, Kakadu National Park, NT. (Source: Neil Pettit.)

Animals and plants use these landscape mosaics at different spatial and temporal scales. The degree of connectivity between the aquatic habitats varies among species. For example, waterbirds in the Kakadu wetlands use the landscape well beyond these wetlands to meet their requirements for feeding, nesting and resting. The extent and duration of inundation govern their food resources and their nesting success, and may affect their ability to move across the landscape to access resources. In contrast, fishes rely on hydrological connections to move around. During the wet season in the Magela Creek system flowing through Kakadu, fishes can move along the creek, into and out of the floodplain billabongs and, for some species, into or out of the tidal reaches. As the dry season begins, fishes then move to seek refuges in which to wait out the period of hydrological disconnection (drying), sheltering in either flowing or standing permanent waters (Figure 12.2, Bishop *et al*. 1995), depending on the particular species.

This example illustrates how different species respond to the aquatic landscape differently, depending on their requirements and means of dispersal. Body size also affects species' responses; smaller animals tend to respond at finer spatial scales within the landscape. For example, many small freshwater crustaceans seldom move as far as large fishes yet both groups depend on hydrological connections for dispersal. When managing biodiversity at the landscape level, we must acknowledge that different species respond to habitats at different spatial and temporal scales and that their responses depend on connectivity among these habitats.

We also need ways to quantify biodiversity at these different spatial scales to help us assess the success of our efforts to protect it. Of the numerous indices of diversity and taxonomic richness (Gaston 1996, Lindenmayer and Gibbons 2012), three of the most widely used are alpha, beta and gamma diversity. **Alpha diversity** is the number of taxa in a given area, whereas **gamma diversity** comprises the total number of taxa across whole landscapes, and is mostly used in global or continental-scale biodiversity assessments. **Beta diversity**, the 'turnover' or change in taxa composition across a landscape, is also significant for biodiversity conservation. For example, two wetlands might each have 40 species of invertebrates, but if the two wetlands each have 40 different species (i.e. 80 species in total) then diversity is clearly higher than if they share the same set. There are various indices of beta diversity, and they need to be used and interpreted cautiously (Anderson *et al*. 2011).

12.3 PROTECTED AREAS FOR CONSERVING FRESHWATER COMMUNITIES

Protected areas are one of the principal tools used to conserve biodiversity. An intention of a protected area is that threatening processes are minimized, thereby preserving whole ecosystems, communities and their component species. Although protected by law from a range of human uses and activities (particularly vegetation clearing), some uses such as water extraction may still be allowed. In Australia, there is a protected area network that aims to conserve representative areas of all the country's terrestrial ecosystems. However, this network may be less successful in conserving our freshwater ecosystems, which were largely overlooked in the design of the reserve system (Nevill 2007). In addition, threats such as invasive species (Section 12.8) and climate change (Section 12.9) are difficult to exclude (Chessman 2013).

Some freshwater protected areas are designated by international agreements such as the Ramsar Convention on Wetlands whose signatories agree to protect and conserve wetlands, and to use them wisely (Box 12.1). The Ramsar definition of wetlands is:

> *areas of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salt, including areas of marine water the depth of which at low tide does not exceed six metres (www.ramsar.org/)*

and is the basis of the one used in this book (Section 1.2) to collectively define surface waters. Ramsar sites in Australia were nominated as individual aquatic systems rather than as a comprehensive or representative selection of significant waterbodies. Other designated protected areas, ranging from National Parks to different types of conservation reserves, often incidentally contain inland waters but few of these areas were established to explicitly protect Australian rivers and wetlands (Saunders *et al*. 2002). There is certainly scope for improvement.

This lack of adequate comprehensive protection has serious consequences for the conservation of our fresh-

Box 12.1 Ramsar wetlands in Australia

The Convention on Wetlands, agreed in Ramsar, Iran in 1971, is the foremost international environmental agreement for the conservation of freshwater and marine wetlands. As a signatory, Australia is required to designate and conserve Wetlands of International Importance ('Ramsar sites'), make 'wise use' of (sustainably manage) all wetlands and support international cooperation for conservation. By 2012, Australia had designated only 65 Ramsar sites covering nearly 8.1 million ha, but these do not yet represent the diversity or geographic distribution of wetlands. Different Ramsar wetlands in Australia are managed by federal or state government agencies, or in some cases, by non-government organizations and private land holders. The EPBC Act (1999) recognizes Ramsar wetlands as matters of National Environmental Significance, requiring environmental approval of any new 'action' that may have a significant impact. The Ramsar Convention helps conserve freshwater ecosystems in Australia because it codifies global conservation norms, engages the Federal Government in the protection of wetlands in states and territories (including conservation through environmental flows), and because Ramsar sites are a freshwater protected area mechanism that applies across land tenures (Pittock *et al*. 2010).

Jamie Pittock (Australian National University) and Max Finlayson (Charles Sturt University)

Box 12.2 Aquatic biodiversity conservation in urban streams

Cities of the world have been unkind to their streams. Small streams are often obliterated and buried, transformed into stormwater drains. Streams, even in protected areas, that remain downstream of stormwater pipes are usually impaired. Paved urban catchments have larger and more frequent stormflows that erode stream beds and banks and alter water quality. These flashy flow regimes eliminate sensitive species and reduce the channel's capacity to retain contaminants (Walsh *et al*. 2005a). Encouragingly, studies of peri-urban streams (bordering urban areas) show that preventing stormwater runoff from draining directly to streams can protect flow regimes, water quality and the ecology of receiving streams (Walsh *et al*. 2012). To do this, stormwater can either be treated for domestic and industrial use or retained so that it evaporates, is used by plants or infiltrates to recharge the groundwater. Peri-urban streams show us that biodiverse urban stream communities are possible, but only if retention and use of stormwater become standard practice and stream corridors can be protected and vegetated. Slowly, long-standing planning and engineering practices are changing (Fletcher *et al*. 2011), and we can be kind to our streams in future.

Chris Walsh, University of Melbourne

water biota, particularly because of the importance of connectivity across mosaics and networks of surface waters and between them and groundwaters. Often, only parts of surface or groundwater systems occur in protected areas, and the rest of the system lies in agricultural, industrial or urbanized land (Box 12.2) where water regime and water quality are usually adversely affected. Impacts of human activities on groundwaters and rivers in unprotected areas upstream are often transferred down to the protected ecosystems. For example, the Glenelg River in western Victoria has its headwaters in the Grampians National Park and its lowland reaches and estuary in the Glenelg River and Cobboboonee National Parks. However, the middle reaches are exposed to severe sedimentation and water quality problems (Figure 12.3, Robson and Mitchell 2010). Sediment slugs (Section 10.3) in the Glenelg River are slowly moving downstream and there is concern that they will enter the lower river in the protected area.

However, partial protection is not always the greatest problem. Sometimes, other threats such as invasive species or the effects of climate change are more serious. For example, part of Kakadu National Park lies downstream of a uranium mine on Magela Creek, considered a possible threat to water quality through potential releases of uranium, manganese, magnesium and sulfate. An ecological risk assessment (Box 11.5) that compared this threat to those from invasive species, altered fire regime and seawater intrusion caused by sea-level rise showed that the mining risks were orders of magnitude lower than those from these other threats, and invasive para grass *Urochloa* (formerly *Brachiaria*) *mutica* posed the greatest risk to these wetlands (Bayliss *et al*. 2012).

Other problems relate to legislation covering water supply and mineral rights in Australia. Typically, the need for water supply overrides conservation requirements. Sometimes, water catchments become conservation reserves because they are the only areas with intact vegetation, and the protected area contains infrastructure for water extraction. In the Grampians National Park, for example, water extraction has transformed some formerly permanent streams into temporary ones, altering the flora and fauna of these streams arising in and flowing through a protected area. Similarly, mining for fossil fuels and minerals can occur next to or below protected areas, altering hydrological regimes and potentially releasing pollutants into surface and groundwaters (Sections 8.6 and 11.6).

Despite all these difficulties with designing effective protected areas for aquatic biodiversity conservation, Australia boasts several protected areas that include aquatic ecosystems of very high conservation value, including some listed under the Ramsar Convention. We now need to ensure that the ecological significance of lateral, longitudinal and vertical connectivity is fully recognized when protecting these areas, especially given the range of dispersal abilities of aquatic plants and animals.

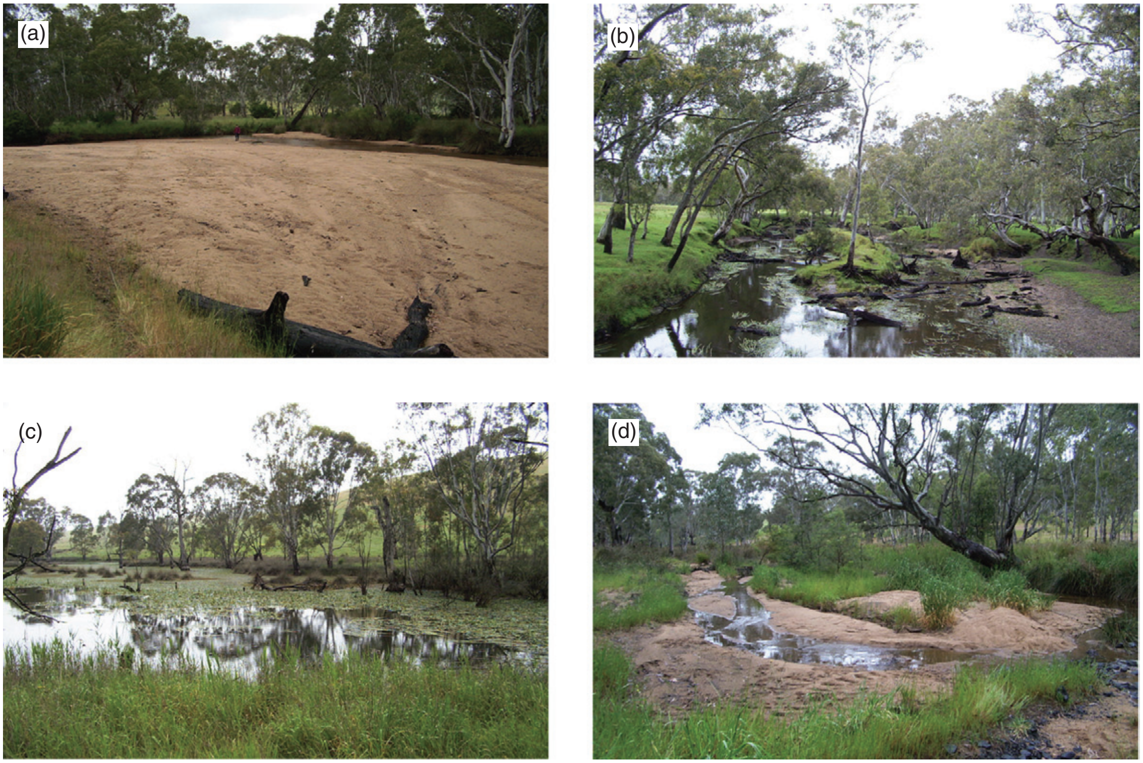

Figure 12.3 Middle reaches of the Glenelg River, western Victoria, (a) a large sediment 'slug' entering the river from a tributary (right-hand side); (b) a reach unaffected by sedimentation in the middle reaches of the river; (c) a tributary junction plug wetland formed when a sediment slug blocks the river channel, creating a wetland; and (d) the main river channel filled with sand. (Source: Belinda Robson.)

12.4 HAVING GOOD CONNECTIONS: DISPERSAL AND CONNECTIVITY IN CONSERVATION

Most inland waters in good ecological condition support biota capable of active dispersal by flying (insects, birds), swimming (fishes, some crustaceans), or walking or hopping across terrestrial areas (amphibious reptiles and amphibians). Others disperse passively, carried by animals such as fishes or birds as passengers (zoochory; for example, some plants, molluscs and other invertebrates). Many are windborne (e.g. spores, seeds, desiccation-resistant stages of many zooplankton) or waterborne. Some travel far between waterbodies, sometimes many hundreds of kilometres apart, whereas others disperse only locally within their waterbody and may never go further than a few hundred metres. This diversity of dispersal abilities leads to very different patterns of landscape-level connectivity that must be considered in the design of protected areas.

Until recently, systematic conservation planning has focused on **longitudinal connections** along river systems (Barmuta *et al.* 2011). This has been because the problems of managing riverine protected areas are most evident where impacts occur upstream of the protected areas. However, other connections are also important (Linke *et al.* 2011), and are now being included in methods to plan freshwater reserves. For example, **lateral connections** between floodplain wetlands and river channels or among groups of wetlands have been included in the conservation planning method 'Marxan' to incorporate the ecological requirements of species such as flying insects and waterbirds that move independently of hydrological connections (Hermoso *et al*. 2012).

Although the ecological significance of **vertical connectivity** between surface and groundwaters has long been known by freshwater ecologists, recognition of its relevance for conservation has been slow. A welcome advance was acknowledgement that diverse types of groundwater-dependent ecosystems were widespread across Australia and threatened by changes to groundwater regime and water quality. Although groundwater faunal assemblages within individual aquifers often have low alphadiversity, there is much short-range endemism (Chapter 8) and adjacent groundwaters, currently or historically, isolated typically have very different species compositions (i.e. high beta and gamma diversity). This means that designing groundwater reserve networks to protect all species may be impractical because of the large areas required to encompass all the species (Boulton 2009). Unfortunately, surface and groundwaters are often managed separately despite being hydrologically connected. Management of an aquifer often differs across political boundaries, even though it is the same groundwater. There is still some way to go in understanding groundwater biodiversity and the processes that sustain it before we can determine how best to use protected areas to conserve groundwater species.

Where possible, we should link freshwater and terrestrial conservation planning to conserve whole landscapes. The reality is that scope for such planning for conservation based on fully protected areas may be limited. In Australia, many existing large protected areas were delimited decades ago (Turak *et al*. 2011), and in most regions there is limited opportunity for designating new ones. Therefore, we need methods other than protected areas to conserve aquatic biodiversity. The most popular approach is now the designation of areas with different degrees of protection or permissible activities, analogous to those in different zones of marine conservation areas (Linke *et al*. 2011; Turak *et al*. 2011). This approach is more aligned with ideas of the sustainable use of ecosystems for their services rather than as fully protected areas that quarantine places or resources from human influence. To use this approach, we need a better understanding of the way that aquatic biota use the landscape, especially in taking refuge from natural and anthropogenic disturbances. This then allows us to focus on controlling human activities that potentially threaten such refuges or their connectivity to surface waters and groundwaters.

