Hierarchical Ecotoxicology

Community Ecotoxicology

William H. Clements
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Community Ecotoxicology

Hierarchical Ecotoxicology Series

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For our families

To Diana for her endless support over the years (WHC)
To Peg, Ben, and Ian (MCN)

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Series Preface

This five-volume *Hierarchical Ecotoxicology Series* is intended to bridge a widening gap between general ecotoxicology textbooks and technical books focused on specific ecotoxicological topics. Important, narrowly focused books abound, and textbooks appear yearly but are necessarily broad treatments of the field of ecotoxicology. This series was conceived from the belief that a synthesis is needed that provides the student with an understanding beyond that afforded by a general textbook but, unlike that from more specialized books, remains focused on paradigms and fundamental methods.

This series has separate volumes for the ecotoxicology of individuals, populations, communities, ecosystems and landscapes, and the entire biosphere. Although these topics are treated separately, the intent is to integrate ecotoxicology as a science across these hierarchical levels.

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1 Introduction to Community Ecotoxicology

1.1 DEFINITIONS – COMMUNITY ECOLOGY AND ECOTOXICOLOGY

> *Ecology is the science of communities.* (Shelford 1913)
>
> *There is little agreement among ecologists about what a community is and how its structure is regulated.* (Ricklefs 1990)
>
> *Doing science at the community level presents daunting problems because the database may be enormous and complex.* (Begon, Harper and Townsend 1990)

1.1.1 COMMUNITY ECOLOGY

A community is defined as a group of interacting populations that overlap in time and space. However, the study of communities transcends simple descriptions of demographic and life history characteristics of individual populations. Instead of describing birth rates, death rates, and other autecological features of isolated populations, community ecologists focus on the interactions among these populations in nature. Rather than measuring fluctuations in abundance of a particular species over time or quantifying differences in population density between locations, the community ecologist considers changes in species diversity and composition of dominant taxa. The primary goal of community ecology is to describe patterns in the organization of communities and to explain the underlying processes that regulate these patterns (Wiens 1984). In particular, the community ecologist seeks to quantify the relative importance of biotic and abiotic factors that influence temporal and spatial variation in community structure. Key issues in contemporary community ecology include questions such as 'Why are more species found in some habitats than in others?' or 'How important are species interactions relative to abiotic factors in regulating community composition?'

The boundaries of communities have been defined based on spatial overlap of populations, trophic structure, strength of species interactions, and taxonomic relationships. In our coverage of community ecology and ecotoxicology, we will not restrict our definition of a community to any arbitrarily-selected taxonomic group, although this is a common practice in terrestrial ecology (e.g. a subalpine forest bird community). We feel that interactions among different taxonomic groups (e.g. between fish and zooplankton or between birds and terrestrial insects) are at least as relevant to ecotoxicology as interactions within these groups. Similarly, instead of limiting our definition of a community to populations within a single trophic level, we will adopt a 'vertical' definition of communities that includes populations within several trophic levels. Our reasoning is that the potential interactions between predators and their prey are among the most interesting, best studied, and most relevant to the field of ecotoxicology. Resource–consumer interactions form the basis for the transfer of energy and contaminants across trophic levels. Finally, we distinguish between the terms 'community' and 'assemblage' based on spatial scale and the potential for interactions among populations. Both terms refer to groups of populations; however, a community consists of populations that have the potential to interact, whereas an assemblage generally consists of populations at a larger spatial scale with no implied interactions.

1.1.2 COMMUNITY ECOTOXICOLOGY

Community ecotoxicology is the study of the effects of chemicals on species abundance, diversity, and interactions. Community ecotoxicologists are also interested in describing patterns in community structure (e.g. number of species, trophic organization) and explaining mechanisms responsible for these patterns. However, unlike research in basic ecology, community ecotoxicologists are especially concerned with separating effects of anthropogenic disturbance, such as chemical stressors, from natural variability. Community ecotoxicology is distinct from population and ecosystem ecotoxicology. While an understanding of the life history characteristics, habitat requirements, and other autecological features of a particular species is important for predicting consequences of exposure to chemical stressors, the endpoints investigated in community ecotoxicology typically integrate responses of numerous species. Finally, community ecotoxicology is unique from ecosystem ecotoxicology in its focus on structural measures such as species diversity and trophic organization instead of ecosystem processes such as energy flow, detritus processing, and nutrient cycling.

Community ecotoxicology has adopted many of the approaches and modified many of the questions derived from basic community ecology to predict effects of chemical stressors. For example, just as community ecologists quantify patterns of species diversity along natural habitat gradients (e.g. elevation, vegetation type), similar study designs allow community ecotoxicologists to measure changes in community composition along pollution gradients. Empirical studies in basic community ecology have provided important insights into how communities respond to contaminants and other anthropogenic disturbances. In particular, the study of community responses to natural disturbance has been a productive area of research in ecology for the past 30 years. Community ecotoxicologists have used these results to help understand ecological responses to chemical stressors. Many of the characteristics of successional change in community composition over time are analogous to patterns of recovery from anthropogenic disturbance.

Finally, basic research on food webs and trophic interactions in community ecology has greatly improved our ability to predict contaminant transport among trophic levels and their effects on trophic structure.

1.2 HISTORICAL PERSPECTIVE OF COMMUNITY ECOLOGY AND ECOTOXICOLOGY

Although the basic definition of a community seems obvious in light of the hierarchical nature of biological organization (e.g. individuals → populations → communities → ecosystems), it underscores several of the more controversial aspects of community ecology. Since the early 1900s ecologists have struggled to delineate communities and their spatiotemporal boundaries. The early history of ecology reveals considerable disagreement over the use of terms such as community, association, assemblage, and guild. A review of major ecology textbooks reveals considerable variation in the definitions of these terms (Fauth *et al*. 1996). Our definition of community ecotoxicology emphasizes the spatial and temporal overlap of populations and the potential for interspecific interactions. We recognize that species interactions in some communities are relatively weak, and therefore the patterns observed are best explained by autecological processes affecting individual populations. However, in communities where interspecific interactions do play an important structuring role, the relative strength of these interactions will influence how communities respond to anthropogenic disturbance. The potential interactions among species represent emergent properties of communities (Odum 1984; Box 1.1) that define this level of biological organization.

Our treatment of community ecology also highlights three significant developments in the history of ecology that greatly influenced the way ecotoxicologists study the fate and effects of contaminants (Table 1.1). First, the deep-rooted

Table 1.1. Historical developments in community ecology and their influence on community ecotoxicology

Historical development in community ecology	Reference	Implications for community ecotoxicology
Debate between proponents of holism and reductionism	Clements 1936 Gleason 1926	Limitations of single species toxicity tests for predicting ecological effects on communities and ecosystems
Importance of food webs and energy flow	Elton 1927 Lindeman 1942	Food chain transfer of contaminants; Importance of trophic structure on contaminant levels in top predators
Rise of experimental ecology	Connell 1961 Paine 1966	Use of microcosms, mesocosms and ecosystem manipulations for measuring ecological effects

philosophical differences between proponents of holism and reductionism in ecology are at least partially responsible for the emergence of ecotoxicology as a distinct discipline. Criticism of the underlying assumption that protection of individual species will protect communities and ecosystem processes motivated researchers to question traditional approaches in toxicology (Cairns 1983, 1986). Second, recognition of the importance of trophic interactions by early researchers influenced a generation of ecologists and significantly contributed to the development of contaminant transport models employed by ecotoxicologists. Finally, the experimental approaches developed by field ecologists who recognized the shortcomings of purely descriptive studies are slowly being integrated into ecotoxicological research. We will show that these historical developments had a profound influence on community ecology and continue to influence the current generation of ecotoxicologists.

1.2.1 HOLISM AND REDUCTIONISM IN COMMUNITY ECOLOGY AND ECOTOXICOLOGY

> *The relationship between classical ecologists and environmental toxicologists has never been a strong one, and an uncharitable person might well describe it as tenuous.*
> (Cairns 1995)

While few ecologists disagree with the definition of communities as groups of interacting populations, the relative importance of these interactions in structuring communities has been the focus of intense debate throughout the history of ecology. Some ecologists argue that species interactions are a basic property of all communities, whereas others describe communities as a random collection of populations that coincidentally occupy the same habitat because of their similar environmental requirements. Thus, since its inception the field of community ecology has struggled to define itself within the broader context of ecology (Box 1.1).

Box 1.1 Historical perspective of holism and reductionism in community ecology

As in other sciences, the philosophical division between proponents of holism and reductionism is prevalent in ecology. Adherents of holistic approaches argue that complex systems have certain emergent properties that cannot be understood by studying component parts in isolation. Supporters of reductionism counter that there are no emergent properties of systems and that the most efficient way to describe the functioning of a system is by detailed study of the component parts. There are few examples in the history of ecology where the debates between holism and reductionism have been more contentious than in the field of community ecology.

One of the most significant developments in the history of ecology was the recognition that different geographic locations supported unique and often predictable associations of plants and animals. As 19th century naturalists began their intercontinental travels to collect field observations on the distribution and abundance of organisms, they were intrigued by the similarity of plant associations that occurred in similar climates. In the early 1900s, Frederick E. Clements, a plant ecologist studying grasslands in Nebraska, proposed that in the absence of disturbance, plant communities progressed in an orderly fashion to a final climax community. This predictable sequence of changes in vegetation, termed succession, was determined primarily by competitive interactions among species and resulted in predictable and discrete boundaries between plant communities. Clements' 'superorganism' concept, which likened the functioning of a community to that of an individual organism, was undoubtedly one of the more extreme holistic interpretations of community ecology. His viewpoints were rigorously challenged by other plant ecologists, particularly Henry A. Gleason, who argued that plant communities lacked definite boundaries and consisted only of fortuitous associations of species. To Gleason, communities were nothing more than stochastic collections of independent species. Because species interactions are the emergent properties which define communities, these ideas challenged not only Clements' view on succession but also the very existence of communities. If species interactions are relatively weak or unimportant, then communities may simply represent ecologists' futile attempts to force random associations of species into nonexistent organizational units. The ultimate demise of Clements' 'superorganism' hypothesis was in part a result of the shift from the study of whole systems to individual populations that began in the 1940s (Simberloff 1980).

Debate over the relative importance of species interactions and the existence of emergent properties of communities is ongoing among contemporary ecologists and ecotoxicologists. At the very least, the concept that communities are organized into functional units has a 'long and troubled history' (Wilson 1997). Strong *et al.* (1984) note that ecology has historically been dominated by the neo-Malthusian perspective that interspecific competition is the major force structuring communities. Some ecologists take the extreme position that communities lack any predictable patterns and have questioned the validity of community ecology as a legitimate science (Schrader-Frechette and McCoy 1993).

Although most contemporary ecologists readily dismiss Clements' superorganism concept (but see papers on the Gaia hypothesis, Lovelock 1979), there is much support for the hypothesis that communities are more than the sum of their component populations. Predictable patterns in species associations exist, and these patterns are often determined by species interactions. Experimental research on multilevel selection theory (Goodnight 1990a,b) suggests that communities are shaped by natural selection and possess functional organization (Wilson 1997). Indeed, some researchers have noted a resurgence of the holistic paradigm in ecology and argue that Clements' superorganism concept provided a foundation for the study of systems ecology (Simberloff 1980). There is also evidence that species interactions can play a major role in structuring communities (Schoener 1974, 1983; Diamond 1978; Schoener). However, this evidence emerged slowly because of the historical focus on descriptive approaches and the late development of experimental procedures in community ecology. The credibility of hypotheses concerning the relative importance of species interactions was further undermined when researchers invoked untestable explanations, such as the 'ghost of competition past' (Connell 1980), to explain the negative results of competition experiments. Because conducting meaningful experiments on communities is challenging, most community ecologists have relied on anecdotal accounts, observations, and mathematical formulations to argue for the importance of species interactions. As described below, the transition of community ecology from a descriptive to an experimental science has greatly increased the credibility of this discipline. We argue that a similar transition is slowly occurring in community ecotoxicology.

The debate between proponents of holistic and reductionist approaches has been especially acrimonious in the field of community ecotoxicology. Because of the need to make definitive regulatory decisions, often without an ecological perspective, there has been an historical focus on reductionist approaches in toxicology (Cairns 1983, 1986). The implicit but often untested assumption that results of single-species laboratory toxicity tests can predict the effects of contamination on more complex systems in nature is a classic example of reductionism in ecotoxicology. Many field assessments of natural systems, especially in terrestrial habitats, also emphasize population-level analyses and dismiss community-level approaches. However, the focus of ecotoxicological research on populations can lead to misleading conclusions regarding the broader impacts of environmental pollutants on higher levels of biological organization. There is an inherent bias that results from the emphasis on economically-important or charismatic species, which often receive special attention under the natural resource damage assessment laws. For example, failure to account for responses of all taxa, including those resilient to oil, provided an incomplete picture of the responses of seabird communities following the 1989 *Exxon Valdez* oil spill in Prince William Sound, Alaska (Wiens *et al*. 1996).

Because of the opportunity to evaluate the responses of numerous species simultaneously, we suggest that community ecotoxicology can provide a much broader context for the assessment of environmental contamination than the study of individual species. Due to differences in life history characteristics and tolerance, different species in a community respond differentially to contaminants and other stressors. Thus, the composition of communities at different locations or at two points in time provides useful information about these environmental conditions. Communities also provide the 'ecological and evolutionary context for populations' (Angermeier and Winston 1999). Variation in responses among taxa due to differences in physiology, feeding habits, habitat use, and reproductive characteristics can provide insight into the direct mechanisms of toxic effects on species.

As illustrated by the quotes at the beginning of this chapter, there is an opinion that results of community and ecosystem studies are complex, highly variable, and difficult to interpret. For example, Luoma and Carter (1991) state that 'at no level of biological organization is it more difficult to adequately understand the dose of a metal to the system than at the level of community'. The primary difficulty in studying higher levels of biological organization is the need to understand both direct and indirect effects of contaminants. Direct effects of contaminants may result in reduction or elimination of local populations and are generally easier to interpret than indirect effects. In contrast, indirect effects of contaminants, such as increased susceptibility to predation or the elimination of an important prey species in the diet of a predator, are much more difficult to detect and interpret. We suggest that a better appreciation of the importance of indirect effects is fundamental to predicting how communities respond to anthropogenic disturbances.

1.2.2 TROPHIC INTERACTIONS IN COMMUNITY ECOLOGY AND ECOTOXICOLOGY

The study of trophic interactions in communities represents the second major development in the history of ecology that has greatly influenced ecotoxicology. Since Lindeman's thermodynamic formalization of Elton's trophic pyramids in the mid-1900s (Lindeman 1942), ecologists have used feeding relationships to characterize the structure of communities. This development triggered a long-standing controversy in ecology: that systems with high diversity and trophic complexity are more stable than less complex systems. Hutchinson's 'Homage to Santa Rosalia' (1959) and the classic paper published by Hairston, Smith and Slobodkin (1960) stimulated a flurry of research attempting to relate population abundance and community structure to trophic complexity.

Information on feeding habits and trophic relationships is of fundamental importance for predicting the transfer of contaminants through communities. It is well established that trophic position greatly influences levels of some contaminants in organisms. The mechanistic explanation for elevated concentrations of organochlorines and other persistent contaminants observed in top predators represented one of the first attempts to integrate basic ecological principles (e.g. trophic ecology) into toxicology. In aquatic ecosystems, an understanding of the relative importance of dietary and aqueous exposure to contaminants is required to predict bioaccumulation (Dallinger *et al.* 1987). Recent studies have shown that, in addition to trophic position, the number of trophic levels determines the levels of certain contaminants in top predators.

1.2.3 IMPORTANCE OF EXPERIMENTS IN COMMUNITY ECOLOGY AND ECOTOXICOLOGY

The final and perhaps most significant development in basic ecology that influenced the field of community ecotoxicology was the recognition that experimental studies are necessary to demonstrate cause-and-effect relationships. The historical focus in ecology was almost entirely on descriptive studies. Early ecologists characterized natural history and habitat requirements, described patterns of plant and animal associations, and relied exclusively on observational studies to determine which biotic and abiotic factors limited the distribution and abundance of organisms. Reliance on these descriptive approaches is at least partially responsible for the relatively slow progress in ecology from the early 1920s until the 1960s. Ecology emerged as a rigorous science only after ecologists began to employ manipulative experiments to test explicit hypotheses. In particular, the pioneering experiments by researchers assessing species interactions in the marine rocky intertidal zone (Connell 1961; Paine 1966) revolutionized the way a generation of community ecologists investigated nature. The profusion of field experiments that followed these classic studies have greatly increased our understanding of the importance of species interactions and our appreciation of the complexity of ecological systems.

The field of community ecotoxicology has experienced a similar transformation in the past 20 years from purely observational approaches to the use of experimental procedures. Prior to 1980, most research in community ecotoxicology was limited to descriptive studies that related species richness, diversity, and community composition to measured levels of chemical stressors. Comparative studies of reference and polluted sites can provide support for the hypothesis that a chemical stressor is responsible for observed differences in community composition. Descriptive studies contribute significantly to our understanding of how communities respond to specific chemicals and remain the primary focus of state and federal monitoring programs in the US. However, as in basic community ecology, the major shortcoming of descriptive approaches is the inability to show cause-and-effect relationships between stressors and community responses. The use of manipulative approaches, such as mesocosms, ecosystem experiments, and natural experiments, have played an increasingly important role in ecotoxicological research over the past 20 years.

1.3 ARE COMMUNITIES MORE THAN THE SUM OF INDIVIDUAL POPULATIONS?

Although general ecology textbooks devote significant coverage to the topic of communities, the focus in most ecotoxicological investigations has been on individuals and populations. Moriarty (1988) questioned the need to study effects of contaminants on communities and concluded that for ecotoxicology, populations are the most appropriate level of organization. Interestingly, Suter's (1993) excellent treatment of ecological risk assessment includes separate chapters on organism, population, and ecosystem-level effects, but there is no corresponding chapter describing community-level responses. Dickson (1995) suggests that the historical emphasis on individuals and populations in ecotoxicological research is unlikely to change because water resource managers and the general public do not appreciate the significance of responses at higher levels of organization. It is much easier to argue for the protection of an economically-important or charismatic species than for the need to maintain ecosystem functional characteristics such as detritus processing or nutrient cycling. However, the study of communities will likely uncover patterns not readily observable through population analyses. We agree with the statement of Sir Robert May (1973) that 'if we concentrate on any one particular species our impression will be one of flux and hazard, but if we concentrate on total community properties (such as biomass in a given trophic level) our impression will be one of pattern and steadiness'.

1.3.1 THE NEED TO UNDERSTAND INDIRECT EFFECTS OF CONTAMINANTS

If communities were abstractions and only represented a tidy way to organize populations into manageable units, then predicting the effects of contaminants at higher levels of organization would be greatly simplified. For example, suppose we knew the direct toxicological effects (e.g. LC_{50} or EC_{50} values) of a particular chemical on all species in a community. If species interactions and indirect effects were unimportant, predicting responses of communities would simply be a matter of book-keeping. With a matrix showing the species names, abundances, and LC_{50} values for all species we could predict the community-level effects at a particular concentration. We know, however, that in many situations species interactions are important and indirect effects complicate ecological assessments. Just as laboratory toxicologists recognize the influences of certain abiotic factors (e.g. temperature, water hardness, dissolved organic carbon) on chemical effects, community ecotoxicologists understand that responses of individual populations cannot be measured in isolation from other populations.

One of the more revealing examples demonstrating the importance of indirect effects occurred when the World Health Organization (WHO), in an attempt to eliminate malaria-bearing mosquitoes, sprayed the pesticides DDT and dieldrin on numerous villages in Borneo. In addition to controlling mosquito populations, the pesticides contaminated cockroaches, which formed the base of an unnatural food chain in the villages. The cockroaches were consumed by geckos, which were ultimately ingested by cats. Biomagnification of DDT and dieldrin by cats resulted in significant mortality and a subsequent increase in rat populations. The somewhat artificial food chain was eventually restored by parachuting large numbers of cats into the villages, a program referred to as ‘Operation Cat Drop’ by the WHO and Royal Air Force.

Numerous examples of indirect effects of contaminants on populations have been reported in the literature; however, separating direct and indirect effects is difficult and often requires field experimentation. Ecosystem manipulation experiments conducted by Schindler (1987) demonstrated that reductions in lake trout abundance resulted from loss of forage fish and not from direct toxicological effects of lower pH. Similar whole-lake manipulations have demonstrated the importance of predator–prey interactions in regulating aquatic communities (Box 1.2). Indirect effects have long been recognized as important causes of reduced abundance of bird populations exposed to pesticides (Powell 1984). Pesticide spray programs are designed to eliminate large numbers of insects, and it should not be surprising that reductions in insect prey may negatively affect bird populations. In addition, spray programs often coincide with critical periods of nestling growth and development because many species have adapted to take advantage of large numbers of prey during periods of insect outbreaks. Reduced prey abundance has been associated with reduced nestling growth and increased risk of predation, presumably because parents are spending more time away from nests searching for prey.

Box 1.2 Trophic cascades in aquatic and terrestrial communities

The most convincing examples demonstrating tight linkages among species and the relative importance of trophic interactions are from a series of studies investigating trophic cascades in aquatic and terrestrial communities (Chapter 8). Whole-lake manipulations conducted by Steve Carpenter and colleagues (Carpenter and Kitchell 1993) have investigated the relative importance of nutrients and top predators on lake productivity. Much of the limnological research conducted in the 1970s focused on the role of nutrients, especially phosphorus, in controlling productivity of lakes. According to the ‘bottom-up’ hypothesis, discharge of nutrients increased phytoplankton biomass, providing greater resources for higher trophic levels. Although there was anecdotal support for the bottom-up hypothesis, it could not explain all of the variation in productivity of the world’s lakes. More recent studies have tested the hypothesis, that while nutrients determine the potential range of productivity, predation regulated actual productivity measured in lakes. In a simple three-level food chain, planktivorous fish reduce abundance of algal-grazing zooplankton and allow phytoplankton populations to expand (Fig. 1.1). Based on the trophic cascade hypothesis, it is expected that algal biomass and primary productivity are generally greater in systems with three trophic levels. In a four-level food chain typical of many lakes, piscivorous fish (e.g. lake trout, bass) control abundance of planktivorous fish, thereby allowing densities of algal-grazing zooplankton to increase. Thus, increased

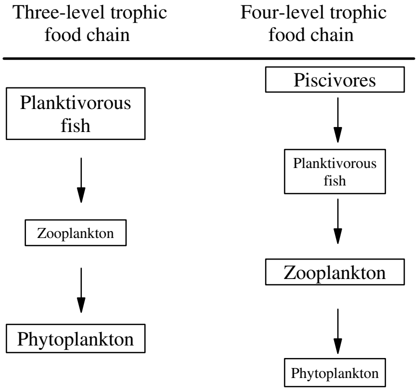

Fig. 1.1. Trophic cascades in three- and four-level food chains. The relative size of each compartment reflects the biomass of the trophic level. In the three-level trophic food chain planktivorous fish control zooplankton, thus allowing phytoplankton to increase in abundance. The addition of piscivores in a four-level trophic food chain reduces abundance of planktivorous fish and allows zooplankton to regulate phytoplankton populations

abundance of top predators releases grazing zooplankton from predation and ultimately limits primary productivity. This ‘top-down’ hypothesis has been tested in a number of biomanipulation experiments where top predators are added or planktivorous fishes are removed (Carpenter and Kitchell 1993). These manipulations have been employed as management tools to control moderate eutrophication in lentic systems (see Box 8.1, Chapter 8).

Analogous cascading trophic relationships between producers and consumers have been observed in terrestrial communities with three trophic levels. Long-term investigations on Isle Royale National Park (MI) have shown that density of moose populations is largely determined by wolf predation. The studies also provided strong evidence for top-down control by demonstrating close linkages between balsam fir, the winter forage of moose, and moose density (McLaren and Peterson 1994).

These examples show that indirect effects and species interactions can play a major role in regulating communities. Because of the importance of species interactions and the difficulty in predicting these indirect effects, community responses to chemical stressors cannot be understood by merely studying individual populations in isolation. To measure effects of contaminants on these systems it will be necessary to account for interactions within and among trophic levels. For example, without information on the role of trophic cascades and top-down control, it would be impossible to predict that the loss of top predators from a chemical stressor could actually increase primary productivity.

In summary, understanding potential indirect effects of contaminants is often cited as a primary justification for testing at higher levels of organization (Cairns 1983). However, indirect effects have received relatively little attention in the ecotoxicological literature (Clements 1999). This paucity of information results from the difficulty of conducting experiments to isolate direct and indirect effects. Developing novel approaches to estimate the influence of contaminants on species interactions and associations is a significant challenge in community ecotoxicology. Although experimental manipulation of contaminant levels and prey abundance is the best way to distinguish direct and indirect effects, conducting planned field experiments in ecotoxicology is difficult. In the absence of direct experimentation, an understanding of natural history requirements of individual species can be used to assess the relative importance of direct and indirect effects on natural communities. Eeva, Lehikoinen and Pohjalainen (1997) compared the breeding success of the Pied Flycatcher and Great Tit to smelter emissions (Cu and SO_4) in southwestern Finland. Because of known differences in feeding habits and habitat preferences between species, these researchers were able to separate

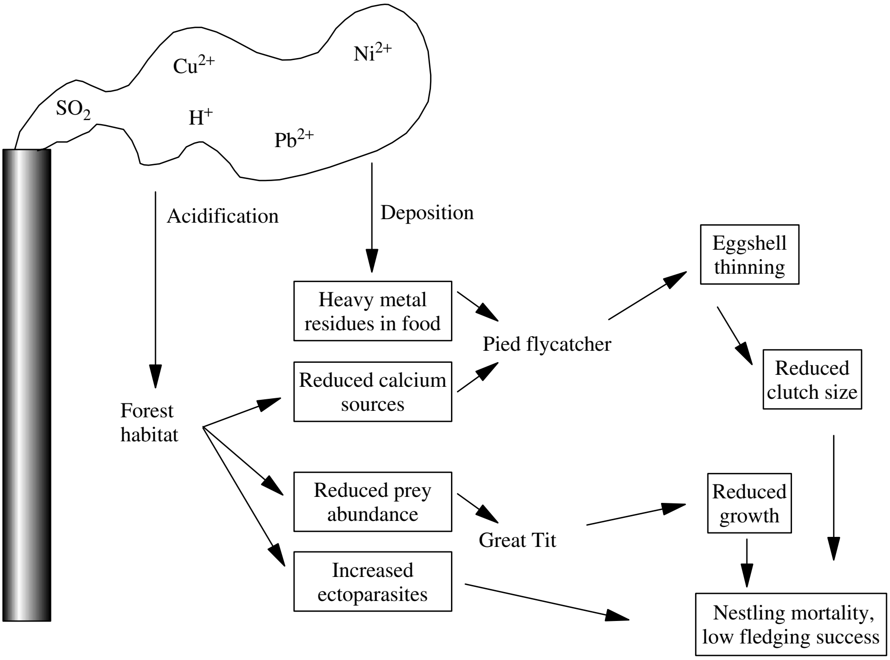

Fig. 1.2. Direct and indirect effects of smelter emissions on breeding success of birds. Pied flycatchers are directly affected by exposure to heavy metals in food, resulting in eggshell thinning and reduced clutch size. In contrast, Great Tits suffer reduced growth due to lower food abundance. (Modified from Figure 12 in Eeva, Lehikoinen and Pohjalainen 1997)

the direct toxicological effects of Cu exposure from the indirect effects of reduced prey abundance (Fig. 1.2). In the absence of experimental evidence, comparative studies among species can provide a reasonable way to estimate the relative influence of direct and indirect effects. In Chapter 2 we will describe experimental and descriptive approaches for assessing the influence of contaminants on species interactions.

1.4 COMMUNITIES WITHIN THE HIERARCHY OF BIOLOGICAL ORGANIZATION

Communities represent an intermediate level of complexity in the hierarchy of biological organization. They are distinct from populations and ecosystems, but have close linkages to these lower and higher levels of organization (Fig. 1.3). The changes in community composition observed at polluted sites are a result of differences in sensitivity among populations as well as the interactions between populations. Many of the measures of contaminant effects developed by community ecotoxicologists exploit these known differences in sensitivity among species. The most frequent observation at polluted sites is the loss of sensitive species and their replacement by tolerant species. The presence or absence of known pollution-tolerant and pollution-sensitive species enables community ecotoxicologists to estimate the relative degree of contamination in the field. For example, since the early 1900s community-level measures of contamination have been employed to assess organic enrichment. The Saprobien system of classification, first developed in Europe, was used to characterize streams as either clean or polluted based on the abundance of sensitive and tolerant species (Kolkwitz and Marsson 1909). Contemporary approaches used by community ecotoxicologists to quantify pollution are generally more sophisticated and include a diverse assortment of biotic, comparative, and diversity indices (Johnson, Wiederholm and Rosenberg 1993). However, most measures are still based on the simple assumptions that the absence of pollution-sensitive taxa and the presence of pollution-tolerant taxa are indicative of degradation. Pollution indices, such as Hilsenhoff's (1987) biotic index, integrate estimates of species-specific sensitivity to pollutants with measures of relative abundance to assess the levels of degradation in aquatic ecosystems. The application of these approaches for assessing contaminant effects in the field will be described in Chapter 3.

There are also close connections between community-level properties and higher levels of biological organization. Recent studies have shown that structural characteristics of communities (species diversity, community composition) influence the functioning of ecosystems (Chapin *et al*. 1998). In a series of field experiments, Tilman and colleagues have shown that species diversity significantly influences plant productivity and nitrogen dynamics, with more diverse plots having greater productivity (Tilman *et al*. 1997). Similar results from model

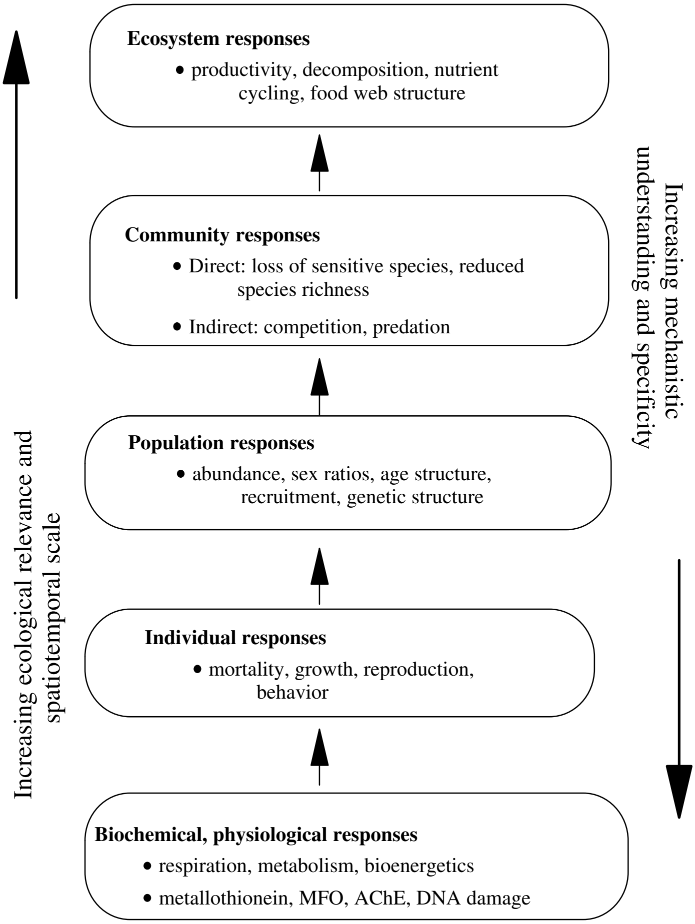

Fig. 1.3. Effects of contaminants across levels of biological organization. Responses at lower levels of biological organization (biochemical, physiological) are generally more specific and are better understood in terms of mechanisms. Consequently, cause and effect relationships are more obvious with sub-individual responses. Responses at higher levels of biological organization (communities and ecosystems) occur at broader spatiotemporal scales and have greater ecological relevance but often lack mechanistic explanations. (Modified from Figure 1 in Clements 2000)

ecosystem experiments showed that depauperate communities had lower productivity and reduced CO_2 uptake compared with species-rich communities (Naeem *et al*. 1994). In addition to demonstrating a linkage between community composition and ecosystem function, these results have important implications for the study of anthropogenic disturbance, especially contaminants. These experiments suggest that loss of functionally important species due to chemical stressors is likely to impact ecosystem processes.

The study of community-level processes also provides insight into the potential effects of natural and anthropogenic disturbance on community stability. The enduring controversy in basic ecology concerning the relationship between species diversity and stability has been tested in grassland plots subjected to severe drought (Tilman and Downing 1994). As predicted, diverse communities were better able to withstand disturbance than species-poor communities. If the relationship between resistance and species diversity illustrated in these experiments is applicable to anthropogenic disturbances, we would expect that naturally depauperate communities would be especially susceptible to chemical stressors. Furthermore, we speculate that communities which have lost species because of exposure to chemical stressors would be more susceptible to other anthropogenic disturbance (e.g. global climate change). The relationship between community structure and functional characteristics of ecosystems and its relevance to ecotoxicology are discussed in Chapter 6.

1.5 CONTEMPORARY TOPICS IN COMMUNITY ECOTOXICOLOGY

The contemporary research topics in community ecotoxicology fall into five general categories: (1) better understanding of the basic ecological factors that regulate communities; (2) development and application of improved biomonitoring approaches; (3) integration of experimental approaches into community ecotoxicology; (4) influence of trophic structure on food chain transport of contaminants; and (5) influence of global atmospheric stressors on community responses to contaminants. Each of these topics will be covered in detail in the chapters that follow. Here, we briefly describe some of the key issues that will be presented in these chapters.

1.5.1 THE NEED FOR AN IMPROVED UNDERSTANDING OF BASIC COMMUNITY ECOLOGY

For community ecotoxicology to thrive as a discipline, researchers must acquire a better understanding of the biotic and abiotic factors that regulate community structure. As noted above, the absence of a sensitive species at a contaminated site is often assumed to be a direct result of contamination. Alternatively, the absence of this species may be a result of a myriad of biotic and abiotic factors unrelated to the stressor. In order to understand how contaminants affect community structure, it is critical that ecotoxicologists develop better tools for distinguishing between natural and anthropogenic variation in communities. The relationship between species diversity and ecosystem function is a good example where basic ecological research could contribute to our understanding of community responses to contaminants. An appreciation of the role that community structure plays in controlling ecosystem function will improve our ability to predict the consequences of reduced biodiversity on higher levels of organization. Similarly, current interest in the relationship between species diversity and stability has significant implications for community ecotoxicology. An understanding of the quantitative relationship between species diversity and natural disturbance may allow community ecotoxicologists to predict which communities will be most sensitive to anthropogenic disturbance. We will examine the influence of biotic and abiotic factors on species associations and interactions within the context of community ecotoxicology in Chapter 2.

Continued research on successional changes in plant and animal communities following natural disturbance will allow ecotoxicologists to predict trajectories in systems recovering from anthropogenic disturbance. Our failure to establish well-defined goals for measuring the success of contaminant remediation impedes our ability fully to characterize ecological recovery. The rapidly emerging field of restoration ecology relies extensively on concepts developed by early plant ecologists studying community succession. Finally, basic community ecologists continue to address issues of spatiotemporal scale in their investigations. Because the spatial and temporal scale of anthropogenic stressors do not necessarily coincide with the endpoints being measured in an ecological assessment (Suter 1993), community ecotoxicologists must also consider scale when investigating effects of contaminants.

1.5.2 DEVELOPMENT AND APPLICATION OF IMPROVED BIOMONITORING TECHNIQUES

The second general area of research in contemporary community ecotoxicology is the development and application of improved biomonitoring approaches. One major goal of these improvements is to streamline biological assessments and reduce costs so that biological monitoring programs can be more efficiently implemented by state and federal regulatory agencies. The cost of quantitative assessments of community structure, especially those that require species-level identification of taxonomically difficult groups, is considered a major impediment to these programs. Research questions related to the appropriate number of samples and the necessary level of taxonomic resolution required to characterize disturbed sites are receiving considerable attention. Chapter 3 will focus on descriptive approaches in community ecotoxicology and highlight recent attempts to streamline biological monitoring programs. Other improvements in biological monitoring involve application of more sophisticated statistical procedures, especially multivariate techniques and the development of regional multimetric indices. Because responses of communities to contaminants and environmental factors are inherently multivariate, the statistical approaches employed to analyze these data should reflect this complexity. Although the relative merits of multivariate and multimetric approaches have been debated in the literature

(Fausch *et al.* 1990; Fore, Karr and Wisseman 1996), recent attempts to integrate these approaches is a promising development in biomonitoring research. We will describe the application of multimetric and multivariate approaches in community ecotoxicology in Chapter 5.