12.5 PROTECTING REFUGES TO CONSERVE AQUATIC COMMUNITIES

There are often dramatic expansions and contractions of inundated habitat in lentic and lotic systems such as the Kakadu wetlands or the floodplains of dryland rivers. Aquatic biota survive dry periods, including supra-seasonal droughts (Lake 2011), in a variety of spatial and temporal **refuges**. Refuges from disturbance are habitats that convey spatial or temporal resistance or resilience to biotic communities affected by biophysical disturbances (Sedell *et al*. 1990). Recolonization and recovery after drought depend on the life-history traits of species (including their dispersal capacity) and the presence and distribution of refuges (Robson *et al*. 2011). In inland waters, where many ecosystems are either not or only partially included in protected areas, the identification and protection of at least some types of refuges may help conserve certain species (Robson *et al*. 2008b).

In theory, if refuges could be identified and included in protected areas, this would help ecosystems recover from disturbances such as drought or fire and maintain biodiversity (Turak *et al*. 2011). For example, some waterholes in dryland rivers remain filled despite years without surface flow in the main channel, and provide a refuge for most freshwater species in the river. In dryland rivers, a spatial and temporal mosaic of refuge waterholes may be necessary to sustain river biodiversity during dry periods (Sheldon *et al*. 2010). This may also apply in seasonal streams and wetlands in Mediterranean-type (dry summer-wet winter) climatic regions (Robson and Clay 2005; Chester and Robson 2011). In waterholes, as the time between floods increases, diversity within a specific waterbody (alpha diversity) declines but, because of environmental differences among waterbodies, gamma diversity remains more stable. Therefore, to conserve the most species, multiple and dispersed refuges are needed.

Furthermore, waterbodies need to be periodically reconnected hydrologically to maintain both local and regional aquatic diversity. Disturbance pressure must recede at times to allow species to disperse and recolonize. In dryland Australian rivers and floodplains that operate in a ‘boom-bust’ cycle of drying and inundation (Section 7.7.1), there are three groups of species that

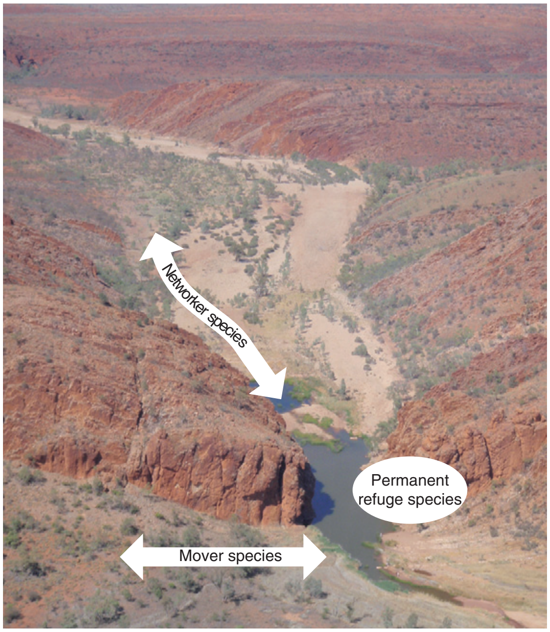

Figure 12.4 Application of the classification by Sheldon *et al.* (2010) to biota of a permanent waterhole at Glen Helen Gorge on the Finke River, NT. 'Mover species' are mainly insects such as dragonflies that can fly among river channels regardless of flow conditions, 'networker species' (e.g. fishes and shrimps) rely on hydrological connections to disperse, and 'permanent refuge species' include molluscs such as freshwater mussels and snails that do not disperse far. (Source: Belinda Robson.)

use waterhole refuges but differ in their capacities for dispersal (Figure 12.4, Sheldon *et al.* 2010): 'mover species' that fly among waterholes, 'networker species' that travel via hydrological connections, and 'permanent refuge species' (the fewest) that seldom disperse and take permanent refuge in the waterholes.

12.6 CONSERVING AQUATIC SPECIES AND POPULATIONS

To conserve biodiversity effectively, we must know what species and populations exist to be conserved. In Australia, many species and even genera remain undescribed, especially of invertebrates, algae and fungi. We know even less about the taxonomic diversity of microbes. Additionally, many aquatic species have complex life histories, comprising several stages with different morphologies and even terrestrial or marine phases, and so their conservation requires consideration of environments other than inland waters. Consequently, we do not know the size or areal extent of the metapopulations of most aquatic species, severely hampering their effective conservation and management.

12.6.1 The special challenge of conserving species with complex life histories

To fully conserve a freshwater species with a complex life history comprising different stages that require different habitats, some of which may be semi-aquatic or terrestrial, we must ensure that the species has access to these habitats at all appropriate times in the life-cycle. Loss of just one stage's habitat may be enough to send a species locally extinct. For example, many freshwater insects have aquatic larvae and terrestrial adults. Appropriate habitat, food and water quality are needed for the larvae whereas adults often require fringing or riparian vegetation, oviposition sites and, for some, adequate food. Although it seems unfashionable to gather data about individual species and their natural history, this knowledge is essential for their adequate protection. It also often reveals the intriguing aspects of behaviour that delight fellow freshwater ecologists.

One example of the importance of knowing about complex life histories and intriguing behaviour is illustrated in conservation efforts to arrest the worldwide decline in freshwater mussels, including the Unionidae (mainly Africa, Eurasia, North America) and Hyriidae (Australasia, South America, Figure 12.5). These mussels release larvae (glochidia) that must spend a brief period as parasites on the gills, fins or skin of a host fish. During the parasitic phase, the glochidia metamorphose to become juvenile mussels, and adopt a benthic habitat as they mature. For freshwater mussels, the parasitic phase on fishes is the primary means for dispersal (Klunzinger *et al.* 2012, Walker *et al.* 2013). However, many Australian freshwater mussels are in decline because human activities have reduced populations and movements of their fish hosts (Brainwood *et al.* 2006) in addition to the direct effects of habitat changes (e.g. through sedimentation and dredging). Strategies to conserve freshwater mussels must ensure that adequate

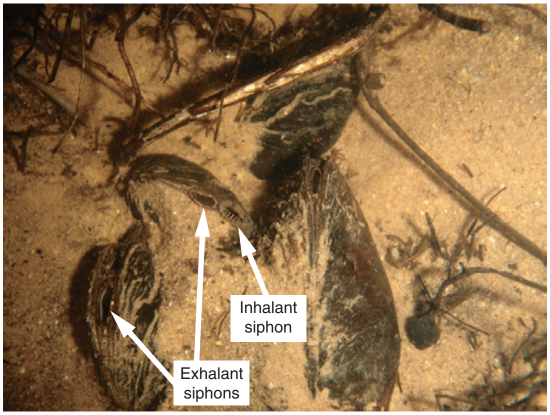

Figure 12.5 The freshwater mussel *Westralunio carteri*, like other Australian species, expels larvae (glochidia) in strings of mucus that float free in the water, awaiting contact with a potential host fish. (Source: Peter O'Toole.)

numbers of their host fish species can move among mussel populations.

12.6.2 The spatial extent of populations and metapopulations

The use of molecular genetics has helped reveal the spatial extent and structure of populations of many aquatic species, and for various lotic species, four models of population structure have been proposed (Section 7.7.2). Life history traits, especially a species' capacity to disperse among stream networks, determine its likely population structure (Hughes *et al.* 2009). However, although sufficient freshwater species have been sampled and analysed using molecular genetics to construct these models, the population sizes of most species have yet to be described and knowledge for species in standing waters is particularly poor. In addition, many populations of freshwater taxa will probably be parts of **metapopulations** (Section 4.1), comprising 'populations of populations' that are linked by sporadic dispersal and interbreeding. Successful conservation and management must maintain these linkages.

Fishes and other large animals can be tracked to ascertain movement patterns (Box 9.7), but many invertebrate population structures can only be described using genetics. Furthermore, few places have been sampled over time, so we know little of how the distributions of populations change across landscapes over the time scales (e.g. months to years) at which we observe changes in water regime. Thus, it is difficult to determine whether protected areas contain whole populations or multiple populations, and whether they allow adequate connectivity and dispersal among waterbodies. Genetic work so far indicates that many aquatic invertebrate populations are smaller and inter-population dispersal is less than expected, rendering them highly vulnerable to landscape changes (Hughes *et al.* 2009).

Figure 12.6 The Australian smelt *Retropinna* from the Murray-Darling Basin. (Source: Tarmo A. Raadik.)

12.6.3 What are 'Evolutionarily Significant Units'?

Conservation biologists frequently refer to **Evolutionarily Significant Units** (ESUs). These are genetically distinct populations within one species, largely reproductively isolated from each other (Waples 1995). They need to be conserved separately from each other because each ESU may have traits enabling it to persist in its particular environment. These may include visible traits such as colouration or pattern, or physiological ones such as greater tolerance to higher temperatures. The ESUs of many species exist both within and outside protected areas, especially for aquatic species that move among standing waters and along river networks. Until we know what ESUs exist for a species of interest, and the spatial limits of each, we cannot plan to effectively protect the species' full suite of genetic diversity.

Let's take two widely distributed Australian fishes as examples. The first is the Australian smelt *Retropinna* (Figure 12.6), a freshwater fish found in rivers across the south-east. It was previously regarded as comprising two species: one on the mainland and one in Tasmania. However, a molecular genetic study (Hammer *et al.* 2007) reveals at least five separate ESUs (probably species): one in the Lake Eyre Basin, at least one in rivers of Tasmania, western Victoria and SA, one in central-eastern Queensland, one in south-eastern Queensland and one along the south-east coast of NSW and Victoria. The second example is the spangled perch *Leiopotherapon unicolor*, common across widely different waters throughout central and northern Australia, even in isolated ones in the desert. Despite its wide distribution, this species shows much less genetic variation across its range and appears to comprise a single ESU (Bostock *et al.* 2006).

What is the conservation relevance of identifying ESUs for these two freshwater species? For the spangled perch, shown to be all one ESU, loss of some populations across its range would not severely reduce the genetic diversity of this species, and the species can be managed as one population. In contrast, smelt populations must be managed as different ESUs to conserve the multiple species (Hammer *et al.* 2007).

12.6.4 Hidden biodiversity: cryptic species

Often, the use of molecular genetics leads to the discovery of **cryptic species**. These are species that are reproductively isolated from each other but morphologically so similar that they had previously been regarded as the same species. Usually, these populations are found in different places but sometimes they co-occur (i.e. are sympatric), causing problems in field identification.

Numerous cryptic species of aquatic vertebrates and invertebrates are being found across Australia, as our example of the Australian smelt shows. Many groundwater habitats harbour cryptic species of stygofauna (Section 8.5.2), adding additional complexity to the conservation of this subterranean environment. The frequency with which cryptic species are being discovered indicates that we have probably severely underestimated the species richness of surface and groundwaters. This underestimate probably also reflects the low number of taxonomists and systematists working in our inland waters. Sadly, despite the importance of this work to conservation and ecology, there is seldom adequate recognition or funding provided to address the huge gaps in our knowledge of freshwater taxonomy for most groups.

12.6.5 Endemic species and relictual faunas

As we saw in Chapters 4, 7 and 8, Australia has numerous endemic aquatic plants and animals. Many are also **short-range endemics**, defined as endemic species with highly restricted distributions (nominally $<10\,000\,\text{km}^2$, Harvey 2002). Groundwater fauna include many short-range endemics (Section 8.5.2) as do some groups of surface water invertebrates, such as gastropod molluscs. Although coastal dystrophic lagoons in Tasmania are considered significant sites for short-range endemic microalgae (Tyler 1996), distributions of other apparently endemic algae within them may actually reflect limited sampling. For example, the desmid *Micrasterias hardyi* pictured in Figure 4.9 was collected in a Simpson Desert waterhole; before then, the species had been considered endemic to an area thousands of kilometres away.

Relictual faunas in freshwater habitats comprise species that evolved in cooler, wetter and often temperate environments and now persist in refuges with suitable micro-climates (usually permanent water, buffered from thermal extremes) surrounded by warmer and more arid landscapes. In the past, much of Australia was wetter and cooler (Section 7.7.3). Subsequent aridification isolated ‘freshwater oases’ in the dry landscape, creating pockets of relictual fauna in several regions (e.g. south-western WA, Davies 2010; central Australia, Davis *et al.* 1993). This aridification and geographic isolation has also promoted endemicity in much of our freshwater fauna, further facilitated by the various sources and modes of dispersal of different taxa and the geological timing of their arrival on the continent.

Complex life histories, numerous cryptic or short-range endemic species and the occurrence of relictual faunas all contribute to the challenges in conserving our aquatic species. Even a single group can include diverse examples. For instance, in one genus of charophytes, there are short-range endemic species (e.g. *Nitella tumida*), annual species (e.g. *Nitella sonderi*) and cryptic species (e.g. *Nitella verticillata*) whose detection may depend on luck or repeated thorough surveys and culture of seed bank material (Casanova and Porter 2013). Until we are fully aware of these issues, successful species conservation will be elusive. In particular, conservation managers must be alert to the need to maintain multiple populations of 'apparent' species across their geographic range to ensure cryptic species are not lost before they are even described. Relictual fauna are already 'on the edge' and will require special protection from threats such as climate change if we are to preserve these species. The situation is further hampered by the poor state of taxonomic and biological knowledge for most aquatic species in Australia.

12.7 THREATENED COMMUNITIES AND SPECIES

Any taxon, population or ecological community can be at risk of extinction, whether naturally or through human activities. When they are subject to an identifiable and usually anthropogenic 'threatening process', we classify them as **threatened**. Biodiversity conservation often focuses on threatened ecological communities: assemblages of species that face particular pressure from human activities. Some threatened communities are relictual, such as several of the groundwater-dependent cave faunas in south-western WA (Guzik *et al*. 2011) where dwindling groundwater supplies increasingly restrict their aquatic habitat (Box 8.10). Others are threatened as a result of widespread anthropogenic alteration of particular habitat types, such as the 'unwooded freshwater wetlands of the southern wheatbelt' (WA) of which only two examples now exist (Jones *et al*. 2009) after widespread secondary salinization.

Although legislation in Australia to protect biodiversity now recognizes ecological communities, there is room for improvement. Revised legislation, combined with the improving knowledge of biodiversity and the distribution of ESUs and short-range endemics, should help us better conserve our precious freshwater communities and ecosystems. However, even the best legislation will fail to protect aquatic systems against changes to their supporting ecological processes (e.g. alteration to water regime) if it is not enforced. Most freshwater communities officially designated as threatened still face hurdles in obtaining funding and other resources for their adequate protection (Box 12.3). Listing does not guarantee conservation action, and prioritization after listing is often piecemeal, varying among jurisdictions, taxonomic groups and threat categories.