Finally, biomonitoring studies designed explicitly to distinguish the effects of natural and anthropogenic variation are a significant improvement in community-level assessments. Natural variation in community composition is a serious problem in most biomonitoring studies, and often confounds interpretation of field results. Situations where natural variation in abiotic characteristics can be quantified and used as covariates provide the best opportunity to assess the relative importance of natural and anthropogenic effects. Similarly, study designs that allow community ecotoxicologists to separate effects of multiple and potentially interacting stressors are also necessary. The practical but simplistic emphasis of toxicology on single stressors provides a very unrealistic perspective of nature. Natural communities are often exposed to several anthropogenic stressors simultaneously, and identifying the relative importance of each stressor is necessary to understand observed community responses.

1.5.3 APPLICATION OF CONTEMPORARY FOOD WEB THEORY TO ECOTOXICOLOGY

The third area of significant research in community ecotoxicology is the integration of contemporary food web theory into fate and transport models to predict the movement of contaminants through communities. It is well established that levels of contaminants in predators are influenced by physiological (e.g. lipid content, metabolism) and life history (e.g. age, sex feeding habits) features. However, recent studies have shown that ecological characteristics, such as the length and type of food chain, also explain a significant amount of variation. Research on the influence of predator–prey interactions and trophic structure on energy flow will make significant contributions to our understanding of contaminant transport through food chains. The application of stable isotope analyses to characterize feeding relationships and to quantify contaminant transport among trophic levels is a significant development in community ecotoxicology (Kiriluk *et al.* 1995). Although most research describing the relationship between food chain structure and contaminant levels has been conducted in aquatic ecosystems (Rasmussen *et al.* 1990), it is likely that similar patterns will be observed in terrestrial habitats. Studies showing trophic linkages between ecosystem types (e.g. terrestrial and aquatic) demonstrate the importance of energy input and potential for contaminant movement between communities. For example, field experiments conducted by Nakano, Miyasaka and Kuhara (1999) illustrated that limiting input of terrestrial arthropods in small headwater streams had dramatic indirect effects on a benthic community food web. We will examine the direct application of food web theory and new methodological approaches to the study of contaminant transport in Chapter 8.

1.5.4 THE NEED FOR IMPROVED EXPERIMENTAL APPROACHES

The fourth general area of contemporary research in community ecotoxicology is the application of experimental procedures, both laboratory and field, to assess effects of contaminants. Motivated by the realization that observational studies alone cannot show causal relationships and the need for better mechanistic understanding of contaminant effects, ecotoxicologists are beginning to employ more complex experimental procedures in community-level assessments. Experimental approaches which include microcosms, mesocosms, and field manipulations have been used to validate traditional single species toxicity tests (Pontasch, Niederlehner and Cairns 1989) and to support results of descriptive studies (Clements, Cherry and Cairns 1988). Recently, more complex factorial designs have been employed to assess interactions of multiple stressors (Genter 1995) and quantify the influence of trophic structure (Pratt and Barreiro 1998), location (Kiffney and Clements 1996), and previous exposure to stress on community-level responses to contaminants (Courtney and Clements 2000). The most serious limitation of microcosm and mesocosm experiments is the loss of ecological realism that occurs when studies are conducted at smaller spatial scales. Some investigators are especially critical of small-scale experiments and have suggested that microcosm studies have little relevance in ecology (Carpenter 1996). Understanding the influence of spatial and temporal scale on responses to contaminants is critical for predicting how communities will respond in natural systems. In Chapter 4 we will highlight the transition of community ecotoxicology from a descriptive to an experimental science and discuss the important tradeoffs between spatial scale, replication, and ecological realism.

1.5.5 INFLUENCE OF GLOBAL ATMOSPHERIC STRESSORS ON COMMUNITY RESPONSES TO CONTAMINANTS

The final area of research in contemporary community ecotoxicology relates to the interactions between chemical and global atmospheric stressors. Although responses to global atmospheric stressors are generally not considered in most ecotoxicological investigations, increased CO_2, ultraviolet radiation (UVR), and acidification are major environmental issues that will significantly affect natural communities. In addition to their well-documented direct effects, these stressors will likely influence the way that communities respond to contaminants. In fact, some researchers speculate that indirect effects of global warming, acidification, and UVR on communities will be greater than direct effects (Field *et al.* 1992). Increased temperatures resulting from global climate change will likely influence contaminant bioavailability, uptake, and depuration in complex and often unpredictable ways. The photoactivation of certain contaminants after exposure to UV-B radiation, most notably the polycyclic aromatic hydrocarbons, is well documented in the toxicological literature (Oris and Giesy 1986). Finally, decreases in pH of soils and in aquatic ecosystems as a result of acid deposition will increase concentrations and bioavailability of certain metals.

In addition to the direct and indirect influence of global atmospheric stressors on community responses to contaminants, interactions among global warming, UV-B radiation, and acidification are also possible. For example, acidic deposition and climate-induced changes in hydrologic characteristics of watersheds will likely alter the quality and quantity of dissolved organic material (DOM) in aquatic ecosystems. Because DOM plays an important role in reducing light penetration and controlling contaminant bioavailability, these changes will influence exposure of aquatic communities to UV-B radiation and chemical stressors. The effects of global atmospheric stressors on communities and the interactions among these stressors are discussed in Chapter 7.

REFERENCES

Angermeier PL and Winston MR (1999). Characterizing fish community diversity across Virginia landscapes: Prerequisite for conservation. *Ecol Appl* **9**: 335–349.

Begon M, Harper JL and Townsend CR (1990). *Ecology: Individuals, Populations and Communities*. Blackwell Scientific Publications, Cambridge, MA.

Cairns Jr J (1983). Are single species toxicity tests alone adequate for estimating environmental hazard? *Hydrobiologia* **100**: 47–57.

Cairns Jr J (1986). The myth of the most sensitive species. *BioScience* **36**: 670–672.

Cairns Jr J (1995). The genesis of ecotoxicology, In *Ecological Toxicity Testing: Scale, Complexity, and Relevance*, ed. by Cairns Jr J and Niederlehner BR, pp. 1–10. CRC Press, Inc. Boca Raton, FL.

Carpenter SR (1996). Microcosm experiments have limited relevance for community and ecosystem ecology. *Ecology* **77**: 677–680.

Carpenter SR and Kitchell JF (1993). *The Trophic Cascade in Lakes*. Cambridge University Press, New York, NY.

Chapin FS, Sala OE, Burke IC, Grime JP, Hooper DU, Lauenroth WK, Lombard A, Mooney HA, Mosier AR, Naeem S, Pacala SW, Roy J, Steffen WL and Tilman D (1998). Ecosystem consequences of changing biodiversity – Experimental evidence and a research agenda for the future. *BioScience* **48**: 45–52.

Clements FE (1936). Nature and structure of the climax. *J Ecol* **24**: 252–284.

Clements WH (1999). Metal tolerance and predator–prey interactions in benthic macroinvertebrate stream communities. *Ecol Appl* **9**: 1073–1084.

Clements WH (2000). Integrating effects of contaminants across levels of biological organization: an overview. *J Aquat Eco Stress Recov* **7**: 113–116.

Clements WH, Cherry DS and Cairns Jr J (1988). The impact of heavy metals on macroinvertebrate communities: a comparison of observational and experimental results. *Can J Fish Aquat Sci* **45**: 2017–2025.

Connell JH (1961). The influence of interspecific competition and other factors on the distribution of the barnacle. *Chthamalus stellatus*. *Ecology* **42**: 710–723.

Connell JH (1980). Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* **35**: 131–138.

Courtney LA and Clements WH (2000). Sensitivity to acidic pH in benthic invertebrate assemblages with different histories of exposure to metals. *J N Am Benthol Soc* **19**: 112–127.

Dallinger R, Prosi F, Segner H and Back H (1987). Contaminated food and uptake of heavy metals by fish: a review and a proposal for further research. *Oecologia* **73**: 91–98.

Diamond JM (1978). Niche shifts and the rediscovery of competition: Why did field biologists so long overlook the widespread evidence for interspecific competition that had already impressed Darwin? *Am Sci* **66**: 322–331.

Dickson KL (1995). Progress in toxicity testing – an academic's viewpoint. In *Ecological Toxicity Testing: Scale, Complexity, and Relevance*, ed. by Cairns Jr J and Niederlehner BR, pp. 209–216. CRC Press, Inc. Boca Raton, FL.

Eeva T, Lehikoinen E and Pohjalainen T (1997). Pollution-related variation in food supply and breeding success in two hole-nesting passerines. *Ecology* **78**: 1120–1131.

Elton C (1927). *Animal Ecology*. Macmillan, New York, NY.

Fausch KD, Lyons J, Karr JR and Angermeier PL (1990). Fish communities as indicators of environmental degradation. *Am Fish Soc Symp* **8**: 123–144.

Fauth JE, Bernardo J, Camara M, Resetarits WJ, VanBuskirk J and McCollum SA (1996). Simplifying the jargon of community ecology: a conceptual approach. *Am Nat* **147**: 282–286.

Field CB, Chapin III FS, Matson PA and Mooney HA (1992). Responses of terrestrial ecosystems to the changing atmosphere: a resource-based approach. *Ann Rev Ecol Syst* **23**: 201–235.

Fore LS, Karr JR and Wisseman RW (1996). Assessing invertebrate responses to human activities: evaluating alternative approaches. *J N Am Benthol Soc* **15**: 212–231.

Genter RB (1995). Benthic algal populations respond to aluminum, acid, and aluminum-acid mixtures in artificial streams. *Hydrobiologia* **306**: 7–19.

Gleason HA (1926). The individualistic concept of the plant association. *Bull Torrey Bot Club* **53**: 7–26.

Goodnight CJ (1990a). Experimental studies of community evolution. I. The response to selection at the community level. *Evolution* **44**: 1614–1624.

Goodnight, CJ (1990b). Experimental studies of community evolution. II. The ecological basis of the response to community selection. *Evolution* **44**: 1625–1636.

Hairston Sr NG, Smith FE and Slobodkin LB (1960). Community structure, population control, and interspecific competition. *Am Nat* **94**: 421–425.

Hilsenhoff WL (1987). An improved biotic index of organic pollution. *Great Lakes Entomol* **20**: 31–39.

Hutchinson GE (1959). Homage to Santa Rosalia or Why are there so many kinds of animals? *Am Nat* **93**: 145–159.

Johnson RK, Wiederholm T and Rosenberg DM (1993). Freshwater biomonitoring using individual organisms, populations, and species assemblages of benthic macroinvertebrates. In *Freshwater Biomonitoring and Benthic Macroinvertebrates*, ed. by Rosenberg DM and Resh VH, pp. 40–158. Chapman and Hall, New York, NY.

Kiffney PM and Clements WH (1996). Effects of metals on stream macroinvertebrate assemblages from different altitudes. *Ecol Appl* **6**: 472–481.

Kiriluk RM, Servos MR, Whittle DM, Cabana G and Rasmussen JB (1995). Using ratios of stable nitrogen and carbon isotopes to characterize the biomagnification of DDE, mirex, and PCB in a Lake Ontario pelagic food web. *Can J Fish Aquat Sci* **52**: 2660–2674.

Kolkwitz R and Marsson M (1909). Ökologie der tierischen Saprobien. *Int Rev Gesaten* **2**: 126–152.

Lindeman RL (1942). The trophic-dynamic aspect of ecology. *Ecology* **23**: 399–418.

Lovelock JE (1979). *Gaia: a New Look at Life on Earth*. Oxford University Press, Oxford, UK.

Luoma SN and Carter JL (1991). Effects of trace metals on aquatic benthos. In *Ecotoxicology of Metals: Current Concepts and Applications*, ed. by Newman MC and McIntosh AW, pp. 261–300. Lewis, Chelsea, MI.

May RM (1973). *Stability and Complexity in Model Ecosystems*. Princeton University Press, Princeton, NJ.

McLaren BE and Peterson RO (1994). Wolves, moose, and tree rings on Isle Royale. *Science* **266**: 1555–1558.

Moriarty F (1988). *Ecotoxicology: the Study of Pollutants in Ecosystems*. Academic Press, New York, NY.

Naeem S, Thompson LJ, Lawler SP, Lawton JH and Woodfin RM (1994). Declining biodiversity may alter the performance of ecosystems. *Nature* **368**: 734–737.

Nakano S, Miyasaka H and Kuhara N (1999). Terrestrial–aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. *Ecology* **80**: 2435–2441.

Odum EP (1984). The mesocosm. *BioScience* **34**: 558–562.

Oris JT and Giesy Jr JP (1986). Photoinduced toxicity of anthracene to juvenile bluegill sunfish (*Lepomis macrochirus* Rafinesque): photoperiod effects and predictive hazard evaluation. *Environ Toxicol Chem* **5**: 761–768.

Paine RT (1966). Food web complexity and species diversity. *Am Nat* **100**: 65–75.

Pontasch KW, Niederlehner BR and Cairns Jr J (1989). Comparisons of single-species, microcosm and field responses to a complex effluent. *Environ Toxicol Chem* **8**: 521–532.

Powell GVN (1984). Reproduction by an altricial songbird, the red-winged blackbird, in fields treated with the organophosphate insecticide fenthion. *J Appl Ecol* **21**: 83–95.

Pratt JR and Barreiro R (1998). Influence of trophic status on the toxic effects of a herbicide: a microcosm study. *Arch Environ Contam Toxicol* **35**: 404–411.

Rasmussen JB, Rowan DJ, Lean DRS and Carey JH (1990). Food chain structure in Ontario lakes determines PCB levels in lake trout (*Salvelinus namaycush*) and other pelagic fish. *Can J Fish Aquat Sci* **47**: 2030–2038.

Ricklefs RE (1990). *Ecology* (3rd edn). WH Freeman and Company, New York, NY.

Schindler DW (1987). Detecting ecosystem responses to anthropogenic stress. *Can J Fish Aquat Sci* **44** (Suppl 1): 6–25.

Schoener TW (1974). The species–area relationship within archipelagos: models and evidence from island land birds. In *Proceedings of the 16th International Ornithological Congress*, ed. by Firth HJ and Calby JH, pp. 629–642. Australian Academy of Science, Canberra.

Schoener TW (1983). Field experiments on interspecific competition. *Am Sci* **122**: 240–285.

Schrader-Frechette KS and McCoy ED (1993). *Methods in Ecology: Strategies for Conservation*. Cambridge Press, Cambridge, UK.

Shelford VE (1913). *Animal Communities in Temperate America*. University of Chicago Press, Chicago, IL.

Simberloff DS (1980). A succession of paradigms in ecology: essentialism to materialism and probabilism. *Synthese* **43**: 3–39.

Strong DR, Simberloff D, Abele LG and Thistle AB (1984). *Ecological Communities: Conceptual Issues and Evidence*. Princeton University Press, Princeton, NJ.

Suter II GW (1993). A critique of ecosystem health concepts and indexes. *Environ Toxicol Chem* **12**: 1533–1539.

Tilman D and Downing JA (1994). Biodiversity and stability in grasslands. *Nature* **367**: 363–365.

Tilman D, Knops J, Wedin D, Reich P, Ritchie M and Siemann E (1997). The influence of functional diversity and composition on ecosystem processes. *Science* **277**: 1300–1302.

Wiens JA (1984). On understanding a non-equilibrium world: myth and reality in community patterns and processes. In *Ecological Communities: Conceptual Issues and the Evidence*, ed. by Strong DR, Simberloff D, Abele LG and Thistle AB, pp. 439–457. Princeton University Press, Princeton, NJ.

Wiens JA, Crist TO, Day RH, Murphy SM and Hayward GD (1996). Effects of the Exxon Valdez oil spill on marine bird communities in Prince William Sound. *Ecol Appl* **6**: 828–841.

Wilson DS (1997). Biological communities as functionally organized units. *Ecol Appl* **78**: 2018–2024.

2 Biotic and Abiotic Factors that Regulate Communities

2.1 CHARACTERIZING COMMUNITY STRUCTURE AND ORGANIZATION

> *The organization of a community results from the outcome of interspecific competition for the available resources, and is expressed both in the relative abundance and the spatial distribution of constituent species.* (Hairston 1959)
>
> *Despite recent advances, both in the acquisition of data and in its analysis, I doubt that any multispecies community is sufficiently well understood for us to make confident predictions about its response to particular disturbances, especially those caused by man.* (May 1984)

As with most scientific endeavors, the field of ecology is concerned with identifying patterns in the natural world and then explaining the underlying processes responsible for these patterns. Community ecologists specifically focus on characterizing variation in the numbers and types of species found at different locations and understanding the role of biotic and abiotic processes responsible for these differences. Changes in species diversity across broad environmental gradients or between habitats have occupied the interest of community ecologists for several decades. Variation in the distribution and abundance of species may be a result of broad geographical patterns (e.g. 'Why are there so many species in the tropics compared with temperate regions?') or small-scale, local phenomena (e.g. 'Why is community composition different between headwater streams and mid-order streams?'). An appreciation of factors that determine natural spatial and temporal variation in community composition is essential for ecotoxicologists. In order to characterize community responses to contaminants and other anthropogenic disturbances, we must first understand the influence of natural spatiotemporal variation on species diversity and composition. This natural variation in community structure is of practical importance because it complicates assessments of anthropogenic disturbances. Similarly, temporal changes in species diversity and community composition provide the context for understanding how communities will recover from anthropogenic disturbance.

In their attempt to identify predictable features of communities, ecologists have identified numerous ways to categorize communities. Taxonomic groupings, trophic organization, morphological features, and life history traits are a few of the characteristics that ecologists have employed to classify community structure.

As evidenced by Hairston's quote, for many ecologists community structure was synonymous with species interactions, specifically competition. Other ecologists felt that definitions of a community should include both biotic and abiotic characteristics. Recognizing that community structure was influenced by factors other than competition, Roughgarden and Diamond (1986) proposed the idea of 'limited membership' as a unifying theme for defining community structure. Basically their approach focuses on a single question: Why does the unique combination of species found in a particular location or region represent only a subset of what *could* occur? Roughgarden and Diamond argue that membership of any species in a community is a result of three primary factors: the physical environment, dispersal ability, and species interactions. The relative importance of these three factors will vary among community types and across habitats.