Individual species that are listed as **endangered species** may gain some priority in conservation. Some are short-range endemics, such as the western swamp tortoise *Pseudemydura umbrina* (Figure 12.7, Box 12.4), and may have characteristics such as long life span or delayed sexual maturity, low fecundity and very specific requirements for certain resources. This resource specialization includes dependence on a narrow range of foods or a complete reliance on a single species to facilitate life-history events such as pollination or

Box 12.3 Endangered aquatic plant communities

In 2013, nearly one third of the communities listed as 'Endangered' or 'Critically endangered' under the EPBC Act were aquatic (18 from 61). About two-thirds of these aquatic communities were listed because of their plant and vertebrate assemblages. This probably still under-represents the threatened aquatic plant communities that exist, particularly when climate change (with sea-level rise and reductions in rainfall) is considered. Aquatic plant communities are threatened by drainage, over-grazing and cropping, unrestricted groundwater use (Fensham *et al*. 2010) and urban development and sea-level rise. Listing is a useful conservation tool that can provide protection at the landscape level, when endemic species are known but not formally described, and when threats are obvious, widespread and uncontrolled. For example, as a consequence of listing, Fleurieu Peninsula Swamps (SA) have been protected from forestry activities and over-grazing, and the Seasonal Herbaceous Wetlands of the Temperate Lowland Plains should now be protected from cropping during their dry phases (Casanova 2012). However, protection is limited by the development of recovery plans and enforcement of the legislation, both of which depend on the vagaries of federal and state government funding.

Michelle Casanova, Federation University Australia

Box 12.4 The western swamp tortoise

The western swamp tortoise *Pseudemydura umbrina*, one of the most threatened turtles on Earth (critically endangered, IUCN Red List), inhabits temporary swamps on the Swan Coastal Plain, where it eats aquatic invertebrates in winter and spring, and aestivates underground or under leaf litter in summer and autumn. In the 1960s, more than 150 tortoises occupied two nature reserves near Perth. However, fox predation and climatic drying reduced the wild population to fewer than 50 by 1985. A recovery plan prescribing predator-proof fencing, groundwater pumping, captive breeding and translocations has been implemented since 1992. The number of tortoises in the wild increased from around 40 in 1992 to more than 150. However, because these tortoises do not mature sexually until they are about 15 years old, and have a lifespan of at least 70 years, most of the population is juveniles. A captive-breeding colony has been established at Perth Zoo and two new translocated populations have been established north of Perth, outside the species' original range. A research project is seeking new translocation sites south of Perth, where the effects of the drying climate should be ameliorated.

Andrew Burbidge, Consultant Conservation Biologist

Figure 12.7 The western swamp tortoise, endemic to south-western WA, is one of the world's most threatened turtles. Although commonly called a 'tortoise', it is actually a turtle because it lives in water. (Source: Gerald Kuchling.)

parasitism (e.g. freshwater mussels, Section 12.6.1). However, many threatened species have few or none of these traits. Instead, they are threatened because of impacts by invasive species or changes in land use.

Some groups of freshwater taxa are more vulnerable than others; for most groups, our knowledge is too poor to tell. Worldwide, the groups of freshwater animals containing the highest proportions of threatened species are molluscs (Figure 12.5) and amphibians (Figure 12.8). Approximately 20% of Australia's frog species are listed as threatened (Hero and Morrison 2004, Figure 12.8), and tend to be upland, short-range endemics (although some formerly had broader geographic ranges) dependent on permanent forested streams and montane wetlands. The chytrid fungus, whose spread has contributed to amphibian decline worldwide, also contributes to increased rarity in some Australian species. However, habitat loss and climate change-related impacts such as increased fire frequency, reduced snow cover and increased drying are associated with declines in almost all the threatened species. Species' traits also play a role; species with short breeding seasons, longer tadpole stages, larger body sizes, greater ages at sexual maturity, larger eggs and lower fecundity are more likely to be threatened.

One strategy for conserving threatened species is to keep and breed them in captivity (termed ***ex-situ* conservation**) before reintroducing them to suitable, safe, natural habitats. The captive population is viewed as 'insurance' in case the species becomes extinct in the wild. If possible, several captive populations are kept, selected to represent the existing genetic diversity of the species (Olden *et al.* 2011). In some cases, so little suitable habitat remains within the species' original geographic range that **translocation** to other locations must be considered (Hoegh-Guldberg *et al.* 2008) as we saw in the western swamp tortoise example (Box 12.4). However, there are serious risks to translocating species (Box 12.5). Overall, captive breeding, reintro-

Figure 12.8 Some Australian frogs listed as threatened: (a) the sunset frog *Spicospina flammocaerulea*, a short-range endemic of south-west WA, only discovered in 1994; (b) the torrent tree frog *Litoria nannotis*, an upland frog formerly found across the wet tropics in north Queensland, but now endangered; (c) the green and golden bell frog *Litoria aurea*, once widespread in the south-east but now rare. (Source: (a) Nicola Mitchell; (b) and (c) Margaret Davies.)

Box 12.5 Risks of translocating native aquatic species

Translocation of native species is one method of assisted adaptation to climate change that is being increasingly considered. However, it comes with risks. One is that translocation will allow inter-breeding, potentially homogenizing stocks, thereby reducing the expression of unique characteristics. This is observed for some freshwater crayfishes. Also, if interbreeding occurs between strains of a translocated species, the locally adapted hybrid may show increased vigour and colonize new areas. Translocated species can physically restructure their surroundings (e.g. digging by the yabbie *Cherax destructor*) or result in predation, resource-competition or aggressive-competition, which may exclude individuals of other species from where they previously occurred. Establishing species that dominate the biomass may have consequences for trophic interactions, especially whenever the ecosystem contains rare or threatened elements (e.g. caves or mound springs). Moving individuals may move diseases, symbionts and parasites. Diseases may affect other species. Translocation of other 'passengers' is serious if they affect host fitness in their new environment or spread and become pests themselves. For example, ectosymbiotic flatworms on translocated freshwater crayfishes subsequently switched hosts in their new environment! All these risks must be assessed before translocating any species.

Pierre Horwitz, Edith Cowan University

duction and translocation are costly and research-intensive, and have been used for only a few aquatic species in Australia, usually vertebrates or larger plants that are charismatic and highly valued by society (e.g. the Lake Pedder galaxias, Lintermans 2013).

12.8 IN THE WRONG PLACE: 'EXOTIC AQUATICS' AND INVASIVE SPECIES

In this book, we use the term 'native' to refer to species found in Australia prior to European settlement whereas species from other countries are called '**exotic**'. Both native and exotic species can be **invasive species**. These are species occurring beyond their usual geographic distribution as a result of human activities, and that threaten valued environmental, agricultural or other resources by the damage they cause (DSEWPAC 2013).

Invasive species often possess traits such as high fecundity and early sexual maturation, or the capacity for vegetative (plants) or parthenogenetic (animals) reproduction. Some aquatic plants are especially invasive because they have broad tolerances to environmental conditions and readily disperse via water (hydrochory) by drifting fragments that can vegetatively develop into new plants. Altered water regime (Chapter 9), clearing of native vegetation (Chapter 10) and direct transfer by human activities assist invasive species to spread and colonize new areas.

Although most invasive species in Australia are 'exotic aquatics', some native aquatic species have become invasive. For example, the cosmopolitan species common reed *Phragmites australis* frequently forms dense beds in rivers where water extraction is occurring. The artificially low river flows allow this wind-dispersed species to establish and, once a reed bed is formed, it traps sediment, resists higher flows and is hard to dislodge (Erskine *et al*. 2012). Water can pool upstream of the reed bed and cause localized flooding.

The introduction of invasive aquatic plants and animals into Australian waterbodies, whether intentional or accidental, has had profound and probably irreversible effects on many aquatic ecosystems. Some species are notorious, such as the cane toad *Rhinella marina* from Central and South America. Others attract little concern, such as the freshwater crayfish *Cherax destructor*, which is native to eastern Australia but has been introduced to Tasmania and WA. Rather than review all the country's aquatic invasive species, we have listed the more common ones (Table 12.1), and focus on several to examine their major ecological impacts.

12.8.1 Invasive predators and competitors

Of all the impacts of invasive species on native aquatic biota and ecosystems, two of the most severe are direct **predation** and interspecific **competition**. Ironically, some predatory invasive species were introduced as biological control agents to eat other species deemed to be a nuisance. For example, early last century, public health authorities in Australia introduced the so-called 'mosquito fish' *Gambusia holbrooki* (Table 12.1) to control mosquitoes, especially in malaria-prone areas. At first, managers were delighted by the ease with which it spread and the fish's hardiness. The species can survive fresh to brackish water with temperatures up to 35°C. Not only do females bear live young, contributing greatly to their success, they mature in four months and may produce as many as 80 offspring at a time. Laboratory fish had been reported to eat up to 225 mosquito larvae in one hour. It seemed the ideal biological control agent.

The species was first introduced into NSW in 1925, Queensland in 1929 and the other States in the 1930s. During World War II, the military took it to camps all over Australia and today it is one of the most widespread freshwater fishes in the country. Today, we are also a little wiser about its devastating impact on native species and aquatic ecosystems. The species, now called eastern gambusia to try at least to eradicate its original misleading name, has proved to be of little value in controlling mosquitoes. Instead, it actually has detrimental effects on native predators of mosquitoes (Harris 2013), and threatens at least seven native fish species in Australia (Jackson 1993) through competition for food and space, and direct predation on eggs and larvae. Eastern gambusia are aggressive and nip fins of adult fishes or bite developing limbs off tadpoles, leading to disease and death of native species. They are now declared a noxious species.

Competition among native and invasive species for some limiting resource usually results from aggressive behaviour by the invasive species that interferes with some aspect such as foraging, reproduction or habitat exploitation by the native one. In WA, the introduced freshwater crayfish *Cherax destructor* from eastern Australia competes aggressively with the native marron *Cherax cainii*. Laboratory studies have shown that *C. destructor* dominates direct encounters between equal-sized individuals of the two species (Lynas *et al*. 2007) and this may partly account for the spread of the species across the marron's former range. However, it is notoriously difficult to unequivocally demonstrate competition in the field, and other attributes of *C. destructor* such as a generalist diet, tolerance of poor water quality and affinity for humans probably assist its invasion.

12.8.2 Domestic and hybridizing invasive aquatic species

Some of Australia's most serious invasive aquatic species arose through **domestication**, and were then distributed by the public (e.g. gardeners, aquarists). For example, the invasive *Salvinia molesta* spread around the world as an ornamental plant for ponds and aquaria (Table 12.1). Another example is the common carp *Cyprinus carpio* (Figure 12.9a) now found across southern Australia. Although various strains of carp have been introduced to Australia since the 1800s, the wild strain (Boolarra) was the one

Table 12.1 Examples and impacts of some of the more common invasive species in Australian inland waters. *Listed as a weed of national significance.

Taxon	Species	Type	Ecological impacts and mode of reproduction
Ferns	Salvinia *Salvinia molesta**	Exotic floating fern	Forms dense floating mats of vegetation. Grows rapidly, restricting light penetration into the water. May cause anoxia. Competes with native floating and submerged vegetation. Spreads rapidly by fragmentation.
Flowering plants	Blackberry *Rubus fruticosus**	Exotic riparian invasive	Out-competes native vegetation. Leaves not consumed by in-stream shredders. Restricts light to stream channel. Spread by birds and water.
	Common reed *Phragmites australis*	Native emergent plant	Forms dense reed beds that slow river flow, causing deposition of sediment. Excludes other native plants and alters stream habitat for fauna and flora. Vegetative spread and wind-dispersed seeds.
	Giant sensitive plant *Mimosa pigra**	Exotic tropical riparian tree	Forms dense stands that exclude native riparian and emergent vegetation in wetlands. Seeds dispersed by floating.
	Canadian pondweed *Elodea canadensis*	Exotic submerged plant	Highly tolerant and can withstand harsh conditions. May compete with native submerged plants. Reproduces by vegetative growth from fragments.
	Water hyacinth *Eichhornia crassipes*	Exotic floating plant	Forms dense floating mats, restricting light to beds of wetlands and rivers, shading out submerged plants. May cause anoxia, altering nutrient cycling. Vegetative and sexual reproduction.
	Willows *Salix* spp.*	Exotic riparian trees	Form dense stands. Change in-stream detrital food web. Change stream bed habitat. May cause anoxia. Spread vegetatively and from seeds.
	Para grass *Urochloa mutica*	Exotic tropical emergent grass	Forms dense stands and excludes native plants. Alters habitat for aquatic fauna. Mainly spread vegetatively.
	Bulrush or cumbungi *Typha orientalis, T. domingensis* (both native), *T. latifolia* (exotic)	Native and exotic emergents	Form dense stands that slow river flow and cause deposition of sediment. Exclude native plants and alter stream habitat for fauna and flora. Spread vegetatively and by wind-dispersed seeds.
Molluscs	New Zealand pond snail *Potamopyrgus antipodarum*	Exotic grazing freshwater snail	Forms dense populations in rivers and lakes. Competes with native grazers and gastropods. Reproduces parthenogenetically.
	Bladder snail *Physa acuta*	Exotic grazing freshwater snail	Now the most abundant gastropod in many permanent and temporary wetlands. Competes with native grazers and gastropods. Hermaphroditic.

(*Continued*)

Table 12.1 *(Continued)*

Taxon	Species	Type	Ecological impacts and mode of reproduction
Crustaceans	Yabbie *Cherax destructor*	Native freshwater crayfish	Aggressive competitor that may compete with local native crayfishes. Reproduces sexually.
	Marron *Cherax cainii*	Native freshwater crayfish	Has displaced other crayfish species, in particular the hairy marron *C. tenuimanus* with which it hybridizes. Reproduces sexually.
Fishes	Eastern gambusia *Gambusia holbrooki*	Exotic small-bodied fish	Was spread deliberately in Australian surface waters to control mosquitoes. Voracious predator and fin-nipper of native fishes and tadpoles. Outcompetes native fishes and consumes invertebrates (including mosquitoes). Reproduces sexually and females bear live young.
	Common carp *Cyprinus carpio*	Exotic fish	Benthic feeder that reduces aquatic plant cover and increases suspended sediment, potentially reducing biodiversity in lowland rivers and floodplain wetlands. Reproduces sexually.
	Salmonidae – several species of trout and salmon	Exotic predatory fishes	Released as sport fishes and still actively stocked (introduced regularly) in some waterbodies. Active predators of native fishes and crayfishes, and may cause local extinction of native fishes. Reproduces sexually.
Amphibians	Cane toad *Rhinella marina*	Exotic toad	Released in Queensland to control cane beetle. Has spread overland across northern Australia. Both tadpoles and adults poisonous to native predators. Reproduces sexually, laying eggs in waterbodies.