Another way to characterize community structure is to consider factors that limit membership in a community as a series of filters operating at different spatial and temporal scales. This idea was proposed by Poff (1997) to describe associations of species traits across spatial scales from microhabitats to entire watersheds. Using this model, Roughgarden and Diamond's (1986) concept of limited membership could be extended to include factors at regional and global scales (Fig. 2.1). While species interactions, physical characteristics, dispersal ability, and anthropogenic factors play a prominent role at local scales, evolutionary and biogeographical factors determine species composition at global and regional scales. As we proceed from global to local filters, the characteristics that limit community membership become increasingly fine. The concept of limited community membership is attractive because it requires that we consider factors operating at the local level as well as historical and biogeographical characteristics. Using this model, species-specific sensitivity to contaminants is simply another filter that restricts community membership. If we are to make significant progress in predicting how communities respond to chemical stressors, an understanding of factors that limit community membership at these different spatial and temporal scales is required.

2.1.1 COLONIZATION AND COMMUNITY STRUCTURE

Ecologists recognize that historical factors and regional-scale processes often interact to regulate local community composition. Colonization studies of newly created habitats provide opportunities to assess the influence of historical factors and species' dispersal abilities on community composition. If communities were regulated entirely by local, deterministic factors, we would expect that communities established in similar habitats would have similar composition. Jenkins and Buikema (1998) tested this hypothesis by measuring structural and functional characteristics of zooplankton communities in 12 newly established ponds. Samples collected over a 1-year period showed that physical and chemical characteristics of these ponds were essentially identical. However, communities established in each of the ponds were distinct, reflecting the unique colonization

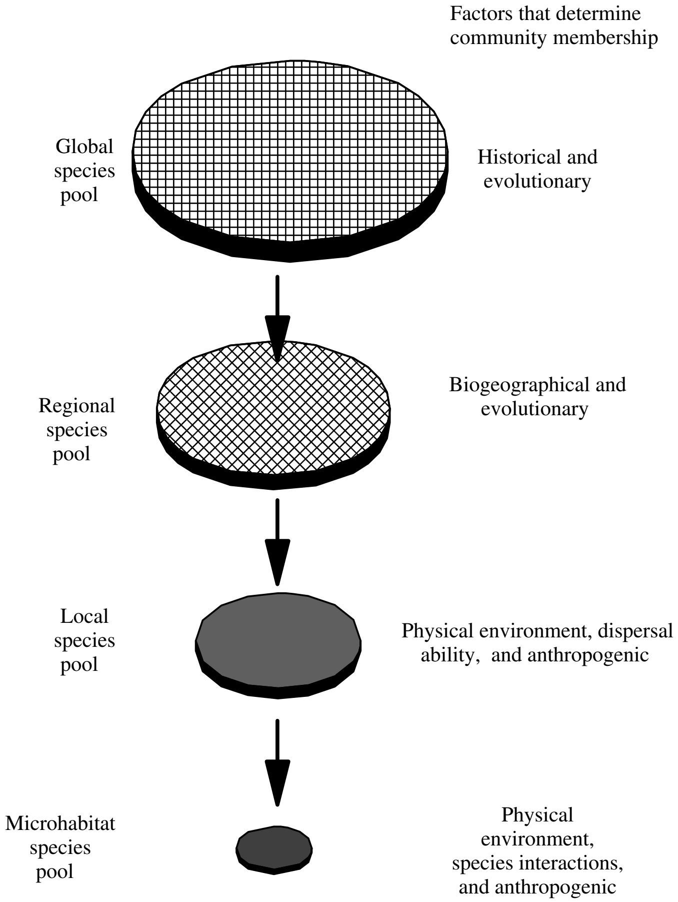

Fig. 2.1. Historical, biogeographical, and environmental factors that determine membership of species in a community. Each factor is represented as a filter that operates at different spatial and temporal scales to determine regional, local, and microhabitat species pools. The pore size of each filter reflects its relative influence on species pools. Using this model, contaminants and other anthropogenic stressors are simply another filter that determines community composition. (Modified from Figure 1 in Poff 1997)

abilities of dominant zooplankton species. Dispersal ability regulated composition among ponds because species that arrived first had a lasting effect on community structure. These results have important implications for how we view the establishment and regulation of communities. Failure to account for regional processes may explain the apparent stochastic behavior observed in some communities. The results also demonstrate that historical factors can have lasting, subtle impacts on communities, thus complicating our ability to locate reference sites and assess the importance of anthropogenic stressors (Matthews, Landis and Mathews 1996; Landis, Mathews and Mathews 1996).

2.1.2 DEFINITIONS OF SPECIES DIVERSITY

A variety of approaches have been developed by community ecologists to define and quantify species diversity. Species richness is a simple count of the number of different species within a local habitat or a region. Some ecologists are uncomfortable with measures of species richness because rare and common species are treated equally. Assuming that abundance of a species is related to its ecological importance, estimating relative abundance of different species may be a more effective way to characterize community structure. Diversity indices that account for both species richness and distribution of individuals among species are commonly used in biological assessments. These measures are described in Chapter 3. Here, our discussion of spatial and temporal patterns in diversity will focus on the number of species within a sample or within a region. To characterize spatial variation in community structure, ecologists distinguish among three different measures of species diversity. Alpha diversity refers to the species richness within a local area. Because assessments of anthropogenic disturbance are generally site specific, alpha diversity is the measure most relevant to ecotoxicologists. Beta diversity is the change in number of species and is an expression of species turnover between two adjacent habitats. Gamma diversity is the total number of species within a relatively large geographic area and represents the species pool available to colonize local habitats. Gamma diversity is a product of alpha and beta diversity and therefore will be greatest in regions with high local diversity and high species turnover.

Although concern about the global loss of species has increased awareness of the importance of biodiversity, this is a relatively recent occurrence. Ecology textbooks published in the 1940s and 1950s made little mention of species diversity, attributing differences in community structure among locations primarily to historical and evolutionary events (Schluter and Rickleffs 1993). In contrast, experimental studies conducted in the 1960s and 1970s emphasized local regulation of diversity by species interactions and environmental heterogeneity, almost to the exclusion of historical features. Today we know that spatial and temporal variation in diversity results from a complex interplay of historical, evolutionary, climatic, energetic, environmental, and anthropogenic phenomena. The challenge in community ecology is to understand the relative influence of these different factors on species diversity. The challenge in ecotoxicology is to interpret anthropogenic effects on species diversity within the context of these local and historical features. Some progress has been made with the recognition that natural variation and historical factors can influence community responses to contaminants (Matthews, Landis and Mathews 1996; Landis, Mathews and Mathews 1996; Clements 1999).

2.2 CHANGES IN SPECIES DIVERSITY AND COMPOSITION ALONG ENVIRONMENTAL GRADIENTS

Natural changes in community composition and species diversity across environmental gradients have fascinated ecologists for many years. Early explorers frequently reported broad scale changes in species diversity and community composition with latitude and elevation. Because these changes were often predictable, ecologists developed confidence that underlying biotic and abiotic mechanisms could be identified by analysis of spatial patterns. In some instances the observed transition from one community type to another was relatively abrupt, whereas in others it was much more gradual. These differences were most often related to species-specific tolerance for a particular environmental factor, such

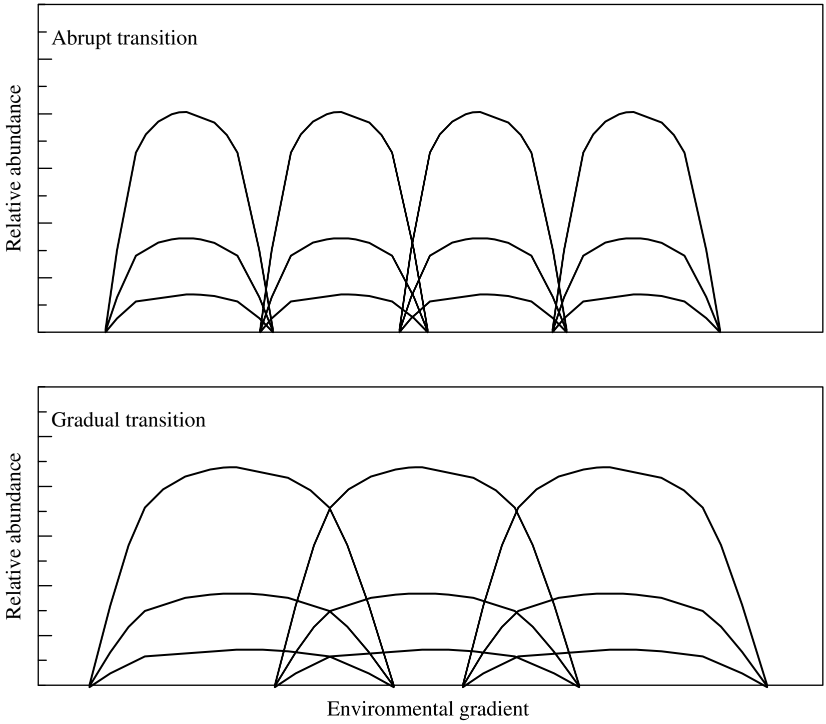

Fig. 2.2. Hypothetical changes in relative abundance of species along an environmental gradient. Some communities show relatively abrupt transition in abundance of dominant species, while others are characterized by gradual changes. Abrupt transitions in community composition are often a result of interspecific interactions (competition, predation). Changes in community composition along a contaminant gradient are likely to be abrupt for some species and gradual for others depending on relative sensitivity to the stressor. (Modified from Whittaker 1975)

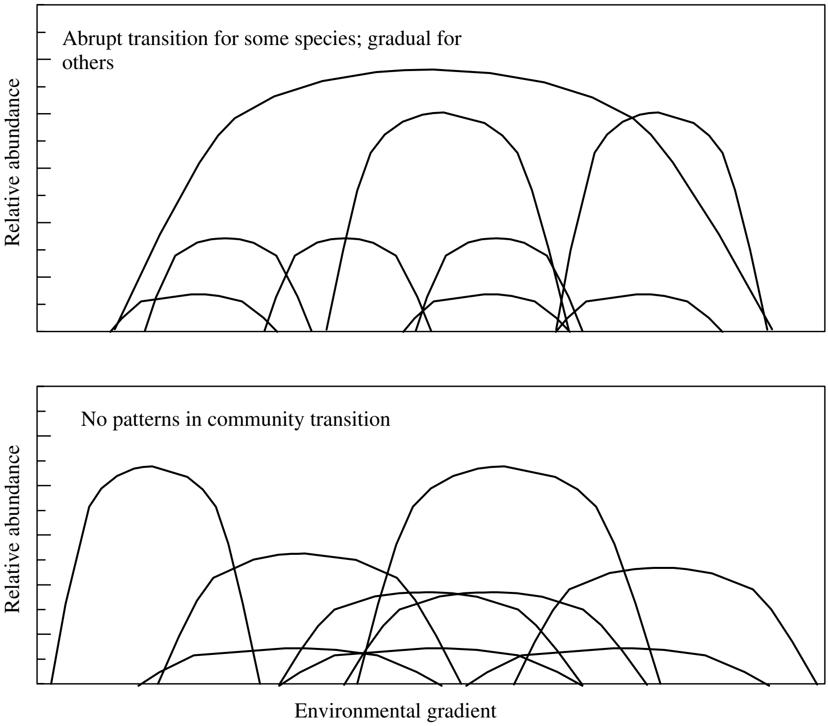

Fig. 2.2. (*continued*)

as temperature, moisture, or soil type. Some species within a community are more tolerant of environmental variation and will be distributed across a broader range of habitats than others. Whittaker (1975) noted that patterns of species replacement along environmental gradients fall into several categories (Fig. 2.2). The forest communities studied by Whittaker and colleagues showed that species replacement was gradual and that species behaved independently of each other. In contrast, marine invertebrate communities in the rocky intertidal zone show relatively abrupt transitions resulting from strong environmental gradients and intense species interactions. Finally, longitudinal changes in stream communities described in the River Continuum Concept (Vannote *et al*. 1980) and geographic changes in community composition across broad latitudinal gradients are relatively gradual, but often show distinct community types.

An understanding of how species respond to natural environmental gradients has direct relevance to community ecotoxicology. First, because contaminants are often distributed along a concentration gradient, the same analytical techniques employed to study natural patterns (e.g. gradient analysis, ordination) can be used to investigate community responses to chemical stressors. Second, understanding the processes responsible for species replacement along natural gradients will allow ecotoxicologists to develop improved models for assessing contaminant-induced variation. We expect that changes in communities in response to contaminants will be relatively abrupt, but that recovery along a contaminant gradient may be more gradual. Finally, natural environmental gradients are often superimposed on contaminant gradients and will complicate biological assessments of community structure. In order to predict community responses to chemical stressors, ecotoxicologists require information on how these natural changes will modify and interact with contaminants.

2.2.1 GLOBAL PATTERNS OF SPECIES DIVERSITY

The most consistent response to an environmental gradient reported by community ecologists at a large spatial scale is the increased species diversity from the arctic to tropical ecosystems. This pattern has been observed for most groups of organisms, and a variety of hypotheses have been proposed to explain the greater diversity in tropical communities (Table 2.1). Tropical ecosystems are more productive, predictable, structurally complex, and are less influenced by extreme climatic events compared with arctic and temperate ecosystems. It is important to note that these four hypotheses are not mutually exclusive, and it is likely that each will play a role in accounting for changes in diversity across latitudinal gradients. For example, Connell and Orias (1964) dismissed environmental harshness *per se* as an explanation for the paucity of species in extreme habitats. Their conceptual model predicts that greater species diversity will be observed in productive habitats with high stability. In his classic paper ‘Homage to Santa Rosalia or Why are there so many kinds of animals?’, G. E. Hutchinson (1959) speculated that the earth’s rich biodiversity was a result of an interplay among energetics, evolution, species interactions, and habitat complexity.

Table 2.1. Four hypotheses to explain the increased biological diversity from arctic to tropical ecosystems

Hypothesis	Explanation
Productivity	Tropical ecosystems have greater primary productivity, thus providing more food resources and greater food web complexity
Heterogeneity	Tropical ecosystems are physically more complex and heterogeneous, thus providing more habitats and opportunities for specialization
Stability	Tropical ecosystems are more stable and predictable, thus allowing species to specialize on a particular resource
Evolutionary time	Tropical ecosystems are ‘older’ in the sense that they have not been subjected to recent glaciation, thus providing more time for speciation

In an assessment of progress over the past 20 years since the publication of Hutchinson's paper, Brown (1981) noted that the inability of contemporary ecology to answer the question 'Why are there so many kinds of animals?' resulted from their failure to focus on energetics. He noted that soon after publication of Hutchinson's seminal paper, ecologists were divided between two camps. The 'ecosystem processes camp' considered energetics, but the research questions were not directed towards community ecology. The 'species interactions camp' focused on community dynamics, but largely ignored the importance of energetics. Brown (1981) proposed a general theory of biodiversity based on availability of energy, the apportionment of energy among species, and environmental harshness. More recently, Brown and Lomolino (1998) presented a more synthetic explanation for patterns of species diversity that included elements of productivity, abiotic stress, and species interactions, all within a broad historical context of time and space. According to this model, abiotic stress in extreme environments limits community composition to a few widely distributed, stress-tolerant species capable of dividing up the limited resources. Biotic interactions in this harsh environment play a relatively minor role. In contrast, abiotic factors are less important in benign environments where predators and competitors limit densities of most species, allowing a large number of relatively uncommon species to partition the abundant resources.

Brown and Lomolino's (1998) synthetic explanation of community organization is intellectually satisfying for several reasons. First, it recognizes the importance of several key factors in controlling species diversity across broad environmental gradients. It is also consistent with the observation that species found in more variable habitats have a greater tolerance for environmental conditions compared with species occupying benign environments (Fig. 2.3). The positive relationship between the range of latitudes occupied by a species and the latitude of its center of distribution is called Rapoport's Rule (Rapoport 1982). A similar phenomenon has also been observed in communities across elevation gradients. The implication is that species found in stable habitats are less able to tolerate variation in environmental conditions than species occupying harsh conditions of higher latitudes or higher elevations. The inverse relationship between species diversity and elevation is probably a result of lower productivity and greater stress of high elevation habitats. This pattern, which has been observed for mollusks, birds, mammals, and trees, may provide important insights into variation in sensitivity to contaminants among locations. Similarly, lower diversity of some plant communities that has been observed along gradients of increased aridity and salt stress is most likely associated with the increased physical harshness of these environments. This explanation is consistent with Menge and Sutherland's (1987) hypothesis of environmental stress gradients, which has been used to account for local patterns of species diversity in benign and stressful environments (see Section 2.5.1). Factors influencing local patterns of species diversity are of particular interest to ecotoxicologists because they may help us understand

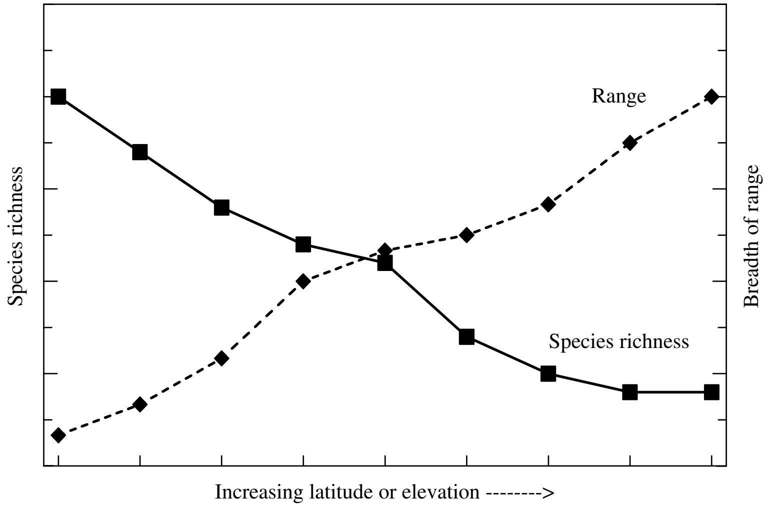

Fig. 2.3. Hypothetical example of Rapoport's Rule showing the relationship between species richness and breadth of distribution along an environmental gradient. Although the total number of species is reduced at higher elevations and at higher latitudes, the tolerance of individual species for environmental conditions is greater. These results suggest that species living in stable environments are less able to tolerate extreme conditions. Variation in tolerance may have important implications for understanding how species from different environments respond to anthropogenic stressors

how communities respond to contaminant gradients. Assuming this pattern is consistent across communities, it suggests that species occupying more predictable environments may be more sensitive to anthropogenic disturbances than species from harsh environments. This hypothesis could be tested by comparing responses of communities from different locations to the same anthropogenic stressor.

Another consistent pattern across broad geographical regions relates to changes in abundance distributions from temperate and tropical habitats. In general, tropical communities are characterized by a more even distribution of individuals among species (Fig. 2.4). In other words, tropical communities not only contain many more species than temperate communities, but the most common species account for a relatively small portion of the total community. In contrast, temperate communities are often dominated by a relatively few species which account for most of the individuals and biomass. Similar patterns have been observed across elevation gradients, suggesting that this may be a general phenomenon (Brown and Lomolino 1998). Because dominance of some species increases in response to stressors, the distribution of individuals among species is a sensitive indicator of anthropogenic disturbance and has been used in biomonitoring studies. These concepts will be further developed in Chapter 3.

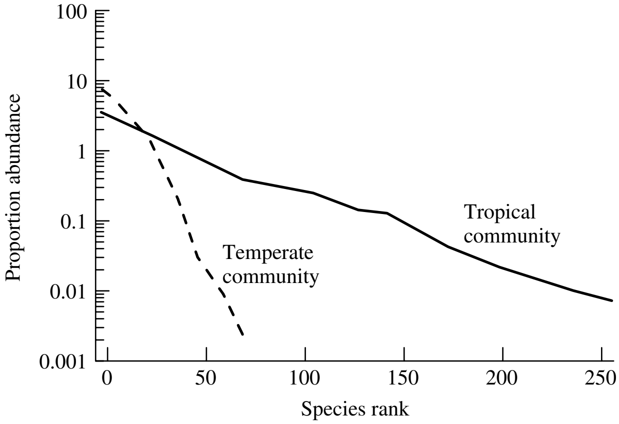

Fig. 2.4. Variation in species abundance curves between temperate and tropical communities. In contrast to temperate systems, tropical communities are characterized by greater species richness and a more even distribution of individuals among species. The shape of species abundance curves is considered a result of species interactions and environmental conditions and has been used to characterize effects of anthropogenic disturbance (see details in Chapter 3)

2.2.2 SPECIES–AREA RELATIONSHIPS

One of the most predictable relationships in community ecology is the increase in number of species with area. The species–area relationship, described as one of the few laws in ecology (Schoener 1974), has been reported across most taxonomic groups and a variety of habitats. In addition to explaining differences in species richness on islands with different area and varying distances from a source of colonists (Box 2.1), the species–area relationship has been applied to conservation biology and the design of wildlife refuges. Contemporary research questions regarding the size, shape, and degree of isolation of wildlife refuges and other natural areas have been addressed using this relationship.

Box 2.1 The special case of islands

MacArthur and Wilson's (1963) theoretical treatment of the equilibrium theory of island biogeography was a major conceptual advance in community ecology. Few discoveries in ecology have had greater impact, and the practical applications of their mathematically simple but conceptually elegant models are still being realized decades later. The equilibrium theory was developed to explain the observation that island flora and fauna often represent a subset of species available from the mainland species pool. Distance from the mainland source of colonists and island area were primarily responsible for variation in the equilibrium number of species among islands (Fig. 2.5). Small, remote

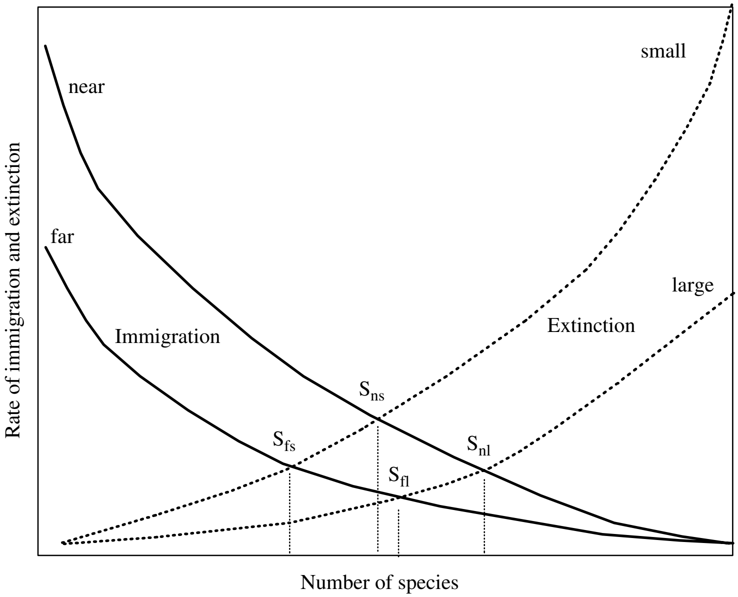

Fig. 2.5. The relationship between number of species and rates of immigration and extinction on islands. Immigration and extinction rates are influenced by island size (large versus small) and distance from a mainland source of colonists (near versus far), resulting in a unique equilibrium number of species (*S*) for each island type. Because recovery of communities from disturbance is largely determined by immigration rate and the proximity of local colonists, these theoretical relationships have important implications for community responses to anthropogenic stressors. (Modified from MacArthur and Wilson 1967)

islands generally had fewer species than larger islands close to a mainland source of colonists. MacArthur and Wilson (1963) also recognized that while the actual number of species was relatively consistent, community composition varied significantly due to species replacement and turnover. The importance of species turnover was evidenced by studies of the recolonization of Krakatau Islands following a massive volcanic eruption in 1883. Surveys of these islands several decades later showed a relatively constant numbers of species, supporting the equilibrium perspective; however, community composition changed significantly over time.

Experimental support for the equilibrium theory of island biogeography was provided by a large-scale manipulation of insect communities in the Florida Keys. Daniel Simberloff, a graduate student working with Wilson, fumigated mangrove islands with the pesticide methyl bromide and followed subsequent recolonization (Simberloff and Wilson 1969, 1970). Results generally supported the equilibrium theory and showed that isolated islands had lower rates of colonization and a lower equilibrium number of species compared with islands located near a mainland species pool.

While much of the research on island size has focused on structural measures (e.g. community composition and species richness), there is evidence that ecosystem function may also be related to area. The theoretical motivation for this concept is based on the observation that individual species in a community are important regulators of ecosystem processes. Wardle *et al.* (1997) tested this hypothesis in an island archipelago of a Swedish boreal forest. Several ecosystem processes, including respiration, decomposition, and nitrogen loss, varied with island area because of differences in community composition. Variation in community composition among islands resulted from the greater frequency of fires due to lightning strikes on larger islands. These results show that historical events (e.g. frequency of fire) play an important role in determining both community composition and ecosystem function. By developing a better appreciation for the role of historical events we can begin to understand how natural communities will respond to anthropogenic disturbance.

The species–area relationship takes the form:

$$S = \mathrm{c}A^z$$

where S = the number of species, c is a constant, A = area, and z represents the slope of the relationship between S and A when both are plotted on a logarithmic scale. Although the constant c varies among taxonomic groups, various field studies have reported that the exponent z is approximately 0.25. The consistency of z among taxonomic groups suggests that some universal principle may be operating (May and Stumpf 2000); however, recent attempts to estimate the slope of the species–area relationship across a range of habitats have reported greater variation than previously believed. Crawley and Harral (2001) measured species richness of plant communities across a wide range of habitat scales (0.01 to 10^8 m^2). They reported that z values were lowest at small spatial scales (due to interactions among species) and at very large spatial scales (due to low species turnover with distance). The greatest rate of species accrual was observed at intermediate scales, where increases in area resulted in increases in habitat diversity. These findings indicate that while species accrual rates may be similar within a small range of spatial scales, different processes operate to determine species diversity across geographic regions.

Despite its intuitive appeal and broad explanatory power in community ecology, the species–area relationship has not received much attention in ecotoxicology. The basic principles of island biogeography have important applications to the study of contaminant effects and recovery. The rate of recovery and the composition of communities during the recovery process are greatly influenced by distance from the source of colonists and colonization abilities of species. These ideas will be considered in Chapter 6.

2.2.3 ASSUMPTIONS ABOUT EQUILIBRIUM COMMUNITIES

MacArthur and Wilson's (1963) equilibrium theory of island biogeography was consistent with the predominant view of ecology at the time. Many ecologists believed that natural communities are orderly, balanced, and maintain a natural equilibrium unless subjected to extrinsic disturbance. Although ecologists recognize the dynamic nature of this equilibrium, the underlying assumption that communities are regulated primarily by biotic interactions remains prevalent in ecology. The emergence of equilibrium theories in ecology was supported by our deep-seated belief that attributes of natural communities are predictable and that historical factors, stochastic events, and small-scale environmental perturbations are relatively unimportant. Much of the controversy surrounding the relative importance of species interactions results from this uncritical acceptance that communities are at equilibrium (see Section 2.4).

Ecologists now recognize that few communities are regulated exclusively by predictable, deterministic processes. Long-term data collected from a variety of systems reveal temporal changes in abundance of dominant species that do not appear to be regulated by equilibrium processes. For example, detailed studies of grassland bird communities have shown few consistent patterns and little indication that biotic interactions are important (Wiens 1984). The most likely explanation for the observed non-equilibrium characteristics of these communities relate to the stochastic environmental conditions of prairie and shrub-steppe habitats.

Studies conducted in streams suggest that communities may shift from equilibrium to non-equilibrium conditions seasonally or among locations along a river continuum (Minshall, Petersen and Nimz 1985). In his classic paper 'The paradox of plankton', Hutchinson (1961) observed that the high diversity of phytoplankton in simple, homogeneous environments was contrary to deterministic predictions of the competitive exclusion principle. The proposed explanation for this paradox was that planktonic communities did not achieve equilibrium conditions. Interestingly, recent studies conducted in lakes suggest that resource competition can structure communities even in environments where equilibrium conditions are rarely observed. Interlandi and Kilham (2001) reported a strong relationship between the number of limiting resources (nitrogen, phosphorus, silicon, and/or light) and diversity of phytoplankton in lakes (Fig. 2.6). Clearly, the dichotomy between equilibrium and non-equilibrium communities is somewhat artificial. Instead of defining communities as either equilibrium or non-equilibrium, Wiens (1984) proposes that communities should be arrayed along a gradient based on a suite of characteristics. This model is analogous to the continuum between r-selected and K-selected species described in population ecology.

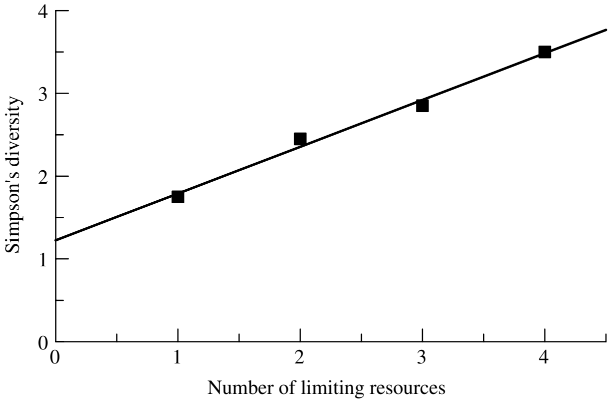

Fig. 2.6. The relationship between the number of limiting resources and species diversity of plankton communities. (Modified from Figure 6 in Interlandi and Kilham 2001)

2.3 THE ROLE OF KEYSTONE SPECIES IN COMMUNITY REGULATION

It is generally accepted that some species have disproportionate effects on community composition and ecosystem function (Power *et al.* 1996). These 'keystone' species are often large, highly mobile consumers, which are especially susceptible to habitat loss and chemical stressors. Because of their impact on communities, loss of keystone species is expected to influence other species in the community. Identifying species that play a significant role in structuring communities is necessary for predicting ecological consequences of contaminants and other anthropogenic stressors.

Determining the relative importance of a species in a community will often require experimental manipulations. Experiments conducted in the marine rocky intertidal zone demonstrated that removal of the predatory starfish *Pisaster ochraceus* had significant effects on other species in the community (Paine 1966). Selective predation of *Pisaster* on mussels, the competitively dominant species in the community, maintained a diverse assemblage of subordinate species. Paine (1969) introduced the keystone species concept to describe a species that has significantly greater effects on a community than expected based on its abundance or biomass. Since the publication of Paine's conceptual paper, investigators have identified keystone species in a variety of ecosystems (Power *et al.* 1996), and the keystone species concept has been referred to as a 'central organizing principle' in community ecology (Menge *et al.* 1994). Currently, we know that keystone species are widely distributed among many ecosystem types and that their effects on structure and function are often far reaching (Table 2.2).

Paine's initial experiments described effects of a keystone predator, and most subsequent studies of keystone species have focused on similar

Table 2.2. Examples of suspected or likely keystone species and their target groups in a variety of aquatic and terrestrial habitats (modified from Power *et al.* 1996)

Habitat	Keystone species	Target group	Reference
Rocky intertidal	Predatory starfish	Mussels	Paine (1966)
Coral reefs	Sea urchins	Algal communities	Carpenter (1990)
Lakes and ponds	Planktivorous fish	Zooplankton	Brooks and Dodson (1965)
Rivers and streams	Predatory steelhead and omnivorous minnow	Invertebrates and fish fry	Power (1990)
Grasslands	Rabbits	Herbs and grasses	Tansley and Adamson (1925)
Woodlands	Wolves	Moose	McLaren and Peterson (1994)
Desert	Kangaroo rats	Seeds	Brown and Heske (1990)

resource–consumer interactions. However, a broad definition of a keystone species should also include effects such as physical restructuring of the environment (ecosystem engineers such as beavers in the Pacific Northwest) and mutualistic interactions (plant-pollinator systems). Similarly, we know that the effects of keystone species extend well beyond regulation of species diversity and include effects on community structure, productivity, nutrient cycling, and energy flow (Ernest and Brown 2001). In fact, an operational definition of keystones species should include any species that has a disproportionate impact on a community, regardless of the mechanism (Power *et al*. 1996). Figure 2.7 shows the relationship between total community impact and relative abundance or biomass in a community. Species that fall on the diagonal line influence the community in proportion to their abundance. Species to the right of the diagonal are dominant in the community but their impact is less than expected based on abundance or biomass. Species to the left of the diagonal are defined as true keystone species because they have a disproportionate influence on community structure or function.

2.3.1 IDENTIFYING KEYSTONE SPECIES

Identifying keystone species and quantifying their effects on community structure are not trivial issues, and criticism of the keystone species concept is at least partially a result of these difficulties. While manipulating density of an individual species remains the most direct approach for assessing its role in a community, conducting experiments at appropriate spatial and temporal scales is logistically challenging. Conclusions about the importance of species interactions relative to abiotic processes are clearly scale-dependent. Because the size of study plots and the duration of experiments may influence patterns that we observe, it follows

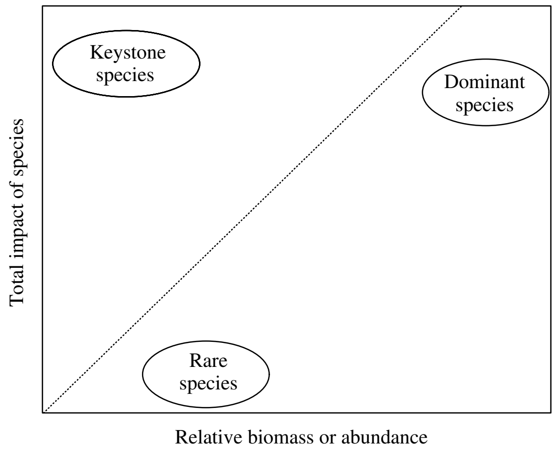

Fig. 2.7. Relationship between total community impact and relative abundance or biomass of a species. The effects of a species on community structure and function are not necessarily related to its abundance or biomass. Species in the upper right hand quadrant are dominant in the community, but their impact is less than expected based on their abundance or biomass. Species to the left of the diagonal have greater impact than expected and are considered true keystone species. (Modified from Figure 3 in Power *et al.* 1996)

that more attention should be given to spatial and temporal scale when interpreting results of manipulative experiments (see Chapter 4). The tremendous success of rocky intertidal ecologists is at least partially a result of the relative ease with which these communities can be manipulated. The reluctance of some ecologists to embrace the keystone species concept is likely due to difficulty obtaining experimental evidence in systems that are less amenable to manipulation (Box 2.2). Comparative approaches and natural experiments, in which community structure and function are measured in areas with and without a particular species, are practical alternatives to actual manipulation and will play an important role in identifying keystone species. Well-designed studies that take advantage of species reintroductions could also contribute to our understanding of keystone species. For example, recovery of otter populations off the California coast and beaver populations in the Pacific Northwest provide excellent opportunities to track ecosystem changes due to increased abundance of keystone species.

Box 2.2 Keystone species in terrestrial communities: an experimental demonstration

Because most experimental evidence for the keystone species concept has been obtained from aquatic ecosystems, many terrestrial ecologists have been reluctant to accept this hypothesis. However, support for the keystone species hypothesis has been obtained from a long-term study in the Chihuahuan desert of southeastern Arizona (USA). To investigate competitive interactions in a rodent community, Brown and Munger (1985) used semi-permeable fences to exclude larger kangaroo rats (*Dipodomys* spp.) from experimental plots. Control and experimental plots were identical except that the fences surrounding controls had slightly larger holes that allowed free movement of both kangaroo rats and smaller species. Populations were sampled monthly for over 20 years, providing one of the few long-term assessments of the effects of species removal. Results of this study showed that the competitively superior kangaroo rats suppressed abundance and altered foraging behavior and habitat use of the smaller species. More importantly, kangaroo rats were shown to have larger than expected impacts on energy flow and community composition of plants, thus satisfying the definition of a keystone species.

Between 1977 and 1996, six species of seed-eating rodents colonized experimental plots where kangaroo rats were removed at densities approximately twice as high as controls. Nonetheless, these species only consumed about 14% of the available energy consumed by kangaroo rats on the control plots. Thus, for almost 20 years there was no evidence of compensation by subordinate species following removal of the keystone species. Remarkably, this changed in 1996 when a species of pocket mouse (*Chaetodipus baileyi*), never previously observed in the study site, colonized the experimental plots at densities 20 times greater than controls (Ernest and Brown 2001). Within 2 years, this species consumed most of the resources and was able to compensate for the excluded kangaroo rats. This experiment demonstrates that previously rare species are capable of restoring community structure and function. It also demonstrates the difficulty of identifying keystone species without experimental and/or long-term data.

Quantifying the relative impacts of keystone species on community structure and function is also complicated by spatial and temporal variation in abundance. Species that regulate community structure in one location or during one time period may be less important in other areas or at other times. This context-dependency of the keystone species concept has been demonstrated in rocky intertidal communities (Menge *et al.* 1994). Power *et al.* (1996) also present several scenarios in which the structuring role of a species could be modified under different environmental circumstances. However, our understanding of the physical, chemical, and biological factors that influence the impact of a particular species is incomplete. Research in rocky intertidal habitats has focused primarily on the role of physical disturbance, and conceptual models have been developed to quantify the relative importance of species interactions under varying levels of physical stress (Menge and Sutherland 1987). These ideas are quite relevant for community ecotoxicology because chemical stressors may directly influence abundance of keystone species as well as modify their structuring role in communities.