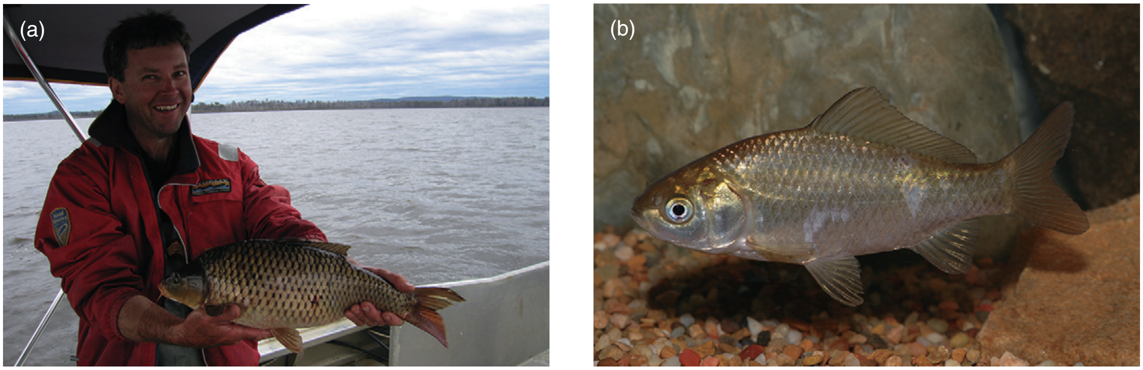

Figure 12.9 (a) A female common carp captured from Lake Crescent, Tasmania. Why the broad smile? Chris Wisniewski (pictured) and other staff of the Tasmanian Inland Fisheries Service had spent many years trying to eradicate this species from Lake Crescent and this was the last one. (b) Goldfish *Carassius auratus*, although a different genus and species from carp, can hybridize with them to sometimes produce fertile offspring. (Source: (a) Scott Hardie; (b) Tarmo A. Raadik.)

that spread swiftly through the Murray-Darling Basin during the 1960s–1980s and now dominates the fish biomass of rivers in the Basin (Davies *et al*. 2010). Common carp now comprise up to 90% of fish biomass in many south-eastern Australian and Tasmanian waterbodies (Koehn 2004).

Common carp exemplify the traits of a successful invasive species. They are highly fecund and may spawn at lower temperatures than native fishes, permitting them to spawn earlier and also in cool water from deep-release impoundments. Eggs hatch quickly and larvae grow rapidly so they quickly escape predation pressure and adult carp have few predators (Koehn 2004). They have been assisted by many of our changes to waterbodies, including slowed river flows and eutrophication. Adult common carp are mainly bottom-feeders and forage by sucking sediment into their mouths. This process suspends sediment and may uproot aquatic plants, increasing turbidity and nutrient levels in the water column and decreasing aquatic plant cover. Common carp breed in shallow waters and on floodplains, and their breeding aggregations damage stands of native aquatic plants.

Attempts to control common carp include traps that take advantage of differences in their behaviour from that of native fishes, water level manipulations that expose carp eggs to desiccation, electrical barriers, non-specific piscicides, blocking nets and exclusion screens to exclude adult carp from spawning sites (Hillyard *et al*. 2010). In river networks, none of these methods provides a single, totally effective control measure. However, in closed waters, carp can sometimes be successfully eradicated as in Lake Crescent, Tasmania, where sustained efforts reduced the population from an estimated 4900 in January 1995 to nil in July 2008; a cause for happiness (Figure 12.9a).

Carp are also able to **hybridize** with goldfish *Carassius auratus* (Figure 12.9b), commonly released from ornamental ponds or when no longer wanted as children's pets. In the Murray-Darling Basin, goldfish now occur at all sites where carp are present, and the two have hybridized (Haynes *et al*. 2012). Hybrids may be fertile and may breed with one of the parent species, leading to increased genetic diversity of these invasive fishes. The consequences of hybridization include the ability to pass on resistance to diseases that might otherwise be used to control carp. Hybrids also possess a greater variety of traits, increasing the range of environments that they are potentially able to invade (Haynes *et al*. 2012). This capacity for hybridization means that these two species must be managed as a single gene pool, and therefore as a single invader when control strategies are developed.

12.8.3 Invasive 'ecosystem engineers'

The impact of invasive species on aquatic communities and ecosystems depends on the degree to which they alter ecosystem processes. Particularly problematic are invasive species that are also **ecosystem engineers**: species able to modify ecosystems through their actions (e.g. burrowing) or through their physical presence (e.g. aquatic plants), thereby changing the physical structure of ecosystems and their ecological processes (Jones *et al*. 1994). One example of invasive ecosystem engineers in many Australian rivers are willows (*Salix* spp.). Similar to the spread of gambusia, the problem mostly began through well-intentioned efforts. To halt bank erosion, willows seemed ideal because they could be planted easily (broken stems stuck into moist ground will grow) and they grew rapidly, quickly stabilizing stream banks. Once planted, many species of willows spread easily downstream because broken stem fragments can take root where they are deposited by the flow. Again we see the familiar attributes of a successful invader: readily dispersed and reproductively prolific, this time by vegetative means (although willows that reproduce sexually also cause serious problems).

Willows have multiple impacts on lotic ecosystems. Unlike the summer-dominated leaf fall of evergreen eucalypts, the leaf fall of deciduous willows occurs in autumn and the leaves are more easily decomposed than eucalypt leaves (Schulze and Walker 1997). This means that streams are less shaded during winter and timing and rates of supply of carbon to food webs are altered. Willow roots form a mat over the stream bed that reduces its complexity, and dense infestations create pools, often with low dissolved oxygen levels (Read and Barmuta 1999). When willows form dense thickets, they may divert stream channels (Figure 12.10) and 'engineer' new islands or backwaters. Willow removal and replanting riparian zones with native vegetation now form a common restoration strategy for streams but complete recovery of the system has yet to be clearly demonstrated (Becker and Robson 2009) and may take longer than a decade.

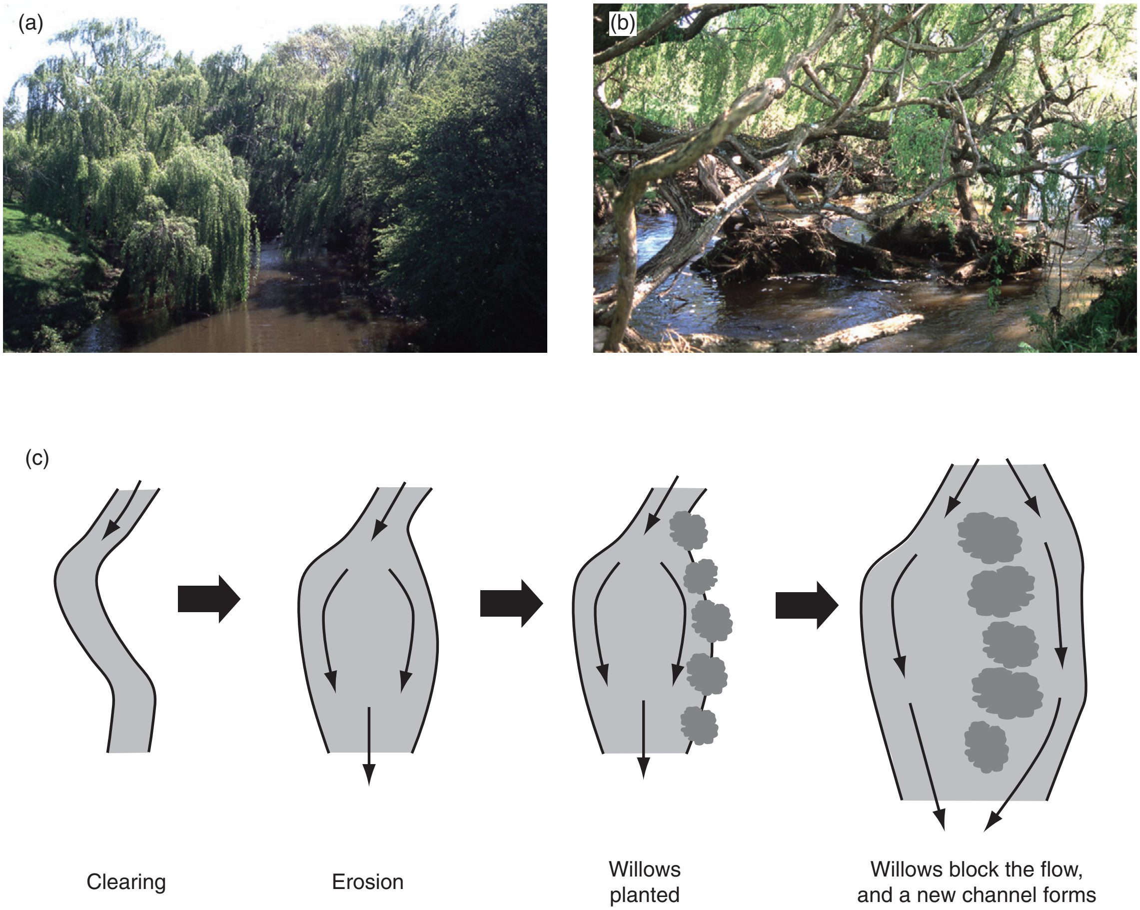

Figure 12.10 Invasive willow trees are ecosystem engineers that alter ecosystem function in riparian zones and within streams: (a) willow infestation on the Merri River in western Victoria; (b) the same infestation showing how fallen and living branches obstruct the river channel; (c) the process of willow infestation and alteration to channel structure. Thin arrows indicate direction of flow. A narrow forested stream channel has the riparian vegetation cleared, causing erosion and channel widening. Willows are planted to stabilize the banks (only one bank shown here). The plants grow and mature, collapsing across the stream channel and blocking the flow. Eventually, the stream cuts a new course around the infestation. (Source: Belinda Robson.)

12.8.4 Potential effects of climate change on aquatic invasive species

The spread and control of invasive species in Australian inland waters are likely to be strongly influenced by climate change (reviewed in Section 12.9). On one hand, some species will probably be favoured. For example, eastern gambusia are likely to increase in abundance across much of the continent because they can tolerate warmer conditions. This will probably intensify their negative impacts on native fishes, tadpoles and invertebrates (Bond *et al.* 2011). Similar responses may allow cane toads and invasive tropical species to move further southwards.

On the other hand, climate change may reduce the abundance or rate of spread of several invasive species (Box 12.6). The ranges of invasive salmonid fishes (Table 12.1) that originated in cooler temperate and

Box 12.6 Modelling the impacts of climate change on freshwater fishes

We need to understand how species' distributions might change if we are to effectively manage and conserve them in the face of projected climate change. One approach to predicting range shifts is to develop correlative statistical models, often called 'niche' or 'species distribution models', which relate present-day distributions ascertained from biological sampling to aspects of climate such as temperature and rainfall, and to use outputs from climate models to predict future species' distributions. Bond *et al*. (2011) used this approach to predict potential range-shifts of freshwater fishes in south-eastern Australia. The models also included likely changes in hydrology in examining changes in fish distributions because water regimes strongly influence the occurrence of some species. Present distributions of most (but not all) freshwater fishes in south-eastern Australia could be adequately predicted from climate, catchment topography and hydrology. Climate change is predicted to induce range contractions for cool-water species, including river blackfish *Gadopsis marmoratus* and introduced brown trout *Salmo trutta*, and range expansions for species such as golden perch *Macquaria ambigua* and flathead gudgeon *Philypnodon grandiceps*, which occupy warmer waters.

Nick Bond, Griffith University

boreal climates may contract as water temperatures increase as a result of climate change (Bond *et al*. 2011). Salmonids are predatory, consuming smaller fishes, crayfishes and other invertebrates. Consequently, contracting salmonid distributions may facilitate recovery of native prey populations, at least of those tolerant of drought and warmer water.

12.9 CLIMATE CHANGE AND AUSTRALIAN AQUATIC ECOSYSTEMS

Climate change is not new – global and regional changes in climate have occurred throughout Earth's history. However, we have now entered an era of rapidly changing global climate partly caused by human activities that have increased concentrations of greenhouse gases in the atmosphere, triggering a general trend of increasing temperatures. Climate change is having, and will continue to have, major effects on virtually every aspect of every aquatic ecosystem around the world, including Australia. These effects include changes to hydrological regimes and water budgets, atmospheric and water temperatures, volumes and timing of precipitation, wind patterns and the frequency of droughts and floods. Every management issue and threatening process covered so far in this book – anthropogenic alterations to water regimes, physical features, water quality and invasive species distributions – will be influenced by climate change and must be considered in this context. Furthermore, these effects are likely to vary regionally across Australia's wide diversity of climatic zones and ecosystems.

A range of scenarios for global climate change depending on varying levels of emissions of greenhouse gases has been produced by the Intergovernmental Panel on Climate Change. **Scenario models** have been developed (CSIRO 2009) to 'downscale' these global ones so that they can be applied at regional scales in Australia. Average air temperatures will increase by 0.6–1.5°C by 2030 and, assuming emissions continue at 2010 rates, 2.2–5.0°C by 2070 (Hobday and Lough 2011). More important are changes to the extremes of temperature and its variability. For example, in some areas the frequency of heat-waves will increase and cold-snaps decrease, along with reduced frequency and duration of frosts (Hughes 2003). Heat-waves are associated with increased frequency of wildfire, which may be compounded by increased fuel loads arising from the CO_2 fertilization effect. Rainfall will also be affected. Since the mid-1970s, annual rainfall has decreased in southern Australia, with a 16% decline below average in the south-west (Silberstein *et al*. 2012). However, total annual rainfall has increased in the tropics, sub-tropics and arid central Australia. Predictions are that these trends will continue.

Sea levels are rising, but the amount varies depending on latitude and local coastal topography. For example, increases along the south-eastern coast are predicted to be greater than the global average (Hobday and Lough 2011). Again, it is the changes to extremes, such as spring tides and storm surges, which will probably have the greatest impact on ecosystems, especially those near the coast. Lastly, the extent and duration of snow cover in alpine areas has declined and this trend is predicted to continue, with a total absence of snow possible under some scenarios (Hughes 2003).

12.9.1 Effects of increased water temperature

Increases in water temperature will directly affect physical and chemical conditions in the water. As temperatures increase, evaporation rates increase and oxygen becomes less soluble. Many microbially mediated processes will also accelerate, increasing biological oxygen demand and further reducing dissolved oxygen. Faster rates of leaf-litter decomposition may occur, altering nutrient cycling and spiralling.

Temperature increases also affect many physiological processes in aquatic organisms (e.g. enzyme activity, egg development). Extremes of water temperature can eliminate some freshwater species. There is evidence that past clearing of riparian vegetation has caused local extinction of invertebrates through increased water temperatures (Davies 2010), and climatic warming may cause further losses. As water temperature is a cue for spawning by many animals such as native fishes, changes in thermal regimes may change reproductive success and habitat use, affecting recruitment of vulnerable species.

12.9.2 Effects of changes to the hydrological cycle and water regimes

Changes to the global hydrological cycle are some of the most profound effects of climate change, and evidence shows this cycle is accelerating (e.g. rates of glacial melting). In parts of the world such as southern Australia, these changes have been particularly severe.

One example is the Mediterranean-climate region of south-west WA, one of the regions globally where climate change impacts were first evident and where they are now more advanced than elsewhere (Pittock 2009). Before 1960, substantial rainfall in winter and spring replenished surface aquifers with freshwater and generated runoff and high flows in rivers and streams. During summer and autumn, when there was much less rain and runoff, surface aquifers continued to discharge into streams and provide baseflow. Surface aquifers also supplied water for deep-rooted riparian vegetation such as flooded gums *Eucalyptus rudis*.