2.3.2 SUMMARY

One of the greatest challenges in ecotoxicology is to develop an understanding of the potential indirect effects of species loss on communities. By definition, the loss of a keystone species due to an anthropogenic stressor will have disproportionate impacts on a community. In keystone-dominated communities, other species have relatively minor effects and are often considered redundant in terms of structure and function. Long-term consequences of the loss of keystone species may be influenced by the ability of these redundant species to compensate and assume similar roles as the keystone species. Compensation for the loss of a keystone predator occurred relatively quickly in a rocky intertidal habitat, and was considered an important contributor to community stability (Navarrete and Menge 1996). In contrast to these findings, experiments by Ernest and Brown (2001) showed that compensation for the loss of kangaroo rats required almost 20 years.

2.4 THE ROLE OF SPECIES INTERACTIONS IN COMMUNITY ECOLOGY AND ECOTOXICOLOGY

> *No living thing is so independent that its abundance and distribution are unaffected by other species.* (Brown and Lomolino 1998)

Considerable research in community ecology is devoted to assessing the relative importance of biotic interactions on distribution and abundance of organisms. As discussed in Chapter 1, while many ecologists define communities by the strength of species interactions, determining the role of competition, predation, mutualism, etc. in community regulation is challenging. Although the evolutionary consequences of competition can be studied at broad scales by measuring character displacement and resource partitioning, these studies cannot demonstrate that competition regulates communities (Schluter and Ricklefs 1993). Despite acrimonious debate among community ecologists over the importance of species interactions, most would agree that positive and negative interactions are common in nature. For example, all heterotrophic organisms necessarily interact with their food supply. However, we do not always know if these interactions significantly influence the abundance or distribution of prey species relative to other factors. In the following sections we will show that contaminants have the potential to change the outcome of species interactions and therefore influence community structure.

Although there is empirical support for the hypothesis that species interactions are common and can play a pervasive role in structuring communities (Diamond 1978; Schoener 1983; Menge and Sutherland 1987), the effects of contaminants on species interactions have been largely ignored by ecotoxicologists. This is somewhat surprising given the prominent role that research on predation, competition, mutualism, etc. has played in basic community ecology. Previous reviews that focused on aquatic ecosystems (Sandheinrich and Atchison 1990; Clements 1997) showed that chemical stressors frequently alter the outcome of species interactions. We suggest that the failure to consider indirect effects of contaminants on species interactions is a major limitation of single species toxicity tests.

2.4.1 DEFINITIONS

Species interactions in natural systems are generally defined by the direction and magnitude of effects (Table 2.3). Although most basic research on species interactions has focused on predation and competition, other types of interactions occur in communities and may be affected by exposure to contaminants. In particular, strong mutualistic interactions, such as those observed in obligate plant-pollinator systems, may be especially sensitive to chemical stressors. One potential limitation to understanding the importance of species interactions in nature has been the emphasis on simple pairwise interactions. A review of 1253 papers published in *Ecology* between 1981 and 1990 showed that >60% considered only one or two species (Kareiva 1994). The emerging view from contemporary ecologists is that higher order interactions or interaction modifications are probably common in natural systems. Trophic cascades are probably the best examples of higher order interactions that have been studied in aquatic communities. Another noteworthy example involves defensive strategies that some plants employ to reduce herbivory. Plants produce a variety of chemicals designed to reduce the incidence of attack by herbivores. Some plants have significantly improved this defensive strategy and 'enlisted' the support of other species. Kessler and Baldwin (2001) showed that emissions of volatile organic compounds by plants during attack by herbivores actually attracted insect predators, thus reducing the number of herbivores by 90%. Identifying higher order interactions in nature will require that ecologists significantly expand the scope of their investigations beyond typical pairwise studies. The greater challenge will be to determine when these complex interactions play an important role in organizing community structure.

Table 2.3. Types of species interactions considered in community ecology. Interactions between two species may be positive (+), negative (−), or neutral (0)

Type of interaction	Effects on species A	Effects on species B
Competition	−	−
Predation	−	+
Parasitism	−	+
Mutualism	+	+
Commensalism	+	0

2.4.2 EXPERIMENTAL DESIGNS FOR STUDYING SPECIES INTERACTIONS

The long history of theoretical research on species interactions has provided an important conceptual framework for designing laboratory and field studies. Relatively simple mathematical models for predation and competition predict how changes in abundance of one species will influence abundance of another species. While verifying these models with experimental studies has proved challenging, manipulations that involved removal or addition of species have provided the most convincing evidence for the importance of competition and predation. A variety of enclosure and exclosure experiments have been conducted in aquatic and terrestrial habitats to quantify species interactions in the field. Key strengths of manipulative experiments are the potential for replication (thus allowing the appropriate use of inferential statistics) and the ability to control confounding variables. One of the more basic questions in studies of competition involves assessing the relative importance of interspecific and intraspecific interactions. Different experimental designs have been used by ecologists to measure the strength of interactions within and between species (Table 2.4). An additive experimental design allows researchers to determine if the presence of a competitor has any effect on a second species, all other factors being equal. This design would be especially useful for studying impacts of an exotic species on a native species (Fausch 1998). A substitutive experimental design holds total density constant and allows researchers to quantify the importance of interspecific competition relative to intraspecific competition. This design would be most appropriate for assessing the effects of contaminants on species interactions.

Because field experiments are often limited in spatial and temporal scale, some researchers advocate the use of natural experiments for assessing the role of species interactions (Diamond 1986). The merits of field experiments and natural experiments are discussed in Chapter 4. Natural experiments often involve

Table 2.4. Two types of experimental designs used to assess the importance of interspecific and intraspecific competition. The table shows the number of individuals that would be included in different treatments for additive and substitutive experimental designs. Additive designs allow for assessment of the presence of a competitive effect. Substitutive designs allow for the quantification of the magnitude of this effect relative to intraspecific competition. (After Fausch 1998)

Design	Treatment 1	Treatment 2	Treatment 3
Additive			
Density of species A	5	5	
Density of species B		5	5
Substitutive			
Density of species A	10	5	
Density of species B		5	10

comparison of abundances, morphological features, and habitat use of species in sympatric and allopatric populations. For example, if competition played an important role in community organization, we would expect that morphological features related to resource use (e.g. beak size in the Galapagos finches is related to feeding habits) would show greater dissimilarity in sympatric populations compared with allopatric populations. This comparative approach has been especially effective for assessing the long-term evolutionary consequences of species interactions over broad spatial scales.

Experimental designs for assessing the influence of contaminants on species interactions add another layer of complexity because they require manipulation of both contaminant levels and predator/competitor abundances. Accomplishing this in the field will be difficult in many types of communities. Previous studies have compared the importance of species interactions in different habitats or under different levels of environmental stress (Menge and Sutherland 1987; Peckarsky, Horn and Statzner 1990). Conducting species enclosure or exclosure experiments at sites with and without contaminants would allow researchers to determine if stressors modified the outcome of species interactions (Clements 1999).

2.4.3 THE INFLUENCE OF CONTAMINANTS ON PREDATOR–PREY INTERACTIONS

Research measuring effects of contaminants on predator–prey interactions falls into two general categories. Some studies consider the ecological consequences associated with alterations in predation intensity. For example, contaminant-induced changes in predation in communities regulated by top-down effects may alter the structure of lower trophic levels. Others studies are primarily concerned with developing a mechanistic understanding of how contaminants influence predator–prey interactions. Many of these predominantly laboratory studies have attempted to relate changes in prey capture efficiency or predatory avoidance to individual bioenergetics.

Much of the laboratory and field research on predator–prey interactions has considered alterations in prey abundance due to direct mortality. However, a more subtle influence on prey populations, which may be more common in some systems, is predator-induced alterations in prey behavior. Changes in prey foraging rates due to predator avoidance may have important consequences for prey fitness (Ball and Baker 1995, 1996). Studies in aquatic systems have shown that prey organisms will alter their behavior in response to biochemical cues emitted by predators (Stirling 1995). Peckarsky and McIntosh (1998) reported that mayflies responded to fish odors by reducing the time spent grazing, resulting in lower size at emergence and reduced fecundity. Increased algal biomass in experimental streams where mayflies were subjected to these chemical cues resulted in a ‘behavioral trophic cascade.’ These subtle responses of prey to predators will be much more difficult to detect than direct prey mortality.

Table 2.5. Behavioral characteristics of predators and prey known to be sensitive to contaminant exposure

Predator behavior	Prey behavior
Prey selection	Predator detection
Searching ability for prey	Predator avoidance and escape responses
Capture and handling time of prey	Defense mechanisms against predators

Contaminants may influence various aspects of predation, and mechanistic studies of predator–prey interactions generally focus on behavioral changes in either predators or their prey (Table 2.5). In order for a predator to feed, it must locate, select, capture, and handle its prey. Any one of these behaviors may be influenced by exposure to contaminants. Predators generally rely on visual, olfactory, and/or auditory cues to locate prey species. Prey selection is often an immediate behavioral response to prey abundance and availability; however, items included in the diet of a predator may be ultimately determined by costs and benefits. Finally, prey capture is a function of predator efficiency (the number of captures per attack) and handling time. Assuming that diet is influenced by natural selection, we expect that prey are selected to maximize caloric gains and minimize expenditures and risks associated with foraging. These basic predictions of the optimal foraging theory have been demonstrated in a variety of organisms including fish, birds, and mammals. Because optimal foraging theory integrates several important aspects of prey selection, capture, and handling, it provides a useful conceptual framework from which to evaluate stressor-induced changes in diet.

Not surprisingly, most field studies of contaminant effects on predator–prey interactions tend to focus on the consequences of reduced foraging success, but are unable to demonstrate clear mechanistic explanations. Field studies of birds have shown reduced foraging success in areas contaminated by organophosphate pesticides compared with uncontaminated habitats (Grue, Powell and McChesney 1982). These reductions in feeding may cause lower growth rates of adults or poor survival of dependent fledglings. However, because pesticides have both direct and indirect effects, it is often difficult to determine if these changes are a result of poor performance by the birds or reduced prey abundance.

Some researchers have attempted to distinguish the direct toxicological effects of contaminants from the indirect effects due to reduced prey abundance. The best examples of this research are from large-scale studies of bird populations exposed to pesticides. Aerial application of insecticides to control grasshoppers in grasslands of the US often exceed 1 million hectares per year (USDA 1987). Because grasshoppers and other non-target species are important prey items for many grassland birds, indirect effects are expected. Furthermore, the breeding season of many birds coincides with peak abundance of grasshoppers, the period when sprays are most likely to occur. Fair, Kennedy and McEwen (1995) measured the direct and indirect effects of the insecticide carbaryl on killdeer (*Charadrius vociferous*) in a large-scale experimental study in North Dakota. Despite dramatic reductions in abundance of grasshoppers and other prey species, killdeer foraging rate was actually greater in sprayed plots compared with controls. Increased foraging rate was attributed to greater numbers of available prey resulting from prey immobilization after pesticide exposure. The increased availability of exposed prey species creates the intriguing possibility that killdeer could receive a large dose of carbaryl while foraging on intoxicated prey.

Mechanistic-based studies of contaminant effects on predator–prey interactions have generally been restricted to the laboratory (Table 2.6). In order to distinguish effects on predator foraging from prey avoidance and escape responses, many experiments focus on behavior of either predators *or* their prey. These experiments have been criticized because they fail to consider the ecological consequences of alterations in predator–prey interactions and because they do not pose hypotheses that can be tested in the field. Sandheinrich and colleagues (Sandheinrich and Atchison 1989, 1990; Bryan, Atchison and Sandheinrich 1995) have conducted some of the most comprehensive analyses of contaminant effects on predator–prey interactions. Their focus on behavioral ecology has provided a solid mechanistic understanding of how contaminants affect various aspects of foraging success.

Equally important in determining the outcome of predator–prey interactions are changes in vulnerability of prey species to predation. The ability of an organism to detect, avoid, escape from or defend itself from predators is likely to be influenced by contaminant exposure. The majority of studies that have exposed both predators and prey species to chemical stressors have shown that prey vulnerability is increased (Beitinger 1990). Similarly, much of the research in terrestrial and wildlife populations has reported that alterations in the behavior of prey species, such as increased activity, will increase susceptibility to predation (Martin *et al*. 1998). Buerger *et al*. (1991) observed increased predation on birds exposed to pesticides compared with unexposed individuals. It was unclear if greater susceptibility to predation resulted from inability to detect or avoid predators. Lefcort *et al*. (1998) reported that exposure of Columbia spotted frog tadpoles (*Rana luteiventris*) to metals decreased predator avoidance response. In a subsequent study, Lefcort *et al*. (1999) showed that predation-induced shifts in habitat use by *R. luteiventris* decreased ingestion of metal-rich sediments and increased ingestion by competing snails. In a community-level assessment of predator impacts, Clements (1999) reported that several macroinvertebrate species collected from a metal-polluted habitat were more sensitive to stonefly predation than those collected from an unpolluted stream. These results suggest that alterations in predator–prey interactions may occur as a result of previous exposure to stressors.

In a novel experiment that investigated the influence of cadmium on foraging success, Wallace *et al*. (2000) exposed grass shrimp (*Palaeomonetes pugio*) to

Table 2.6. Examples of experiments conducted with fish and invertebrates investigating the effects of chemical stressors on predator–prey interactions

Predator	Prey	Stressor	Result	Proposed mechanism	Reference
Brook trout	Atlantic salmon	Organophosphate	Increased predation	Impaired learning ability of prey	Hatfield and Anderson (1972)
Largemouth bass	Mosquitofish	Gamma radiation	Increased predation	Abnormal behavior of prey	Goodyear (1972)
Largemouth bass	Mosquitofish	Mercury	Increased predation	Impaired escape behavior of prey	Kania and O'Hara (1974)
Largemouth bass	Fathead minnows	Cadmium	Increased predation	Greater prey vulnerability	Sullivan *et al*. (1978)
Largemouth bass	Mosquitofish	Ammonia	Decreased predation	Lower prey consumption	Woltering, Hedtke and Weber (1978)
Largemouth bass	Daphnia	Pentachlorophenol	Decreased predation	Lower prey capture rate	Brown *et al*. (1987)
Smallmouth bass	Daphnia and tubificids	Acidification	Decreased predation	Lower visual acuity and reduced capture success	Hill (1989)
Bluegill	Daphnia, Hyalella, and damselflies	Copper	Decreased predation	Lower capture success and increased handling time	Sandheinrich and Atchison (1989)

Atlantic salmon	Brine shrimp	Fenitrothion	No significant effects	No change in capture success; increased reactive distance	Morgan and Kiceniuk (1990)
Rockfish	Chinook salmon	Fungicide	Increased predation	Greater prey susceptibility	Kruzynski and Birtwell (1994)
Bluegill	Daphnia	Cadmium	Lower predator growth	Lower attack rates	
Stonefly	Macroinvertebrate communities	Copper	Increased predation	Greater vulnerability of prey	Clements Cherry and Cairns (1989)
Stonefly	Macroinvertebrate communities	Mixture of heavy metals	Increased predation	Greater vulnerability of prey	Kiffney (1996)
Hydra	Daphnia	Lindane	Variable results	Differential effects on prey recruitment	Taylor *et al*. (1995)
Turbellarian	Isopod	Cadmium	Reduced predation	Lower predator capture or reduced hunger	Ham, Quinn and Pascoe (1995)
Rotifer	Rotifer	Pentachlorophenol	Increased risk of predation	Greater prey swimming speeds and increased encounter rates with predators	Preston, Cecchine and Snell (1999)
Grass shrimp	Brine shrimp	Cadmium	Lower predation	Reduced capture success	Wallace *et al*. (2000)

prey organisms collected from contaminated sites in the Hudson River (Foundry Cove, NY). Experiments showed that prey capture was significantly reduced in predators exposed to cadmium compared with unexposed organisms. These researchers also showed that capture success decreased with body burdens of cadmium and with the fraction of metals bound to high molecular weight proteins (Fig. 2.8). The significance of this study is that environmentally realistic levels of a contaminant in the field significantly altered the outcome of predator–prey interactions.

In summary, the majority of studies attempting to measure the influence of contaminants on predator–prey interactions have shown significant effects. In some instances, effects were observed at concentrations below those considered toxic, based on single species toxicity tests (Sullivan *et al*. 1978; Clements, Cherry and Cairns 1989; Sandheinrich and Atchison 1990; Ham, Quinn and Pascoe 1995; Kiffney 1996). These findings highlight not only the sensitivity of behavioral endpoints to contaminants but also the inadequacy of testing procedures based exclusively on single species. This does not imply that results of single species toxicity tests are totally ineffective for predicting indirect effects. The most consistent pattern that emerges from an analysis of these data is that the outcome of predator–prey interactions is dependent on the relative susceptibility of predators and prey to a particular stressor. Thus, information on species-specific differences in sensitivity derived from single species tests may provide some insight into the direction of effects (e.g. increased or decreased predation); however, understanding the magnitude and ecological consequences of these effects relative to

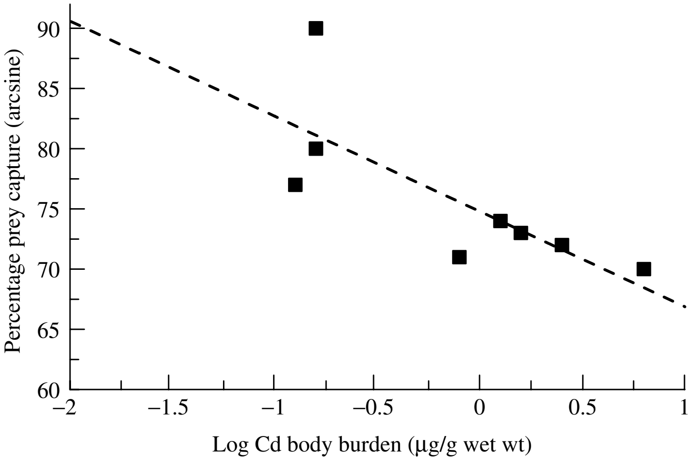

Fig. 2.8. The influence of cadmium levels in grass shrimp (*Palaeomonetes pugio*) on prey capture ability. Predators fed cadmium-contaminated prey showed reduced capture success compared with unexposed predators. (Modified from Figure 5 in Wallace *et al*. 2000)

direct toxicity will require integration of field experiments with mechanistic-based laboratory research.