As a result of climate change in the past few decades, declining winter-spring rainfall is now seldom sufficient to fill surface aquifers. Streamflows have declined by more than 50% following a 16% drop in rainfall (Silberstein *et al.* 2012), so many streams that flowed perennially are now intermittent while formerly intermittent streams seldom flow at all. This imposed seasonal drying has reduced aquatic biodiversity and profoundly changed the ecology of many streams in the region. For example, there are fewer and smaller permanent pools to provide dry-season refuges for aquatic organisms that cannot withstand drying, especially native fishes. Shallower and more slowly flowing streams are now warmer, contain less dissolved oxygen, and may have higher salinity and lower pH (Kinal and Stoneman 2011), further stressing aquatic life.

Years with especially low rainfall create a 'water debt' such that subsequent years with higher rainfall have less runoff because the soil and surface aquifers must be saturated first. Sequences of dry years can lead to widespread mortality of trees and steadily increase the depths to the water tables of surface aquifers. However, this may be beneficial in some parts of the landscape. During salinization, deep saline aquifers rise towards the surface, waterlogging the soil (Section 11.4). As a result of climate change, recharge of surface aquifers declines, surface soils dry out and the rate of salinization slows (Kinal and Stoneman 2011).

Reduced volumes in standing and running waters, combined with higher evaporation rates, are likely to lead to increased concentrations of nutrients and salts and possible acidification (Chapter 11) across southern Australia. In some cases, this may be sufficient to transform freshwater systems into saline ones (Nielsen and Brock 2009). Complex interactions among decreasing water levels and increasing salinity, water temperatures and frequency of short and intense rainfall events can prompt system-specific responses by permanent and temporary aquatic ecosystems (Table 12.2). Multiple stressors frequently cause non-linear responses (Section 11.9), and these must be considered in the context of the different effects of climate change across different parts of Australia and over time.

Table 12.2 Predicted changes in wetlands and their biotic communities in response to climate change across southern Australia. (Source: Adapted from Nielsen and Brock 2009. Reproduced with permission of Springer Science and Business Media.)

	Changes in permanent wetlands		Changes in temporary wetlands	
Driver	**Wetland changes**	**Biotic changes**	**Wetland changes**	**Biotic changes**
Decreased rainfall	Reduced connectivity and flushing. Increased salinity. Fewer wetlands.	Reduced biodiversity. Simpler habitat structure. Longer dispersal distances.	Less time inundated. Less flushing. Increased salinity.	Less time for reproduction. Simpler habitat structure. Greater seed bank depletion with longer time dry.
Increased temperature	Increased evaporation; shallower.	Simpler habitat structure. Less time for reproduction.	Less time inundated. Increased salinity.	Simpler habitat structure. Reduced biodiversity. Greater seed bank depletion with longer time dry.
More frequent and intense, short rainfall events	Reduced connectivity, inundation, and number of wetlands.	Reduced biodiversity. Simpler habitat structure. Longer dispersal distances.	Less time inundated. More aseasonal inundation.	Simpler habitat structure. Greater seed bank depletion with longer time dry.
Salinity	Increased from less flushing, more evaporation, and intrusion of saline groundwater.	Reduced biodiversity.	Increased from less flushing and more evaporation.	Reduced biodiversity.
Management intervention	Maintained as permanent for water supply, so less variability in water regime.	Simpler habitat structure. Reduced biodiversity.	Increased cropping; decreased inundation and reliability as seasonal water.	Less time for reproduction. Simpler habitat structure. Greater seed bank depletion through mechanical disturbance and longer time dry.

12.9.3 Effects of sea-level rise

The impacts of sea-level rise on aquatic ecosystems are predicted to be most severe in the wet-dry tropics of northern Australia where the tidal range is large. Seawater is expected to penetrate further upstream into coastal rivers and their floodplain wetlands, potentially affecting most of the low-lying sections. Many species depend on these rivers and their floodplain wetlands, including magpie geese and estuarine or saltwater crocodiles, which breed in freshwater wetlands. If these freshwater ecosystems become brackish or saline estuarine wetlands or mangroves, there will be a substantial and likely irreversible loss of freshwater biodiversity. Most lentic waters, including some Ramsar-listed wetlands, will be profoundly altered (Traill *et al*. 2010). Barrages, similar to those used on the lower lakes of the Murray River in SA, may need to be used to protect coastal freshwaters in northern Australia from sea-level rise. However, these barrages have negative ecological consequences (Section 9.3), because they also bar movement and dispersal of many aquatic species.

Sea-level rise is also likely to influence Australia's coastal groundwaters (Ivkovic *et al*. 2012), although the ecological implications of this process have received much less attention than their potential effects on surface waters. The main impact is via **seawater intrusion**, the landward migration of seawater into freshwater coastal aquifers. Many coastal aquifers are already facing pressures from extraction for agricultural, urban and industrial needs, and often the seawater intrusion replaces extracted freshwater. Where coastal aquifers are in hydraulic contact with seawater, the fresh water typically sits above the denser saltwater. Predicted rises in sea-level increase the likelihood of a saltwater wedge intruding landwards (Werner and Simmons 2009), below the freshwater aquifer and sometimes mixing with it in a transition zone that ranges from a few metres to several kilometres thick. Effects on the biodiversity of stygofauna are unknown but are likely to be negative. Microbial processes that mediate most nutrient and other chemical transformations in freshwater aquifers (Section 8.4) are also likely to be impaired by the rise in salinity as well as the changes in flow pathways and exchanges with surface waters, many of which may have been inundated with seawater.

12.9.4 Effects of changes to atmospheric conditions

Other than air temperatures, climate change is predicted to cause other changes to atmospheric conditions including reduced humidity and altered concentrations of some nutrients (e.g. ammonium) as a result of increasingly frequent electrical storms. There is also the **fertilization effect** caused by the rising concentrations of atmospheric carbon dioxide, predicted to increase plant growth (Pittock 2009). Increased plant growth will raise water demand, further lowering groundwater because of the greater rates of evapotranspiration (Kinal and Stoneman 2011).

Increased plant growth will generate larger loads of leaf-litter on forest floors, especially during summer when eucalypt leaf-fall is greater. The drier climate projected for southern Australia lowers the humidity and dries out the forest litter. Combined with more frequent summer storms and lightning strikes, there will be more frequent and more intense wildfires, with implications for sedimentation and other impacts on surface and groundwaters (Section 10.3). As the beds of streams and shallow standing waters will dry out more frequently, there is a greater chance of direct exposure to flames and radiant heat, adversely affecting plants and animals dormant in or on the sediments. Permanent pools and other refuges will be exposed to greater temperatures and ash loads during and after fires.

12.9.5 Effects of reduced snow cover and alpine warming

Reductions in snow cover will affect all freshwater species restricted to alpine streams and wetlands because they cannot tolerate warming or desiccation, relying completely on permanent water fed by snowmelt. In tropical areas, mountain tops provide a suitably cool-climate habitat for species that have narrow thermal limits. Aquatic habitats on all mainland and Tasmanian ranges are potential '**summit traps**' for many freshwater species (Sauer *et al*. 2011) because these species tend to be isolated on mountain tops. Many have limited powers of dispersal (leading to a high frequency of short-range endemics) and small population sizes. Habitat area declines with increasing elevation, and this limits their capacity to move to higher elevations to remain within their required temperature range. In short, they are trapped.

These factors have been implicated in the decline of most of our montane frogs. At least 15 Australian montane frog species are short-range endemics, usually found only above a certain altitude (Figure 12.8b), and most of them are listed as threatened (Tyler and Knight 2011). Similar patterns of altitude dependence and short-range endemism are observed in many of Australia's freshwater crayfishes, especially within the genus *Euastacus* which includes several threatened species.

12.9.6 How do these climatic changes affect freshwater species and ecosystems?

We have reviewed the major repercussions of climate change on relevant attributes of Australia's inland waters and their catchments, giving occasional examples of the effects on several species of freshwater plants and animals. Are there particular traits that render these species especially vulnerable to climate change? Who will be the 'winners' and what determines success or failure of species to adapt to climate change? In general, the likely persistence of a **species** in the face of climate change depends on three factors:

its life-history traits, its exposure to the effects of climate change, and its adaptive capacity (e.g. allelic diversity, physiological tolerance and behavioural plasticity) (Chessman 2012).

Life-history traits of species least at risk from climate change include broad physiological tolerances, short generation times and early sexual maturity, high fecundity, generalist resource requirements (e.g. flexible omnivory), large populations with high genetic diversity, good dispersal capacity and a broad geographic range. Note the similarity to the traits of successful invasive species. As we saw in Section 12.8.4, many invasive species in Australia will cope well with climate change, largely because they possess at least some of these suitable traits. In contrast, the species most at risk from climate change will probably have narrow physiological tolerances, low genetic diversity and small population sizes, long generation times and late sexual maturity, specialized resource requirements, poor dispersal and short-range endemism (Steffen *et al*. 2009).

However, this contrast in traits alone does not always allow us to easily pick a 'winner'. For example, what would you predict for the western swamp crayfish *Gramastacus insolitus* (Figure 12.11), one of the world's smallest crayfish species? This species has large eyes and small chelae (nippers), traits not found in burrowing species. Endemic to south-eastern SA and western Victoria, it lives in seasonal wetlands where it must escape drying. Without the ability to construct a burrow, it relies on occupying the burrows of two larger crayfish species (Johnston and Robson 2009) and is therefore restricted to wetlands where these larger species occur. Nevertheless, it is capable of forming large populations, reaches sexual maturity relatively quickly, and is highly fecund (Johnston *et al*. 2010). It is likely to be a poor disperser and little is known of its physiological tolerances, but it occupies a relatively large geographic range. Therefore, this species has life-history traits that are mostly those of a species likely to cope with climate change.

Figure 12.11 An adult western swamp crayfish *Gramastacus insolitus*. (Source: Kerrylyn Johnston.)

However, its degree of exposure is likely to be quite high because wetlands in its geographic range are predicted to be inundated for shorter periods. This may affect its ability to complete its late spring-early summer reproductive cycle and it could be threatened by climate change. If the two larger species of burrowing crayfishes survive, *G. insolitus* will probably prove quite resistant to increased drying. Local extinction may be more likely in wetlands where inundation is no longer annual and, because dispersal will be difficult, the species may become threatened. As you can see, it is not always that easy to pick winners and losers, especially when our knowledge of the ecology of most Australian freshwater species is so incomplete.

It is also challenging to predict which freshwater **communities and ecosystems** are likely to be especially vulnerable to the effects of climate change. There are various possible pathways and mechanisms, most of which interact (Figure 12.12). Changes in the timing of aspects of species' life-cycles (i.e. phenology, including spawning, emergence from pupae, migration timing, etc.) will affect when species require particular resources or provide them for others. For example, if aquatic insects emerge earlier, this will change the timing of aquatic-terrestrial subsidies (Section 4.6.9) but may also remove predation pressure on certain species, leading to changes in biodiversity. Where the impacts of climate change interact with stressors such as salinization and acidification, physiological tolerances of some species may be exceeded, which will also alter species composition and distribution.

Range extensions might occur but only if suitable habitats can be reached. Some of Australia's most threatened freshwater ecosystems lie in Mediterranean-type climates. Their adaptation to climate change is strongly constrained by the inability of species to move southward, because southwards lies only ocean and there are few mountain ranges to offer temperature

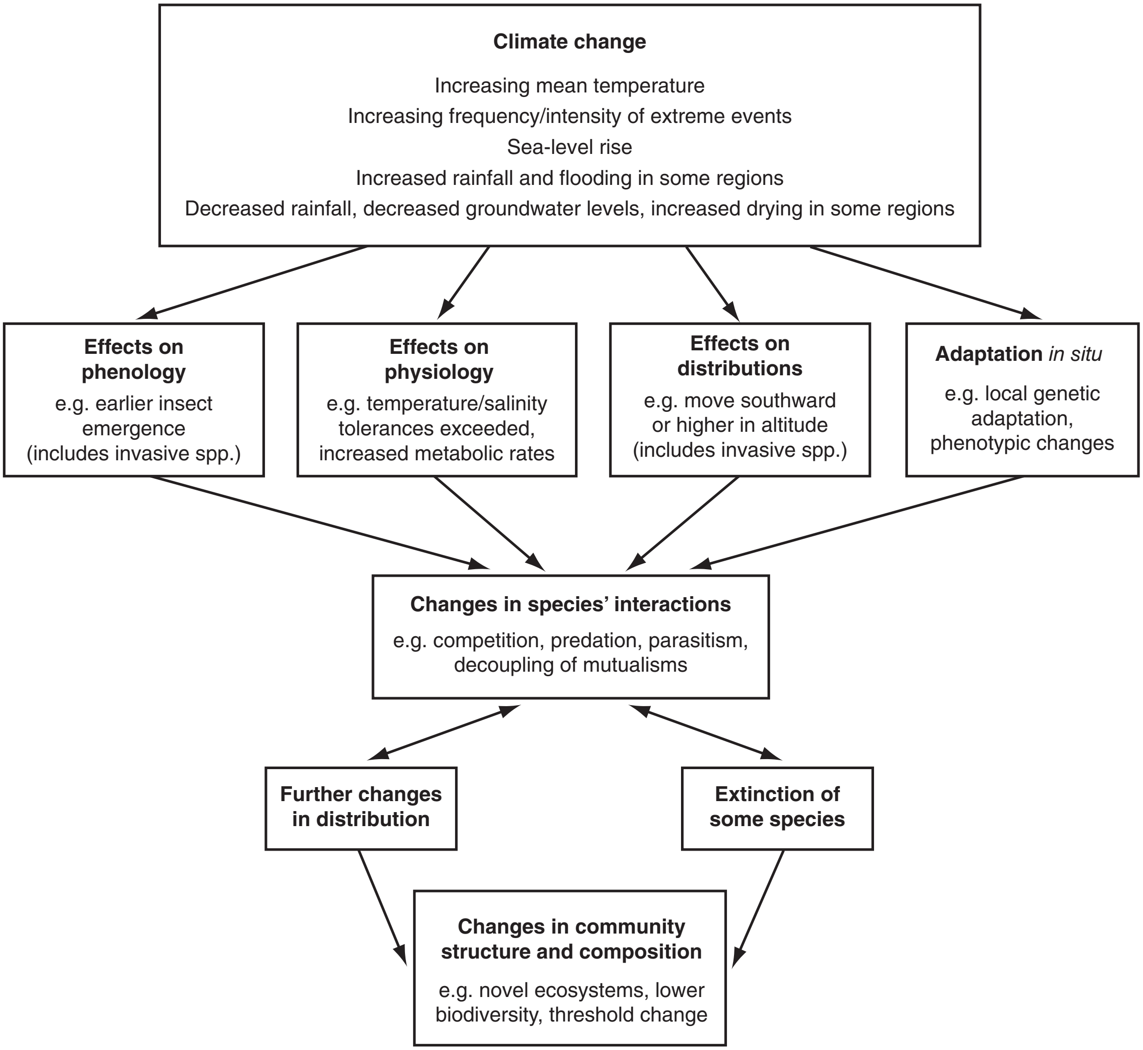

Figure 12.12 Potential pathways of community change in freshwater ecosystems flowing on from species-specific responses to climate change. (Source: Adapted from Figure 5.2 in Steffen *et al.* 2009. Reproduced with permission from CSIRO Publishing. Originally adapted from Hughes 2000.)

refuges (Davies 2010, Sauer *et al.* 2011). Another pathway of change will arise when particular species enter or disappear from ecosystems. These may be top predators capable of controlling trophic cascades (Section 4.6.8) or ecosystem engineers whose activities provide or remove crucial resources for a suite of dependent species. All of these changes in species' interactions will lead to further extinctions and changes in distributions (Figure 12.12), resulting in potentially novel ecosystems and marked shifts in regime when thresholds are crossed. We are only just beginning to observe and identify changes in Australian aquatic ecosystems in response to climate change (e.g. Box 12.7), and we know little about specific responses by organisms such as microbes or stygofauna. This leads to further uncertainty when plan-

Box 12.7 Range shifts by freshwater species in response to climate change

Geographical distributions of some freshwater invertebrates are shifting as the Earth's climate changes. In Europe, aquatic invertebrates are expanding their ranges north (at up to 88 km per year for some dragonfly species, Flenner and Sahlén 2008). Although expansion northwards is sometimes dramatic, contraction from the south is usually less prominent. In Australia, we generally lack the data to track changes in species' distributions precisely. However, analysis of survey data from New South Wales collected before and during the 'Millennium Drought' (1997–2010) suggested that many families of river invertebrates expanded their distributions at the cooler and wetter ends of their geographic ranges but contracted from the warmer and drier ends (Chessman 2012). Several families had overall range contractions. In general, families adapted to warm conditions and still water fared better than those adapted to cool environments and fast-flowing water. Will these shifts reverse with the return of somewhat cooler and wetter conditions since 2010? Climate modelling suggests that these milder conditions may be only a temporary respite from a long-term warming and drying trend across much of the state.