2.4.4 THE INFLUENCE OF CONTAMINANTS ON COMPETITIVE INTERACTIONS

While the evidence that predation is an important organizing force in communities is generally unequivocal, the role of competition in nature has been the subject of intense debate. In contrast to the direct and readily observable effects of predation, competition is generally much more subtle and difficult to quantify. While predation almost invariably involves the removal of individuals from a population, effects of competition may include habitat shifts, changes in feeding habitats, reduced growth, and delayed reproduction. Ecologists recognize that these subtle changes have important consequences for fitness, but there is serious disagreement over their importance relative to abiotic factors.

In general, relatively few studies have measured the influence of contaminants on competitive interactions. Early research on competition and chemical stressors was initiated by Antonovics, Bradshaw and Turner (1971) and their classic studies of metal tolerance in plants (see Newman 2001 for a detailed description of these experiments). Observations that metal-tolerant species performed poorly when grown on uncontaminated soils suggested these species were at a competitive disadvantage. Hickey and McNeilly (1975) measured competitive interactions in four species of metal-tolerant plants. Results showed that fitness and competitive ability of tolerant species was significantly lower than for intolerant species. Taylor, Johnson and Anderson (1994) report that alterations in forest communities due to air pollution may result from both direct phytotoxic effects and changes in competitive ability. They suggest that phytotoxicity can reduce growth and ability to acquire resources, thus changing competitive relationships among dominant species.

Several studies have tested the hypothesis that acidification can alter competitive interactions among species. Hunter *et al*. (1986) measured growth rates of black ducks (*Anas rubripes*) in acidic and non-acidic ponds. They noted significant overlap in the diets of ducklings and fish and speculated that the higher growth rates of ducks in acidic ponds resulted from the elimination of fish competitors. Observations of tree frog populations (*Hyla andersonii*) showed that the distribution of this species was primarily limited to acidic ponds (Pehek 1995). Competition experiments between *H. andersonii* and two other anuran species tested the hypothesis that acidity created a refuge from predation for this acid-tolerant species. Despite strong competitive interactions among the three species, there were no differences in breeding success between low ($pH = 3.9$) or ambient ($pH = 6.2$) treatments. Graham and Vinebrooke (1998) conducted exclosure experiments to investigate trade-offs between resistance to grazing and competitive ability in periphyton communities from acidified lakes. Certain algal growth forms are known to be highly sensitive to grazing and competition. While filamentous growth forms generally outcompete closely attached, adnate species for light and nutrients, these species are generally more sensitive to herbivory. Graham and Vinebrooke developed a conceptual model to contrast how recovery of grazers and improvements in water quality in acidified lakes differentially affected these growth forms (Fig. 2.9). They suggest their model can be used to understand the relationship between chemical and biological recovery in acidified lakes.

Most studies of the influence of chemical stressors on competition have either measured changes in population abundance in the field or focused on mechanisms in the laboratory. For example, Blockwell *et al.* (1998) developed a laboratory bioassay to measure the effects of several contaminants on competition between amphipods (*Gammarus pulex*) and isopods (*Asellus aquaticus*). Results showed that effects of the pesticide lindane on amphipod feeding rates were greater in the presence of the competitor (Fig. 2.10). While these laboratory investigations are useful for demonstrating that species interactions are sensitive to chemical stressors, they provide little context for understanding the significance of these changes in natural systems. If ecotoxicologists are to develop an understanding of the role of species interactions, integration of laboratory and field experiments is essential. Lefcort *et al.* (1999) used field and laboratory experiments to develop a mechanistic understanding of heavy metal effects on

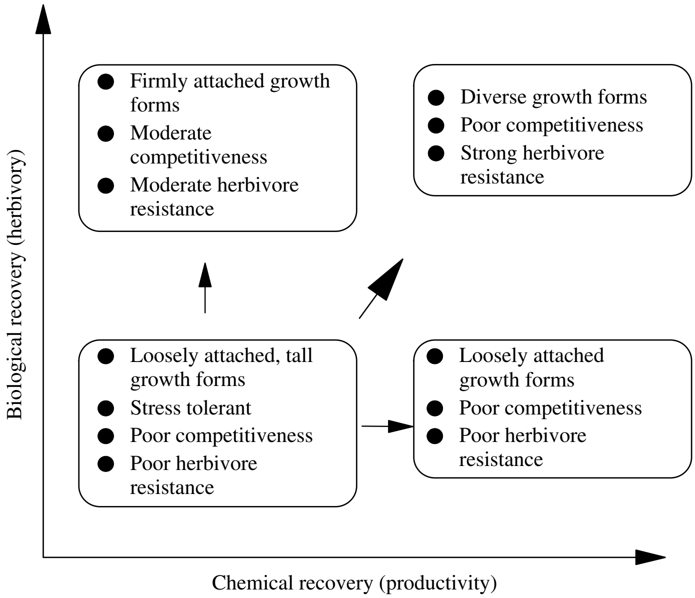

Fig. 2.9. Conceptual model contrasting how biological and chemical recovery will result in different growth forms of algae in an acidified lake. (Modified from Figure 6 in Graham and Vinebrooke 1998)

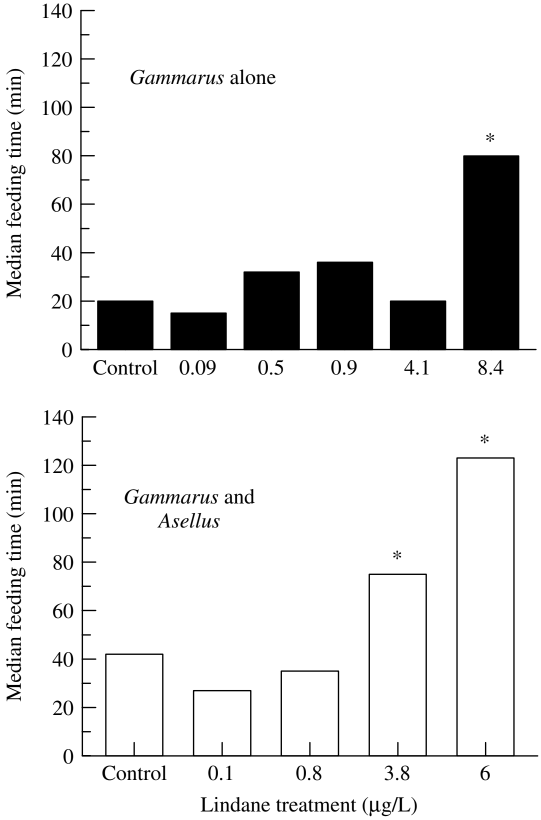

Fig. 2.10. Effects of lindane on competitive interactions between amphipods (*Gammarus*) and isopods (*Asellus*). Feeding time of *Gammarus* is significantly increased only at the highest lindane concentration in the absence of competitors. When *Asellus* is present, effects of lindane on feeding time are increased due to competitive interactions. *Significantly different from controls ($P = 0.05$). (Data from Tables 1 and 3 in Blockwell *et al.* 1998)

competition between snails (*Lymnaea pulustris*) and spotted frogs (*Rana luteiventris*). Results showed that in the absence of heavy metals, tadpoles were able to reduce snail recruitment. However, because tadpoles were more sensitive to metals than snails, the presence of metals eliminated this competitive advantage and had a net positive effect on snails. This research was especially significant because it not only described ecological changes associated with altered competitive interactions but it also identified the mechanisms responsible for these interactions. Contaminant-induced changes in competition have also been observed in terrestrial communities. Sheffield and Lochmiller (2001) exposed a small mammal community to diazinon in replicate 0.1 ha (32 × 32 m) enclosures.

Results showed that the normally strong competitive interactions between hispid cotton rats (*Sigmodon hispidus*) and prairie voles *(Microtus ochrogaster*) were altered by insecticide exposure that favored the competitively inferior species.

2.4.5 SUMMARY

As the previous 20 years of experiments in ecology have shown, demonstrating that predation and competition are important organizing forces in communities has been difficult. Quantifying the influence of chemical stressors on species interactions will be especially challenging and may not be possible in many systems because of difficulties conducting experiments at appropriate spatial and temporal scales. However, there is strong evidence that species interactions are context-dependent and that environmental factors will determine the intensity and outcome of these interactions. If community ecotoxicologists accept that species interactions are important, then some focused research should be directed at understanding the influence of contaminants on these interactions. Because of the sensitivity of behavioral endpoints to contaminants it may be possible to use behavioral responses as an assay to measure species interactions. Clearly, behavioral avoidance of predators is adaptive, and alteration of this response would be detrimental to populations in the field. Thus, one relatively simple test would be to measure behavioral avoidance in the presence or absence of chemical stressors. Stirling (1995) developed a 'behavioral bioassay' with Daphnia to detect the presence of predatory fish. Similar experiments investigating alterations in behavioral responses in other communities could provide an efficient way to assess the indirect effects of chemical stressors.

2.5 ENVIRONMENTAL FACTORS AND SPECIES INTERACTIONS

After several decades of attempting to identify individual factors that organize communities, ecologists now accept that multiple and often interacting factors are most likely responsible for the patterns observed in nature. There is also general agreement that the importance of biotic and abiotic processes vary with location, trophic level, and spatial scale. Simple theoretical treatments of the relative importance of disturbance, environmental variability, or species interactions have been replaced by more sophisticated models that integrate each of these processes. In a 10-year analysis of factors that organize stream fish communities, Grossman *et al*. (1998) determined that environmental variation was much more important than predation or competition. There is also increased awareness that environmental factors can interact with biotic processes in complex and often unpredictable ways. Peckarsky, Horn and Statzner (1990) reported that the role of predation in community regulation decreased with environmental harshness. Although ecologists have long recognized the direct influence of abiotic factors on populations, there have been few attempts to determine how these environmental characteristics influence species interactions. Dunson and Travis (1991) attribute this shortcoming to a cultural gap between community ecologists and physiologists. A similar cultural gap between ecologists and toxicologists may account for our poor understanding of how contaminants influence species interactions.

Recognition that the 'winners' and 'losers' in resource competition depend on environmental conditions is nothing new. Indeed, early laboratory experiments investigating species interactions showed that the outcome of competition was influenced by abiotic conditions (Park 1954). Dunson and Travis (1991) provide a conceptual framework for fish communities, suggesting that the ability of an organism to tolerate physiological stress is inversely related to its competitive ability. They argue that in addition to limiting the pool of species in a specific area, abiotic factors may also determine the outcome of species interactions. By exposing closely related species to a variety of stressors, they show that differences in physiological tolerance can strongly influence resource competition. This finding has significant implications for ecotoxicological investigations because it suggests that species-specific differences in tolerance to chemical stressors may be related to differences in competitive ability.

Some researchers have taken exception to the emerging paradigm that competitive interactions are reduced and coexistence is favored in harsh environments. Because environmental harshness may directly reduce population growth, the opportunities for coexistence in stressful environments may be limited. Chesson and Huntly (1997) present a model that accounts for both the positive effects of reduced competition and negative effects of stress in harsh environments. Results show that the ability of a population to tolerate competition may be reduced in harsh environments. In other words, lower levels of competition may have disproportionate effects on populations when species are competing for resources in harsh environments. These are the types of changes we would expect to see in response to chemical stressors.

2.5.1 ENVIRONMENTAL STRESS GRADIENTS

Menge and Sutherland's (1987) model of community regulation is a promising development in the field of ecology with direct applications in ecotoxicology. The Menge and Sutherland (hereafter, MS) model presents a conceptual framework of community organization that recognizes the importance of disturbance, competition, and predation along gradients of environmental stress. The model integrates several previous attempts to synthesize factors that determine community organization, including Hairston, Smith and Slobodkin's (1960) trophic model and the intermediate disturbance hypothesis. Although developed in marine rocky intertidal systems, Menge and Sutherland suggest that their model could be applied to a variety of terrestrial and aquatic habitats. More importantly, because environmental stress gradients may include physical and chemical stressors, the model is relevant to the study of contaminants.

One major goal of the MS model is to provide a framework for testing the hypothesis that communities respond predictably to variation in disturbance, competition, and predation. The model also examines how these processes vary along a gradient of environmental stress (Fig. 2.11). The stress gradient may be physical (e.g. waves crashing into organisms on the rocky intertidal shore), chemical (e.g. exposure to contaminants), or physiological (e.g. temperature and desiccation stress of organisms exposed during low tide). Important community responses to changes in the relative importance of disturbance, competition, and predation include species diversity, food chain length, and trophic complexity. The MS model predicts that predation will be a major regulator of communities under conditions of low environmental stress, whereas competition plays an increasingly important role at intermediate levels of stress. Under harsh environmental conditions, the importance of these biotic interactions will diminish and communities will be controlled largely by disturbance. The model also considers the influence of trophic level and recruitment on these processes.

The strongest support for the MS model is from rocky intertidal communities where the primary limiting resource is space (Menge and Sutherland 1987).

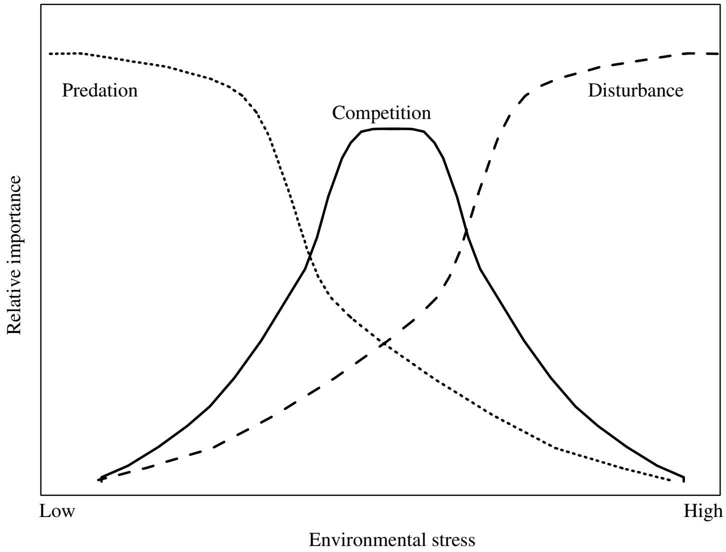

Fig. 2.11. Conceptual model showing the influence of environmental stress on the relative importance of species interactions. At low levels of environmental stress, predation is considered the major factor regulating community structure. As environmental stress increases, predators become less effective and interspecific competition regulates the community. The role of species interactions is generally reduced under high stress conditions. Based on this model, we expect that contaminants would reduce the importance of species interactions in a community. (Modified from Figure 4 in Menge and Sutherland 1987)

Attempts to verify this model in more complex systems have met with mixed success. Locke (1992) analyzed zooplankton communities from acidified lakes and found that only three of 10 studies showed the expected increase in species richness at intermediate levels of pH stress. In a subsequent study, Locke and Sprules (1994) analyzed zooplankton communities from 46 lakes (pH range = 3.8 to 7.2) sampled in the 1970s and again in 1990. The results supported two of the four predictions of the MS model (increased food web complexity and food chain length with stress). The presence of tolerant fish predators in some acidic lakes was cited as a potential explanation for the poor performance of the model. The relationship between physical disturbance and chemical stressors will be described in Chapter 6.

Despite relatively weak support in lentic communities, the MS model should be tested in other aquatic and terrestrial systems. The MS model is of

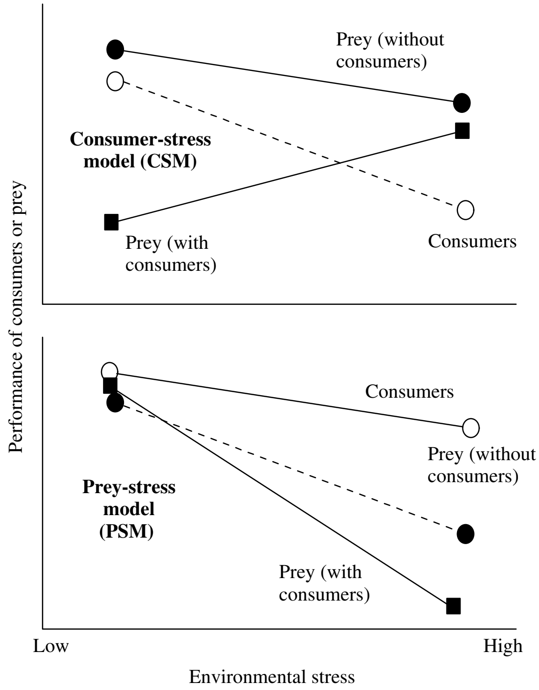

Fig. 2.12. Consumer-stress and prey-stress models showing expected differences in performance of consumers and prey based on differences in sensitivity to stress. If consumers are more sensitive to stress than prey species, the CSM predicts that abundance of prey species will increase and abundance of consumers will decrease along a stress gradient. If prey species are more sensitive, the PSM predicts that abundance of prey will decrease more in the presence of predators. (Modified from Figure 2 in Menge and Olson 1990)

particular relevance to ecotoxicology because it can be applied directly to chemical stressors. One key requirement is to locate systems with well-defined stressor gradients, a task familiar to researchers conducting environmental assessments of contaminants. Clearly one of the critical questions that must be addressed before the MS model can be applied to the study of contaminants is how effects of physical disturbances will compare with those of chemical stressors.

A refinement of the MS model that may have greater applicability to ecotoxicology was proposed by Menge and Olson (1990). They distinguish between two types of environmental stress models: consumer stress models (CSMs) and prey stress models (PSMs) (Fig. 2.12). They propose that the influence of environmental stress on the outcome of consumer–resource interactions is a result of differences in species-specific sensitivity. If consumers are more sensitive to the stressor than their prey, as predicted by CSMs, consumer effects should be reduced in stressful habitats. Conversely, if prey are more sensitive to the stressor, as predicted by PSMs, consumers should have greater effects on prey populations in stressed habitats. Results shown in Table 2.6 indicate that there is support for both PSMs and CSMs in the literature. Similar models could be developed to predict the outcome of competitive interactions based on species-specific sensitivity to other environmental stressors (Dunson and Travis 1991).

REFERENCES

Antonovics J, Bradshaw AD and Turner RG (1971). Heavy metal tolerance in plants. *Adv Ecol Res* **7**: 1–85.

Ball SL and Baker RL (1995). The non-lethal effects of predators and the influence of food availability on life history of adult *Chironomus tentans* (Diptera: Chironomidae). *Freshw Biol* **34**: 1–12.

Ball SL and Baker RL (1996). Predator-induced life history changes: antipredator behavior costs or facultative life history shifts? *Ecology* **77**: 1116–1124.