Bruce Chessman, University of New South Wales

ning mana gement actions to protect freshwater biodiversity and ecosystems facing climate change. Their future trajectories are far from certain.

12.9.7 Planned adaptation to climate change in aquatic ecosystems

Planned adaptation refers to human use of active management strategies to sustain biodiversity and assist ecosystems and species to survive climate changes. Many of these strategies resemble current practices in biodiversity conservation because approaches that support biodiversity subjected to multiple stressors should also sustain it during climate change. These strategies aim to reduce the effects of anthropogenic stressors (Chapters 9–11), enhance connectivity among protected and other conservation areas, and develop and refine landscape-scale conservation actions. The underlying assumptions are that species and ecosystems in good condition will be more able to resist climate change, and that enhancing connectivity will enable species to disperse among waterbodies, to find refuge habitat or to change their geographic range. However, in enhancing connectivity, care must be taken not to assist the spread of invasive species.

Some adaptation strategies are specifically directed at ameliorating the impacts of climate change. These strategies include translocation of native species, creating refuges for species and stockpiling genetic diversity (e.g. the Millennium Seed Bank Project, a global-scale project aiming for long-term storage of 10% of the world's flora, mostly from dryland regions). Translocation of rare and highly valued freshwater species has been done for other reasons (e.g. Box 12.4) but recommendations for translocation have increased as a response to climate change because many species have limited capacity to move to places with a more suitable climate.

Artificial selection to alter the genetics of populations may be another approach (Hoegh-Guldberg *et al.* 2008), increasing the proportion of species that have, for example, greater temperature tolerance. This type of selection occurs under natural conditions for many invasive freshwater fishes, and may be possible for species where culture techniques are well developed (e.g. fishes and crayfishes). However, given our limited knowledge of the population genetics of most freshwater species, this option does not seem especially viable at present. Similarly, the use of captive populations or means of genetic storage (Hoegh-Guldberg *et al.* 2008) does not appear especially feasible for many groups of invertebrates, which comprise a large proportion of Australia's freshwater diversity. Facilitating movements by species also faces challenges because freshwater species have often shown poorer dispersal ability than expected (Hughes *et al.* 2009). At local and regional scales, translocation of aquatic seed banks for restoration under different water regimes (Section 10.4.3) may have conservation potential.

Another approach for planned adaptation to climate change is to create refuges for Australian aquatic species. These may comprise refuges from rising temperature, increased drying or both. Potential strategies for creating refuges from rising temperatures include riparian replanting (Box 12.8), mixing cool water from deep-release impoundments with normal flows to lower temperatures at ecologically critical times, and using anthropogenic permanent ponds to create refuges where formerly permanent waters have all become temporary (Box 12.9). Undoubtedly, further strategies for conserving freshwater biodiversity facing climate change will be developed in the future (e.g. Pittock and Finlayson (2011). To be successful, these need to reduce the impacts of anthro-

Box 12.8 Riparian replanting to control temperature in streams

High water temperatures in streams can reduce local biodiversity by exceeding threshold values of less tolerant species. Temperature also controls fundamental ecological processes, including leaf-litter breakdown and ecosystem metabolism. Many south-western Australian freshwater species are Gondwanan relicts and generally intolerant of high temperatures. However, shade provided by riparian vegetation can reduce water temperatures and, with appropriate replanting, can maintain them below critical threshold values of sensitive aquatic species. Methods for optimizing replanting for temperature control incorporate stream latitude, orientation, width and existing topographical shade. Typically, cleared streams orientated east-west receive more sunlight and consequently have higher water temperatures than those orientated north-south. Our catchment-scale analysis has shown benefits of replanting upstream reaches before downstream and concentrating on the north bank before the south. Water cooled by riparian shading propagates downstream, improving the condition in lower cleared reaches. With climate change raising temperatures, increased and targeted replanting could be used to produce a 'biophysical envelope' that maintains water temperatures below threshold values of existing freshwater species. This 'over-restoration' will increase the overall resilience of freshwater species and enable the maintenance of biodiversity *in situ*.

Peter M. Davies, University of Western Australia

Box 12.9 Using anthropogenic freshwaters as refuges from climate change

Human disturbances reduce aquatic biodiversity, but anthropogenic waterbodies can, incidentally, also provide opportunities for freshwater species. Should anthropogenic waters be considered in conservation planning? In a drying world, species' life-cycles may not be sustainable in remaining natural waters, and survival might depend on drains, ornamental ponds, farm dams and other places where differences from the natural regime (e.g. controlled water levels or temperatures) might constitute refuges. The big question is whether anthropogenic habitats need to look and function like natural ones. Ecologically, anthropogenic waters will comprise a diffuse network with intermittent connections to other parts of the landscape, and we should not necessarily expect to find representative biodiversity in each place. For example, there may be small refuges that support a critical life stage for only one species. There is also the possibility of 'novel ecosystems' evolving within the future climate regime, with as-yet unpredicted habitats and assemblages. With the availability of aquatic habitat inextricab tied to human-induced climate change, increasing proportions of fresh water will be drained, redirected, impounded and channelled. We will need to look to where the water is to find aquatic life.

Edwin Chester, Murdoch University

pogenic stressors to enhance the opportunities for colonization and persistence by threatened species or communities.

12.10 SYNTHESIS

There are compelling ethical and utilitarian reasons to preserve biodiversity. Biodiversity promotes the resilience of aquatic ecosystems to multiple stressors and climate change, and consequently protecting biodiversity will enable us to continue to benefit from the ecosystem goods and services provided by Australia's surface waters and groundwaters. As we have seen in this chapter, managers strive to conserve biodiversity in diverse aquatic landscapes by relying on appropriate legislation and policy, maintaining strategic scientific assessment and monitoring, and adjudicating conflicting demands for the goods and services provided by waters. Biodiversity conservation also takes place at the smaller scales of communities, species and even genes. All of these levels of conservation pose particular challenges and all require input from aquatic ecologists.

In addition to the threats from modifications of water regime, physical structure and water quality (Chapters 9–11), invasive species negatively affect natural biodiversity. Species that have been accidentally or intentionally introduced into aquatic ecosystems have caused irreversible changes to ecological processes and often led to local extinctions of native fauna and flora. Seldom is eradication possible and so we must manage ecosystems that include invasive species and their interactions.

It is now time to explore the 'bigger picture' and see how aquatic ecologists can best contribute to resolving the complex problems of water resource management in an era of global climate change and rapidly evolving political, economic and social forces. Most aquatic ecologists now find themselves drawn into passionate debates about water use. Instead of feeling overwhelmed and threatened by such attention, ecologists should welcome the opportunity to apply their knowledge and understanding. In Chapter 13, we identify challenges and opportunities for aquatic ecologists in integrating their science with successful management and conservation of Australia's surface and groundwaters.

CHAPTER 13

Integrating ecology and management: a synthesis

13.1 THE ‘BIG PICTURE’: INTEGRATING ECOLOGY AND MANAGEMENT

Back in Chapter 1, we introduced several themes of this book. One is that we should seek to manage our aquatic ecosystems by addressing the causes rather than the symptoms of the problems where possible. This requires a good understanding of how our aquatic ecosystems ‘work’, how they vary across multiple spatial and temporal scales, how they are influenced by the components of their water regime, and how they interact with other ecosystems via lateral, longitudinal and vertical linkages (Chapters 2–8). Human activities have altered these processes, interactions, water regimes and linkages (Chapters 9–11), along with added stressors of invasive species, climate change, increasing human population and biodiversity loss (Chapter 12). The challenge for aquatic ecologists now is to see how best to help manage our impacts on surface and groundwaters so that we can protect and sustain aquatic ecosystems, their goods and services, and their natural resilience.

Some ‘**inconvenient truths**’ exacerbate this challenge. One is that despite our rapidly growing ecological knowledge of Australian aquatic ecosystems, we still lack adequate understanding of how most of these systems function and respond to multiple stressors, especially in the long term. Basic ecological knowledge about our aquatic species, even our most common ones, remains incomplete. Another relates to the mismatches that often occur between the spatial and temporal scales at which most research information is collected, those at which many ecological processes function and interact, and those at which resource managers typically operate. Yet another inconvenient truth is that the variable and non-linear responses of aquatic ecosystems to the effects of human activities complicate predictive modelling and other management tools, constraining their reliable use in many situations.

We are becoming increasingly aware that fresh water is not plentiful, groundwater is not limitless and that water flowing unimpounded to the sea is not wasted. Examples in this book show that fresh water is scarce and unsustainably exploited across much of Australia. Groundwater levels and quality are declining as this finite resource is mined faster than it is replenished (Section 8.6), and unimpounded rivers flowing to the sea provide water, sediments and other vital materials that sustain downstream estuaries and near-shore coastal ecosystems, maintaining their beauty and other ecosystem services (Figure 13.1).

Consequently, there is much for Australian aquatic ecologists to do. We have active roles to play in improving the knowledge and understanding about how our aquatic ecosystems function and how best to tackle these ‘inconvenient truths’. Ecological research opportunities abound in a wide variety of surface and groundwaters. However, it is not just a question of ‘more research and better science’. We also have golden opportunities to share our ecological knowledge with others to illustrate potential threats to our water and its quality. For the public, this can be through direct

Australian Freshwater Ecology: Processes and Management, Second Edition. Andrew J. Boulton, Margaret A. Brock, Belinda J. Robson, Darren S. Ryder, Jane M. Chambers, and Jenny A. Davis.

Companion Website: www.wiley.com/go/boulton/freshwater

Figure 13.1 Estuaries rely on natural river flows to sustain their ecological processes and ecosystem goods and services. When the timing, frequency or volume of flows is altered by upstream impoundments, there are often declines in fish stocks and water quality in estuaries downstream. (Source: Andrew Boulton.)

Figure 13.2 Active involvement in field days is an excellent way to share ecological knowledge and stimulate appreciation of the values of our aquatic ecosystems. (Source: Darren Ryder.)

education, involvement in field days (Figure 13.2) and on-ground community workshops, and collaborating with water managers to achieve an optimal balance between the use and protection of water resources. Aquatic ecologists also work with policy makers to devise legislation to guide the wise use of water in growing cities and regional areas, with economists to determine how best to trade water and access rights with suitable environmental provisions, and with social scientists to understand how aquatic ecosystem health relates to human quality of life.

These roles for aquatic ecologists require a **broader perspective** that extends beyond the scientific perspectives in this book. Up to now, this book has intentionally understated the importance of the social, economic and political elements that govern research (often via funding) and management of Australian aquatic ecosystems. However, these elements are essential to any successful management strategy, and the ecological aspects covered in the chapters so far are only one facet of a complex combination of factors that must be considered when assessing and resolving environmental problems and conservation issues, especially in minimizing our impact on aquatic ecosystems.

13.2 THE 'BIGGER PICTURE': INTEGRATING SOCIAL, ECONOMIC AND POLITICAL GOALS

To be successful, integration of these goals must be *active* not passive. Each group of players, including scientists, consultants, managers, economists, politicians, policy makers and community members must take a proactive role in wise water resource management and must be prepared to present their perspectives in ways that encourage dialogue, creativity and open-mindedness. Clear **communication** that acknowledges differences in discipline backgrounds ('knowledge structures' as defined in Benda *et al.* 2002) is essential. The ideal situation is inclusive and includes collaborative governance rather than divisive conflict. To achieve successful collaboration, all players must be actively involved from the outset, there must be time for proper consultation and full consideration of environmental, economic and social issues, and short-term 'reactive' solutions must be viewed with suspicion and concern. Nonetheless, swift action to recover a threatened species or avert an ecological disaster (e.g. a chemical spill) should not be hampered by administrative red tape, and appropriate plans for prompt responses to such eventualities are essential.

The results of successful collaboration in tackling complex issues in water resource management can be personally rewarding. Many aquatic ecologists become consultants and, despite the frequently tight

Box 13.1 Challenges and satisfaction in being an aquatic ecology consultant

Consultants work in a space bounded by science, policy, legislation, governance, economics, social values – everything that affects the management of natural resources. It can be a demanding space to be working in. Answers are needed, and must be given within a set time, even with imperfect knowledge. Political imperatives and public opinion hover around the edge of this space. It is also an immensely rewarding space to work in because the work is relevant and wanted. Good efforts are appreciated and a pleased client becomes, over time, a colleague. Playing a part in developing or implementing new political initiatives – whether environmental flows, policy development, or setting diversion limits as part of the Murray-Darling Basin Plan – is exciting, frustrating and satisfying. An aquatic ecologist enters this space as a scientist but develops new expertise through opportunity and work-flow. Skills are developed in communicating science around this space; this means bringing in new ideas and giving fresh understanding. But ultimately, it is mainly problem-solving, attention to detail, conceptualizing, and being positive.

Jane Roberts, Independent Consultant

deadlines and other constraints, find themselves immersed in a satisfying and stimulating career (Box 13.1). Maintaining flexibility and an open mind to possibilities are crucial personal attributes as is a willingness to work in a team and to communicate complex scientific issues, even when the implications are unpopular for short-term exploitation of water, minerals or other resources. Often, the distinctions between consultant, scientist, manager and information broker are blurred ones, reflecting the diverse roles and skills that are required.

Current water resource management in Australia has moved beyond the 'scientist-manager dichotomy' parodied by Cullen (1990) where conflicting perspectives, values, backgrounds and goals seemed fatal to ever resolving any water resource issue successfully. Fortunately, this has been replaced by a wider appreciation of the parallels. These parallels include that all players agree that clear goals are essential, progress is iterative and builds on previous experience, learning is continuous, and water resource problems are complex and involve multiple conflicting interests (Cullen 2006). Of course, perspectives and goals still often differ but the interactions are now more collaborative and open-minded. Increasingly, such collaborations operate within management frameworks that make allowances for the different perspectives of all concerned – managers, consultants, ecologists, hydrologists, social scientists, economists, engineers, politicians, policy makers and community groups, to name a few.

One such framework is **adaptive management**, broadly described as the cyclical process of identifying the problem, proposing possible solutions, assessing these options, selecting and implementing the most appropriate, evaluating its success, and learning from the experience to modify future solutions and approaches (Allan and Stankey 2009). This cyclical process resembles the scientific method, and therefore it appeals intuitively to scientific researchers. Furthermore, the adaptive management framework is formally embedded in many Australian management policies and guidelines (e.g. Brodie *et al.* 2007, National Water Commission 2012).

Early proponents of adaptive management in the 1970s promoted scientific experimentation as its central strategy but criticism of this narrow focus and its inadequate attention to policy heralded a broadening of perspective in the early 2000s. Emphasis is now placed on promoting a **strategic** approach that adaptively integrates science into social, economic and governance processes. There is a greater focus on the progressive identification of goals and objectives through a logical hierarchy (Section 13.3). Not surprisingly, these goals and objectives are heavily value-laden and should, ideally, result in optimal management of aquatic ecosystems and their goods and services (Section 1.1) to ensure ecological sustainability and intergenerational equity, preserve future options and be economically, socially and politically acceptable. This optimal management seeks to balance social, economic, political and ecological aspects, and relies

Box 13.2 What is 'best available science'?

As policy changes become more fiercely contested, there is an increased expectation that policy will be based on 'best available science'. The term, although widely used, remains ill-defined and there is little guidance on its practical application to policy development. Although evidence and quality assurance are important attributes of best available science, relevance, availability and utility are just as important. Uncertainty, risk and communication are further challenges to the successful application of science to policy. To overcome these challenges, Ryder *et al*. (2010) proposed nine principles to guide the development of a context-specific definition of best available science. These principles are based on the attributes needed for a standardized approach to applying science in natural resource planning and management. For example, the process should be interdisciplinary and facilitate understanding of discipline-based knowledge structures, articulate uncertainty and risk about the scientific information, and promote engagement and trust among the generators and users of information. Ultimately, successful management of aquatic ecosystems will rely on scientists, managers and decision makers who have the skills and courage to apply the best science available and not wait for the best science possible.

Ben Gawne, Murray-Darling Freshwater Research Centre

heavily on effective integration of the 'best available science' (Box 13.2).

13.3 STRATEGIC ADAPTIVE MANAGEMENT IN AQUATIC ECOLOGY

The ecological processes of groundwaters, surface waters and their catchments are tightly linked with human livelihoods, forming socio-ecological systems that are complex, dynamic and often unpredictable. For these systems to be sustainable and resilient, they need to maintain their social and ecological diversity (Walker and Salt 2006). Inevitably, management of these socio-ecological systems must be strategic, and will involve trade-offs where there will be 'winners' and 'losers'. Historically, the environment has been a 'loser' in water resource developments in Australia. However, there is now greater appreciation of the significance of intact aquatic ecosystems for providing essential goods and services and, indeed, for human survival on this planet. **Strategic adaptive management** seeks to balance short-term requirements for ecosystem goods (e.g. water, hydropower) with long-term requirements for services such as self-sustainable and functional aquatic ecosystems that retain their resilience to disturbance.

Strategic adaptive management follows four steps (Figure 13.3). The first is to set the **desired future condition**. This consists of a vision statement, documentation of the vital attributes, determinants, threats and current risks, a list of objectives arranged as a hierarchy from general intent down to specific measurable goals, and the thresholds and their key indicators that will demonstrate achievement of these objectives. Listing the indicators, mechanisms and thresholds that will indicate their successful achievement is essential. Failure to do this has led to ill-defined goals that have been impossible to attain. This first step must also integrate the full context of social, technological, economic, environmental and political values. If these values are not integrated at the outset, setting mutually acceptable goals for the desired condition is virtually impossible. At this stage, full engagement with all players is critical to identify the complete set of values as well as to establish effective institutional support and cooperation among various agencies (Kingsford *et al.* 2011b).

The second step identifies the **management options**, predicts possible outcomes and assesses their acceptability to all stakeholders before making a choice. Again, the full context of social, technological, economic, environmental and political values is needed to guide this choice so that the rationale for final selection of an option is clear and has been agreed upon by all players. The third step entails **planning, implementing and monitoring** the chosen management option. Selected indicators are measured and monitored at suitable spatial

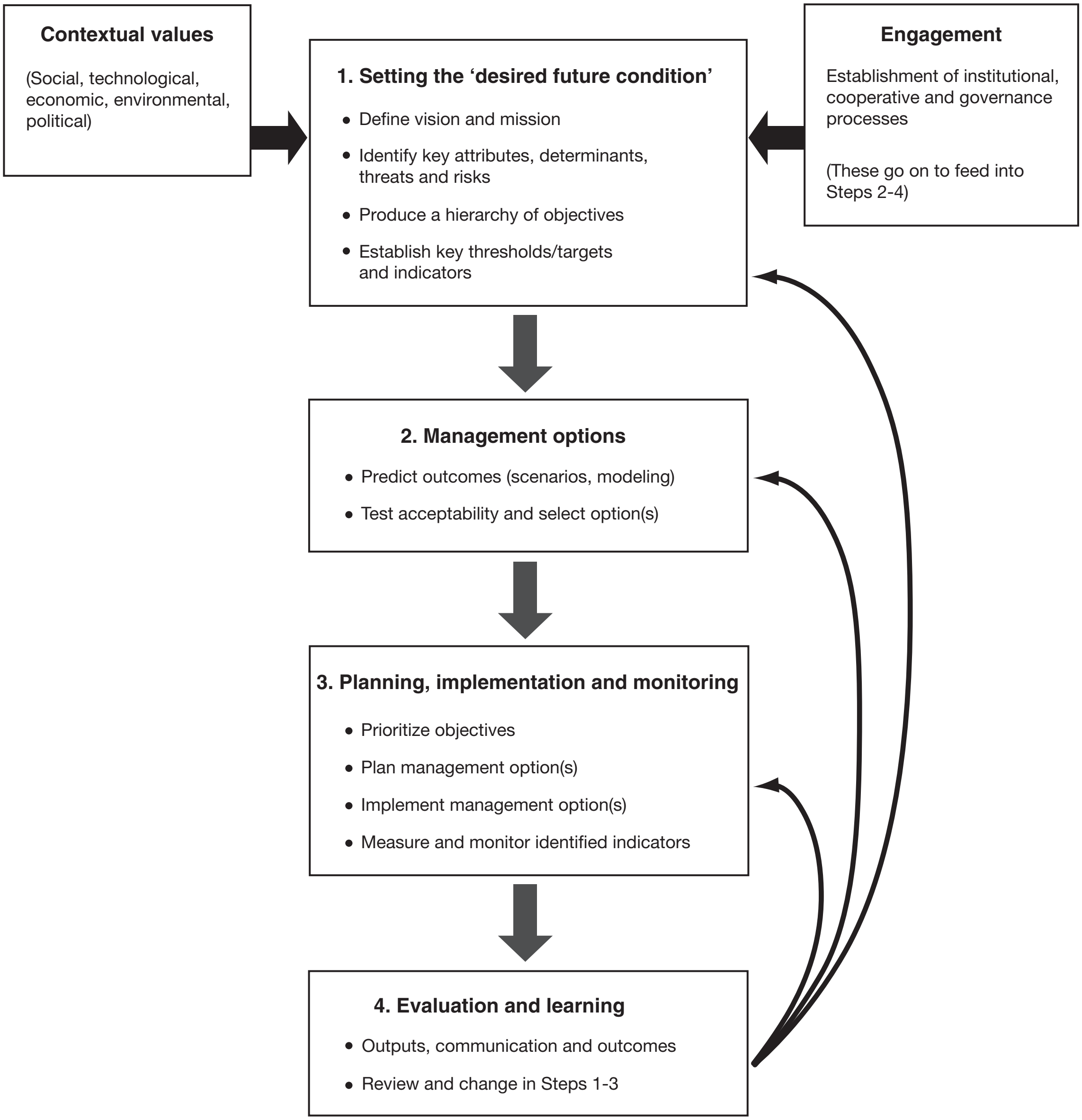

Figure 13.3 The four steps in strategic adaptive management. Goals are informed by social, technological, economic, environmental and political values. Full engagement of all players at the outset leads to establishment of institutional, cooperative and governance processes that then feed into all steps of the framework and help retain adaptive flexibility to changes in the context and values. (Source: Redrawn from Kingsford *et al.* 2011. Reproduced with permission of Elsevier.)

and temporal scales. Part of the planning at this step is to ensure that the human and financial resources are available to achieve the objectives, and that the indicators have a firm scientific basis for their hypothesized response. In steps two and three, models such as decision-support systems are often helpful. These models must be capable of assessing likely outcomes across long timescales as well as dealing with 'surprises' such as extreme events (e.g. floods, droughts). Retaining flexibility in the monitoring program means that this process can also be adaptive and able to deal with 'surprises' as well as incorporating new technology or concepts as they arise.

The final step of **evaluation and learning** feeds back into the other three steps and occurs throughout the full cycle (Figure 13.3). For example, the vision is evaluated during the development of the hierarchy of objectives. Management needs explicit feedback loops from data collection to planning and intervention. After an intervention such as the environmental watering of a wetland (Section 9.5), indicator data must be analysed to assess the intervention's effectiveness in progress towards the desired ecological condition (Section 11.8). This may include adjustment of the models or objectives – changes that must be communicated to all stakeholders – and it is fundamental to learning from the adaptive management process.

Strategic adaptive management is a complex process and takes much time, commitment and cooperation to become established. However, as the stakes in environmental, social, political and economic values are immense, transparent and logical frameworks are increasingly sought to manage and conserve water resources across Australia. One example is the Macquarie Marshes in NSW where several decades of experience have accumulated on the management of environmental water allocations and the conservation needs of protected areas in the Marshes. Formal strategic adaptive management was implemented in 2010, building on the long-term engagement with stakeholders and strong efforts to clarify institutional responsibilities. Although the process has not always gone smoothly, results have been promising (Kingsford *et al.* 2011b) and echo the successful use of this approach in other parts of the world (e.g. Kruger National Park in South Africa).

The strategic adaptive management framework is powerful because it integrates across diverse perspectives and institutions, promotes co-learning, provides explicit and transparent guidelines for decision-making, and increases the confidence and morale of managers. Most importantly, this framework can incorporate the complex social and ecological dimensions that characterize all water resource management. In the past, failure to incorporate this social and ecological complexity has often led to failure in previous management efforts, destroying trust and credibility in the process. Finally, the framework acknowledges the inherent uncertainties of dynamic and unpredictable ecosystems and provides a way of explicitly linking science to management in an effort to assess the boundaries and risks associated with these uncertainties. These uncertainties, along with the ethical negotiation of trade-offs necessary among water users (including the environment), often lead to complex conflicts of interest. Thus, a central aspect of adaptive management is **conflict resolution**.

13.4 RESOLVING CONFLICTS IN FRESHWATER MANAGEMENT: A ROLE FOR AQUATIC ECOLOGISTS?

Aquatic ecologists often become drawn into debates and conflicts about water resource management, especially when their research findings are seen as relevant to the issue. For many researchers, this situation is stressful. Firstly, a research ecologist might consider that their findings are not yet ready for application to a management problem, despite intense pressure to apply them. Most ecological research takes many years to complete whereas resolution of management problems is attempted far more rapidly. Secondly, there is the risk of misinterpretation or misapplication of the research findings, especially when the researcher is not directly consulted or when results are being used selectively and caveats are ignored. Thirdly, many ecologists and researchers do not fully grasp the different approach applied by most managers and politicians when resolving conflicts in water use. Whereas a scientist seeks better understanding by making observations and testing hypotheses to produce reliable predictions, managers and politicians seek negotiated outcomes that will be acceptable to relevant interest groups, and will use whatever arguments might help win their case. In this situation, science is just one line of argument, along with economics, ethics and the law (Cullen 2006). This does not mean that scientific facts and findings are negotiable. Scientists cannot be expected to accept some compromise value. However,

Figure 13.4 Aquatic ecosystems in Australia continue to be degraded by human activities such as this modification of Bannister Creek in Perth (a) when issues are either unknown, ignored or mired in stalemate, sometimes leading to sarcastic signs like this one (b), erected by a council upset that a government water agency would not fund water to sustain a now-dry lake. Although the text of this sign is hard to read in this photo, the images of a dried frog and cracked mud convey the issue eloquently. (Source: (a) Edwin Chester; (b) Belinda Robson.)

managers and politicians view compromises differently, and this is sometimes hard for scientists to appreciate. Finally, most researchers in academic institutions fear that active involvement in environmental conflicts will consume precious research time and may even harm their scientific reputation or funding prospects.

Meanwhile, surface and ground water ecosystems in Australia continue to be degraded by human activities (Figure 13.4). This degradation occurs for many reasons. Regulatory agencies and the public may either be unaware of the issue, do not care about it or do not know what to do about it. People often feel disempowered and helpless when they see environmental degradation, and this leads to frustration but does not solve the problem. Conflicts among competing water users often reach a stalemate, also preventing resolution of the problem. Meanwhile, funding is far greater for research and action on human health and condition than on environmental health and condition, and so the degradation continues.

Aquatic ecologists and other scientists usually want (and have an obligation) to share their knowledge and insights in identifying situations where degradation is occurring and in helping to manage the problem. Most water resource problems require policy for their resolution and so ecologists need to contribute to these policy debates. However, ecologists' policy positions will be influenced by their own values, and other players may hold different values. For example, an ecologist might identify that a management action will remove the habitat of a particular species. Although this is useful scientific input to a decision, it does not mean the habitat must be preserved. Instead, society, represented by managers and politicians, must weigh up the costs and benefits of removing the habitat and then make a decision. If ecologists do not provide their knowledge, the decision may be flawed by the lack of this information. However, they can only inform the debate, not replace it (Cullen 2006).

How best can aquatic ecologists participate in resolving conflicts in water resource management? Although this depends heavily on the personality, experience and employment situation of the ecologist, there are some general recommendations. The first is to be aware of the differences in perspectives between scientists, managers and other players, and to enter the debate properly prepared. This includes being willing to spend the time needed to build up trust. The second is to try to present the evidence and information as clearly and simply as possible, and to 'stay on message'. Repetition will be necessary to different groups. The third is to try to present solutions as well as outline problems. Ecologists sometimes bring unwelcome evidence about environmental degradation, and this information (and perhaps the messenger) can be perceived negatively by other water users. Consequently, efforts to suggest

Box 13.3 Crossing the bridge: from scientist to policy maker

The divide between the realms of science and policy is often highlighted. However, this gap is shrinking as more scientists, particularly those early in their career, become policy makers. This option can be an attractive career choice. Applied scientists may spend time as policy makers and then return to research with a first-hand understanding of political processes, policy and how their research findings could be best used. Alternatively, they may find great satisfaction in being able to write policy, allocate funding and continue their career in this field. I made the switch from scientist to policy maker whilst finishing my PhD on invasive species. When I worked on the Victorian Waterway Management Strategy, I was able to introduce a chapter regarding the management of aquatic invasive species, a topic that had received little attention in the previous strategy and one that I was interested in. As more scientists become policy makers, the gap between the two realms narrows. The individuals who speak both languages are best placed to help bridge the divide between science and policy.

Sarina Loo, Department of Environment and Primary Industries, Victoria

plausible solutions are welcomed, such as the 'Blueprint for a National Water Plan' by the Wentworth Group (2003). The fourth is to work directly with policy makers if the opportunity arises because this can be a powerful way to integrate scientific findings with legislation and policy guidelines (Box 13.3). Few ecologists fully appreciate the power of policy in water resource management (Sarewitz and Pielke 2007), yet their involvement by providing clear scientific advice may avert future conflicts and protect ecosystem services of exploited water resources. Many aquatic ecologists also work with or as consultants. Consultants often have a more direct link with various state agencies and their work involves repackaging and application of research findings to particular management and policy issues (Box 13.1). This is another effective way to contribute to water resource management and conflict resolution, especially in fields such as mining, forestry and agriculture.

13.5 FUTURE CHALLENGES AND OPPORTUNITIES: WHERE TO FROM HERE?

Aquatic ecology underpins wise water management in Australia and overseas. Active, innovative and inspirational aquatic ecologists are urgently needed to provide advice on how to protect, sustain and wisely use our limited surface and groundwaters. Well-funded and multidisciplinary fundamental research is also essential to understand how aquatic ecosystems function and interact, especially at large spatial and temporal scales. Water-dependent ecosystems sustain all of our livelihoods, industries and aesthetic pleasures, and we must endeavour to preserve their ecosystem goods and services by protecting their biodiversity and ecological functions. There is much to do and many challenges for us to tackle.

Perhaps our biggest challenge is finding the **appropriate balance** between reliably informing people about the environmental problems facing Australian inland waters and yet empowering and inspiring them to act. Evidence from diverse social sciences (see Garnett and Lindenmayer 2011) shows that achieving public and political support along with lasting behavioural change requires 'bad news' to be balanced by empowerment. Dire warnings and grim presentations of widespread environmental degradation pervade the media but there is little media coverage of 'success stories' in aquatic conservation, protection or management. Not surprisingly, people feel demoralized about the deteriorating environment and powerless to reverse or slow the damage. Where negative stories are not counterbalanced by some positive ones, denial of the evidence and the science can occur, as seen in the debate about climate change (Kerr 2009). Of course, there are other reasons for denial such as economic and political forces but discussion of these are beyond this book's scope.

We have an opportunity to use our ecological knowledge to identify ways in which environmental problems in aquatic ecosystems can be addressed and ways in which public efforts can be best focused. Using frameworks such as strategic adaptive management and integrating our insights in social, technological, economic and political arenas, we can propose strategies that range from policy guidelines and initiatives by government agencies all the way through to on-the-ground actions by land-holders and the general public. Community engagement is essential. One of the most powerful approaches to help solve problems in aquatic ecosystems is to physically involve the local community in actions such as restoration and biodiversity conservation (Boxes 13.4 and 13.5). Not only is this direct action effective at the local scale, the broader ecological benefits can be explained during the process. For example, while trees, shrubs and grasses are being planted in a riparian zone (Figure 13.5), an aquatic ecologist can explain the benefits of the plantings for the waterway and the reasons for the choice of plant species and planting location. Involving local communities in monitoring the ecological responses to restoration ('citizen science' Tulloch *et al.* 2013) is also powerful education strategy, creates ownership and

Box 13.4 Integrating science and practice to educate, motivate and inspire

People who achieve great things feel a strong sense of purpose that is shared with others and is underpinned by knowledge that enables them to act. Fostering these three elements of belief, belonging and behaviour is what magazines like *RipRap*, and organizations such as the Australian River Restoration Centre, Murray Darling Wetlands Working Group and WetlandCare Australia seek to do. The approaches these organizations take is to value science and technical information, but to place it within the wider social, economic and cultural context within which it needs to operate. Science, when kept in isolation from this wider context, risks becoming irrelevant and obsolete. By integrating scientific knowledge within the broader life of a community, it becomes better understood, able to be applied and a powerful force for change. To do this, we need to weave science through stories, create opportunities for shared experiences, and empower people by providing them with access to knowledge in many different forms. When scientific knowledge is shared in this way it grows and flourishes, inspiring people to act and to achieve shared goals.

Siwan Lovett, Australian River Restoration Centre

Box 13.5 Waterhole monitoring in central Australia

One major threat to central Australian waterbodies is large feral herbivores, including camels, horses and cattle that pollute the water and denude the surrounding vegetation. As part of the Australian Feral Camel Management Project, NT government scientists work closely with the Central Land Council, Traditional Owners and Aboriginal rangers to monitor waterbodies (Figure 13.6) across some 30 000 km^2, tracking ecological recovery as feral animal numbers are reduced. This 'two-way approach' benefits both scientists and the local people. By providing training and guidance to Aboriginal rangers and custodians, aquatic ecologists have implemented monitoring and management efforts on a larger geographical scale than would otherwise have been possible. In turn, scientists have had the opportunity to use the intimate knowledge and historical perspective of Traditional Owners about waterbodies in their traditional lands and to learn how Aboriginal people traditionally managed waterholes to provide both cultural and ecological benefits (e.g. through increasing the area and persistence of surface water). In addition, the encyclopedic knowledge that Traditional Owners and rangers possess of waters within their traditional areas is a critical element in successfully managing waterholes and working together on country.

Jayne Brim Box, Department of Land Resource Management, Northern Territory

Figure 13.5 Community engagement in aquatic restoration programs is enhanced when an aquatic ecologist is on site to explain the reasons for the activities. (Source: Darren Ryder.)

inspires confidence and enthusiasm for involvement in other environmental projects. Aquatic ecologists can also be involved in field days (Figure 13.2) or as guest presenters in local schools where environmental education is on the curriculum.

Another challenge and opportunity for aquatic ecologists is in addressing the mismatch between the spatial and temporal scales at which much ecological research is done (<10 years and $<1\,\text{km}^2$) versus the scales at which most environmental problems occur and at which fundamental ecological processes occur (>10 years and $>1\,\text{km}^2$). Extrapolation of results from fine-scale studies to entire catchments and aquatic landscapes is perilous. Although various models have some value in this process and have been proposed for predictions of, for example, recovery after flow restoration in rivers (Robson *et al.* 2011), we still lack adequate understanding of the broader linkages among catchments, groundwaters and atmospheric inputs for many aquatic ecosystems. Most of the environmental problems described in Chapters 8–12 reflect the result of disruptions of these linkages and their collective effects at broad scales.

Large-scale research needs large-scale and long-term investment of money, effort and resources. Opportunities exist for large, well-coordinated, multidisciplinary teams to address landscape-level issues, using appropriate technology and specifically designed projects to explore how multiple stressors interact on inland waterways and their dependent ecosystems (e.g. the dryland rivers research in Queensland). Aquatic ecologists are often asked what needs to be done to achieve a given environmental state. They are then required to demonstrate the success of their predictions. Large-scale experiments are crucial but need careful coordination and planning, reliable long-term funding and clearly stated scientific and management goals (Box 13.6, Figure 13.7). They are also excellent showcases for the wider community to see what can be achieved and to be inspired by 'success stories' of effective management and conservation.

Figure 13.6 Central Land Council ranger Ricky Kenny, from Kalkaringi, at a water monitoring workshop held at the 2013 CLC Ranger Camp at Harts Range, NT. (Source: Jane Hodson.)

We now recognize that recovery of crucial aspects of the natural flow regime and the allocation of water to the environment are powerful ways of protecting

Box 13.6 The Riparian Restoration Experiment

In 2004, the Riparian Restoration Experiment (www.mdba.gov.au/riparian-restoration-experiment/) was established along three Victorian streams as a long-term (>10 years) study to evaluate ecological responses to the common management practice of fencing and replanting riparian zones. Using a conceptual model, we predicted aquatic and terrestrial responses to livestock removal and replanting. The experiment set out to test our hypotheses and identify reliable indicators for measuring restoration responses. We have control and treatment sites (Box 11.7), with data collected before and after restoration. Spatial extent reflects that typically adopted by management (1 km stream length, ~20 m width each bank). Hydrological and land use data were collected to disentangle responses to restoration from those generated by site-specific differences. Plant cover and tree recruitment responded quickly despite a long drought. However, responses of aquatic biota were influenced by the reduced flows. Aquatic biota might not respond positively to the riparian restoration given the highly variable flows, the limited riparian restoration and the degraded condition of the creeks and their catchments. This endorses the need to adopt a long-term, large-scale perspective when implementing and assessing the effectiveness of stream restoration.

Paul Reich (Arthur Rylah Institute) and Sam Lake (Monash University)

Figure 13.7 Riparian regeneration in (a) 2008, (b) 2009, (c) 2010 and (d) 2011 at Joyces Creek (far left of photos), Victoria. The distant tree, centre left, provides a reference point, obscured in 2011. (Source: Paul Reich.)

Box 13.7 Governance arrangements and aquatic ecology in engineered rivers

Many impoundments and much of the flow-control infrastructure along rivers were designed and built in a different era of water management, mainly to service towns and irrigators and guided by the ‘engineered river’ paradigm. In some cases, this creates flow regimes that depart far from the natural one (e.g. seasonal reversal of flow, Section 9.2.1). There is now current investment into providing more environmental flows, undertaking works to reduce the adverse effects of infrastructure, or providing additional infrastructure to make environmental water delivery and outcomes more efficient and achievable. Consequently, a river may be operated for environmental outcomes, but at the same or another period of the year, it is being run to meet traditional demands. This is a curious interaction and one where the overall ecological outcomes would seem quite uncertain. Equally, the current governance arrangements of water management are based on the ‘engineered river’ paradigm. Although some changes to governance are evident, many of these arrangements will probably continue to inhibit the likelihood of an ecologically optimal outcome. Is the money spent on environmental water allocations spent wisely even if the provisions are suboptimal?

Paul Wettin, Independent Consultant

and, in some cases, partially restoring surface waters and groundwaters where excessive extraction occurs. In some catchments such as the Murray-Darling Basin, the cost of such water allocations runs into billions of dollars. Understandably, taxpayers, politicians and the Treasury want to see evidence for the effectiveness of this investment in the cost of repair. Aquatic ecologists are pivotal to this process of monitoring catchment-scale ecological responses to these allocations, especially in highly regulated systems where ‘optimal’ conditions are absent (Box 13.7). This opportunity ties in with the involvement of aquatic ecologists in strategic adaptive management where goals have been agreed, outcomes of water allocations have been predicted, and ecological responses over multiple scales of space and time can now be monitored and modelled accordingly.

The final challenge and opportunity lie in effectively integrating research findings in aquatic ecology into wise water resource management at a national level so that the best available science can be incorporated along with the relevant social, political and economic aspects. One way for this to occur is through active membership of professional societies such as the Australian Society for Limnology (www.asl.org.au/). This society, formed in 1961, holds annual conferences on aquatic science and management where students, researchers and resource managers present talks and posters on their research, debate topics at special sessions and share their experiences and enthusiasm. There is a satisfying long-term ‘security’ about professional societies as well because these persist over time while many water management agencies frequently alter their names, structure and priorities in response to political, economic, social and environmental changes.

Another way for best available science to be contributed by aquatic scientists is through direct involvement with consultants and government agencies. One example of the latter (in 2013) is the National Water Commission, responsible for progress towards sustainable management and use of the country’s water resources. This progress is guided by a ‘blueprint’ for water reform, the National Water Initiative (http://nwc.gov.au/nwi) that includes preparation of water plans with provision for the environment in catchments across Australia. Aquatic ecologists have provided insights from their research to inform these plans and the management strategies needed to balance water use and environmental needs in different regions. There have been some substantial advances, such as the recognition that the connectivity of surface and groundwater resources requires them to be managed as a single resource. However, more work remains to be done, especially in nationally coordinated collaborative and strategic research into aquatic ecosystem function and response to disturbance (e.g. to guide environmental watering strategies, Section 9.5).

13.6 SYNTHESIS

By now, you will have a good appreciation of the natural complexity of aquatic ecosystems and their linkages with adjacent systems. We have explored physical, chemical and biological processes in standing and running waters, seeing parallels in the ways these systems function and interact. Most of the ecological processes are controlled by the water regime in these waters, and this applies to groundwater-dependent ecosystems as well. Human activities have altered water regimes as well as the physical structure and water quality of most of Australia's inland waters. These changes are further complicated by changes to native biota, the spread of invasive species and the global effects of climate change and human population pressure.

For many aquatic ecosystems in Australia, there is still time to prevent serious loss of biodiversity or irreversible damage to their ecological integrity. Aquatic ecologists have crucial roles to play in this work, through fundamental research as well as guiding management strategies from policy development to environmental monitoring. Many of the themes in this book are the tenets of good adaptive management and effective research. Yet, there is still much to learn about our surface waters and groundwaters and their ecology. Whether your interests are purely scientific or are motivated by a desire to be involved in wise waterway management and to make a difference, we hope this book has met your needs and inspired you to wish to learn more. All of us find aquatic landscapes among the most beautiful sights on Earth (Figure 13.8). A knowledge of their ecology and the capacity to protect them significantly increase the pleasure and wonder.

Figure 13.8 The lower reaches of the Pieman River on Tasmania's west coast are an excellent example of a pristine riparian zone comprising cool, temperate rainforest species. This vegetation provides part of the wilderness experience enjoyed by tourists taking a river cruise on the dark, humic waters, in addition to sightings of platypuses and sea eagles. (Source: Jenny Davis.)

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