Beitinger TL (1990). Behavioral reactions for the assessment of stress in fishes. *J Great Lakes Res* **16**: 495–528.

Blockwell SJ, Taylor EJ, Jones I and Pascoe D (1998). The influence of fresh water pollutants and interaction with *Asellus aquaticus* (L.) on the feeding activity of *Gammarus pulex* (L.). *Arch Environ Contam Toxicol* **34**: 41–47.

Brooks JL and Dobson SI (1965). Predation, body size and composition of plankton. *Science* **150**: 28–35.

Brown JA, Johannes PH, Colgan PW and Mathers RA (1987). Impairment of early feeding behavior of largemouth bass by pentachlorophenol exposure: a preliminary assessment. *Trans Am Fish Soc* **116**: 71–78.

Brown JH (1981). Two decades of homage to Santa Rosalia: toward a general theory of diversity. *Amer Zool* **21**: 877–888.

Brown JH and Heske EJ (1990). Control of a desert–grassland transition by a keystone rodent guild. *Science* **250**: 1705–1707.

Brown JH and Lomolino MV (1998). *Biogeography* (2nd edn). Sinauer Associates, Inc., Sunderland, MA.

Brown JH and Munger JC (1985). Experimental manipulation of a desert rodent community: Food addition and species removal. *Ecology* **66**: 1545–1563.

Bryan MD, Atchison GJ and Sandheinrich MB (1995). Effects of cadmium on the foraging behavior and growth of juvenile bluegill, *Lepomis macrochirus*. *Can J Fisheries Aquat Sci* **52**: 1630–1638.

Buerger TT, Kendall RJ, Mueller BS, De Vos T and Williams BA (1991). Effects of methyl parathion on northern bobwhite survivability. *Environ Toxicol Chem* **10**: 527–532.

Carpenter RC (1990). Mass mortality of *Diadema antillarium*. I. Long-term effects on sea urchin population-dynamics and coral reef algal communities. *Mar Biol* **104**: 67–77.

Chesson P and Huntly N (1997). The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *Am Nat* **150**: 519–553.

Clements WH (1997). Effects of contaminants at higher levels of biological organization in aquatic systems. *Rev Toxicol* **1**: 269–308.

Clements WH (1999). Metal tolerance and predator–prey interactions in benthic macroinvertebrate stream communities. *Ecol Appl* **9**: 1073–1084.

Clements WH, Cherry DS and Cairns Jr J (1989). The influence of copper exposure on predator–prey interactions in aquatic insect communities. *Fresh Biol* **21**: 483–488.

Connell JH and Orias E (1964). The ecological regulation of species diversity. *Am Nat* **98**: 399–414.

Crawley MJ and Harral JE (2001). Scale dependency in plant biodiversity. *Science* **291**: 864–868.

Diamond JM (1978). Niche shifts and the rediscovery of competition: Why did field biologists so long overlook the widespread evidence for interspecific competition that had already impressed Darwin? *Am Sci* **66**: 322–331.

Diamond J (1986). Overview: laboratory experiments, field experiments, and natural experiments. In *Community Ecology*, ed. by Diamond J and Case TJ, pp. 3–22. Harper and Row, Publishers, New York, NY.

Dunson WA and Travis J (1991). The role of abiotic factors in community organization. *Am Nat* **138**: 1067–1091.

Ernest SK and Brown JH (2001). Delayed compensation for missing keystone species by colonization. *Science* **292**: 101–104.

Fair JM, Kennedy PL and McEwen LC (1995). Effects of carbaryl grasshopper control on nesting killdeer in North Dakota. *Environ Toxicol Chem* **14**: 881–890.

Fausch KD (1998). Interspecific competition and juvenile Atlantic salmon (*Salmo salar*): on testing effects and evaluating evidence across scales. *Can J Fish Aquat Sci* **55** (Suppl 1): 218–231.

Goodyear CP (1972). A simple technique for detecting effects of toxicants or other stresses on a predator–prey interaction. *Trans Am Fish Soc* **101**: 367–370.

Graham MD and Vinebrooke RD (1998). Trade-offs between herbivore resistance and competitiveness in periphyton of acidified lakes. *Can J Fish Aquat Sci* **55**: 806–814.

Grossman GD, Ratajczak RE, Crawford M and Freeman MC (1998). Assemblage organization in stream fishes: Effects of environmental variation and interspecific interactions. *Ecol Monogr* **68**: 395–420.

Grue CE, Powell GVN and McChesney MJ (1982). Care of nestlings by wild female starlings exposed to organophosphate pesticide. *J Appl Ecol* **19**: 327–335.

Hairston NG (1959). Species abundance and community organization. *Ecology* **40**: 404–416.

Hairston Sr NG, Smith FE and Slobodkin LB (1960). Community structure, population control, and interspecific competition. *Am Nat* **94**: 421–425.

Ham L, Quinn R and Pascoe D (1995). Effects of cadmium on the predator–prey interaction between the turbellarian *Dendrocoelum lacteum* (Muller, 1774) and the isopod crustacean *Asellus aquaticus* (L). *Arch Environ Contam Toxicol* **29**: 358–365.

Hatfield CT and Anderson JM (1972). Effects of two insecticides on the vulnerability of Atlantic salmon (*Salmo salar*) parr to brook trout (*Salvelinus fontinalis*) predation. *J Fish Res Bd Can* **29**: 27–29.

Hickey DA and McNeilly T (1975). Competition between metal tolerant and normal plant populations: a field experiment on normal soil. *Evolution* **29**: 458–464.

Hill J (1989). Analysis of six foraging behaviors as toxicity indicators using juvenile smallmouth bass exposed to low environmental pH. *Arch Environ Contam Toxicol* **18**: 895–899.

Hunter Jr ML, Jones JJ, Gibbs KE and Moring JR (1986). Duckling responses to lake acidification: do black ducks and fish compete? *Oikos* **47**: 26–32.

Hutchinson GE (1959). Homage to Santa Rosalia or Why are there so many kinds of animals? *Am Nat* **93**: 145–159.

Hutchinson GE (1961). The paradox of plankton. *Am Nat* **95**: 137–145.

Interlandi SJ and Kilham SS (2001). Limiting resources and the regulation of diversity in phytoplankton communities. *Ecology* **82**: 1270–1282.

Jenkins DG and Buikema Jr AL (1998). Do similar communities develop in similar sites? A test with zooplankton structure and function. *Ecol Monogr* **68**: 421–443.

Kania HJ and O'Hara J (1974). Behavioral alterations in a simple predator–prey system due to a sublethal exposure to mercury. *Trans Am Fish Soc* **103**: 134–136.

Kareiva P (1994). Higher order interactions as a foil to reductionist ecology. *Ecology* **75**: 1527–1528.

Kessler A and Baldwin IT (2001). Defensive function of herbivore-induced plant volatile emissions in nature. *Science* **291**: 2141–2144.

Kiffney PM (1996). Main and interactive effects of invertebrate density, predation, and metals on a Rocky Mountain stream macroinvertebrate community. *Can J Fish Aquat Sci* **53**: 1595–1601.

Kruzynski GM and Birtwell IK (1994). A predation bioassay to quantify the ecological significance of sublethal responses of juvenile chinook salmon (*Oncorhynchus tshawytscha*) to the antisapstain fungicide TCMTB. *Can J Fish Aquat Sci* **51**: 1780–1790.

Landis WG, Matthews RA and Matthews GB (1996). The layered and historical nature of ecological systems and the risk assessment of pesticides. *Environ Toxicol Chem* **15**: 432–440.

Lefcort H, Meguire RA, Wilson LH and Ettinger WF (1998). Heavy metals alter the survival, growth, metamorphosis, and antipredatory behavior of Columbia spotted frog (*Rana luteiventris*) tadpoles. *Arch Environ Contam Toxicol* **35**: 447–456.

Lefcort H, Thomson SM, Cowles EE, Harowicz HL, Livaudais BM, Roberts WE and Ettinger WF (1999). Ramifications of predator avoidance: predator and heavy-metal-mediated competition between tadpoles and snails. *Ecol Appl* **9**: 1477–1489.

Locke A (1992). Factors influencing community structure along stress gradients: zooplankton responses to acidification. *Ecology* **73**: 903–906.

Locke A and Sprules WG (1994). Effects of lake acidification and recovery on the stability of zooplankton food webs. *Ecology* **75**: 498–506.

MacArthur RH and Wilson EO (1963). An equilibrium theory of insular zoogeography. *Evolution* **17**: 373–387.

MacArthur RH and Wilson EO (1967). *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ.

Martin PA, Johnson DL, Forsyth DJ and Hill BD (1998). Indirect effects of the pyrethroid insecticide deltamethrin on reproductive success of chestnut-collared longspurs. *Ecotoxicology* **7**: 89–97.

Matthews RA, Landis WG and Matthews GB (1996). The community conditioning hypothesis and its application to environmental toxicology. *Environ Toxicol Chem* **15**: 597–603.

May RM (1984). An overview: Real and apparent patterns in community structure. In *Ecological Communities: Conceptual Issues and the Evidence*, ed. by Strong DR, Simberloff D, Abele LG and Thistle AB, pp. 3–16. Princeton University Press, Princeton, NJ.

May RM and Stumpf MPH (2000). Species–area relations in tropical forests. *Science* **290**: 2084–2086.

McLaren BE and Peterson RO (1994). Wolves, moose, and tree rings on Isle Royale. *Science* **266**: 1555–1558.

Menge BA, Berlow EL, Blanchette CA, Navarrete SA and Yamada SY (1994). The keystone species concept: variation in interaction strength in a rocky intertidal habitat. *Ecol Monogr* **64**: 249–286.

Menge BA and Olson AM (1990). Role of scale and environmental factors in regulation of community structure. *Trends Ecol Evol* **5**: 52–57.

Menge BA and Sutherland JP (1987). Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *Am Nat* **130**: 730–757.

Minshall GW, Petersen Jr RC and Nimz CF (1985). Species richness in streams of different size from the same drainage basin. *Am Nat* **125**: 16–38.

Morgan MJ and Kiceniuk JW (1990). Effect of fenitrothion on the foraging behavior of juvenile Atlantic salmon. *Environ Toxicol Chem* **9**: 489–495.

Navarrete SA and Menge BA (1996). Keystone predation and interaction strength: interactive effects of predators on their prey. *Ecol Monogr* **66**: 409–429.

Newman MC (2001). *Population Ecotoxicology*. Wiley and Sons, Ltd, Chichester, UK.

Paine RT (1966). Food web complexity and species diversity. *Am Nat* **100**: 65–75.

Paine RT (1969). A note on trophic complexity and community stability. *Am Nat* **103**: 91–93.

Park T (1954). Experimental studies of interspecies competition. II. Temperature, humidity, and competition in two species of *Tribolium*. *Phys Zoo* **27**: 177–229.

Peckarsky BL, Horn SC and Statzner B (1990). Stonefly predation along a hydraulic gradient: a field test of the harsh–benign hypothesis. *Freshw Biol* **24**: 181–191.

Peckarsky BL and McIntosh AR (1998). Fitness and community consequences of avoiding multiple predators. *Oecologia* **113**: 565–576.

Pehek EL (1995). Competition, pH, and the ecology of larval *Hyla andersonii*. *Ecology* **76**: 1786–1793.

Poff NL (1997). Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *J N Am Benthol Soc* **16**: 391–409.

Power ME (1990). Effects of fish in river food webs. *Science* **250**: 811–814.

Power ME, Tilman D, Estes JA, Menge BA, Bond WJ, Mills LS, Daily G, Castilla JC, Lubchenco J and Paine RT (1996). Challenges in the quest for keystone species. *BioScience* **46**: 606–620.

Preston BL, Cecchine G and Snell TW (1999). Effects of pentachlorophenol on predator avoidance behavior of the rotifer *Brachionus calyciflorus*. *Aquat Toxicol* **44**: 201–212.

Rapoport EH (1982). *Aerography: Geographical Strategies of Species*. Pergamon Press, New York, NY.

Roughgarden J and Diamond J (1986). Overview: The role of species interactions in community ecology. In *Community Ecology*, ed. by Diamond JM and Case TJ, pp. 333–343. Harper and Row, New York, NY.

Sandheinrich MB and Atchison GJ (1989). Sublethal copper effects on bluegill, *Lepomis macrochirus*, foraging behavior. *Can J Fish Aquat Sci* **46**: 1977–1985.

Sandheinrich MB and Atchison GJ (1990). Sublethal toxicant effects on fish foraging behavior: empirical vs. mechanistic approaches. *Environ Toxicol Chem* **9**: 107–119.

Schluter D and Ricklefs RE (1993). Species diversity – an introduction to the problem. In *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*, ed. by Ricklefs RE and Schluter D, pp. 1–10. University of Chicago Press, Chicago, IL.

Schoener TW (1974). The species–area relationship within archipelagos: models and evidence from island land birds. In *Proceedings of the 16th International Ornithological Congress*, ed. by Firth HJ and Calby JH, pp. 629–642. Australian Academy of Science, Canberra.

Schoener TW (1983). Field experiments on interspecific competition. *Am Sci* **122**: 240–285.

Sheffield SR and Lochmiller RL (2001). Effects of field exposure to diazinon on small mammals inhabiting a semienclosed prairie grassland ecosystem. I. Ecological and reproductive effects. *Environ Toxicol Chem* **20**: 284–296.

Simberloff DS and Wilson EO (1969). Experimental zoogeography of islands: the colonization of empty islands. *Ecology* **50**: 278–296.

Simberloff DS and Wilson EO (1970). Experimental zoogeography of islands: a two-year record of colonization. *Ecology* **51**: 934–937.

Stirling G (1995). Daphnia behaviour as a bioassay of fish presence or predation. *Funct Ecol* **9**: 778–784.

Sullivan JF, Atchison GJ, Kolar DJ and MacIntosh AW (1978). Changes in the predator–prey behavior of fathead minnows (*Pimephales promelas*) and largemouth bass (*Micropterus salmoides*) caused by cadmium. *J Fish Res Bd Can* **35**: 446–451.

Tansley AG and Adamson RS (1925). Studies of the vegetation of the English chalk. III. The chalk grasslands of the Hampshire–Sussex border. *J Ecol* **13**: 177–223.

Taylor Jr GE, Johnson DW and Anderson CP (1994). Air pollution and forest ecosystems: a regional to global perspective. *Ecol Appl* **4**: 662–689.

Taylor EJ, Morrison JE, Blockwell SJ, Tarr A and Pascoe D (1995). Effects of lindane on the predator–prey interaction between *Hydra oligactis* Pallas and *Daphnia magna* Strauss. *Arch Environ Contam Toxicol* **29**: 291–296.

United States Department of Agriculture (1987). *Rangeland Grasshopper Cooperative Management Program, Final Environmental Impact Statement. FEIS 87-1.* Animal and Plant Health Inspection Service, Washington, DC.

Vannote RL, Minshall GW, Cummins KW, Sedell JR and Cushing CE (1980). The river continuum concept. *Can J Fish Aquat Sci* **37**: 130–137.

Wallace WG, Brouwer TMH, Brouwer M and Lopez GR (2000). Alterations in prey capture and induction of metallothioneins in grass shrimp fed cadmium-contaminated prey. *Environ Toxicol Chem* **19**: 962–971.

Wardle DA, Zackrisson O, Hornberg G and Gallet C (1997). The influence of island area on ecosystem properties. *Science* **277**: 1296–1299.

Whittaker RH (1975). *Communities and Ecosystems* (2nd edn). Macmillan, New York, NY.

Wiens JA (1984). On understanding a non-equilibrium world: myth and reality in community patterns and processes. In *Ecological Communities: Conceptual Issues and the Evidence*, ed. by Strong DR, Simberloff D, Abele LG and Thistle AB, pp. 439–457. Princeton University Press, Princeton, NJ.

Woltering DM, Hedtke JL and Weber LJ (1978). Predator–prey interactions of fishes under the influence of ammonia. *Trans Am Fish Soc* **107**: 500–504.

3 Biomonitoring and the Responses of Communities to Contaminants

3.1 BIOMONITORING AND BIOLOGICAL INTEGRITY

Biomonitoring is defined as the use of biological systems to assess the structural and functional integrity of aquatic and terrestrial ecosystems. Karr and Dudley (1981) define biological integrity as the ability of an ecosystem 'to support and maintain a balanced, integrated, adaptive community of organisms having a species composition, diversity, and functional organization comparable to natural habitats in the region'. Measurements (endpoints) used to assess biological integrity may be selected from any level of biological organization; however, historically the focus has been on populations, communities, and ecosystems. Community-level biological monitoring, which is the focus of this chapter, is based on the assumption that composition and organization of communities reflect local environmental conditions and respond to anthropogenic alteration of those conditions. A second important assumption of community-level biomonitoring is that species differ in their sensitivity to anthropogenic stressors, resulting in structural and functional changes at polluted sites.

Karr and Dudley's definition of biological integrity underscores the two most significant challenges to the development and implementation of community-level monitoring: the selection of endpoints and the identification of reference conditions. Although Karr and Dudley provide some suggestions for endpoints (e.g. species diversity and composition), there is little consensus among ecologists as to what key features of communities are the most appropriate indicators of biological integrity. There is, however, widespread agreement that no single measure will be effective and that approaches integrating several endpoints are often necessary to assess effects of contaminants.

The selection of appropriate reference sites and the determination of what exactly constitutes 'natural habitats in the region' have been equally troublesome to natural resource managers. Identifying reference conditions and separating natural variation from contaminant-induced changes are currently major areas of research interest. Community ecotoxicologists have utilized a variety of study designs to distinguish the effects of contaminants from natural variation. If natural changes in community composition are predictable and occur along well-defined gradients (e.g. the longitudinal changes in stream communities along a river continuum), then this variation can be explained using an appropriate study design and statistical analyses. In situations where natural variation is more stochastic, it may be difficult to quantify all but the most extreme examples of perturbation. Regardless, an understanding of the natural spatial and temporal variation of community structure is essential for any biomonitoring program.

Although biomonitoring studies have been conducted in almost every type of aquatic and terrestrial ecosystem, community-level assessments of contaminant effects are largely restricted to aquatic habitats. Excellent historical descriptions of the early development of biological monitoring in aquatic habitats have been published (Cairns and Pratt 1993; Davis 1995). Biological monitoring of community attributes in aquatic systems has occurred since the early 1900s. More recently, conservation biologists have begun to employ community-level monitoring techniques to estimate biodiversity and to prioritize sites for preservation. However, assessments of contaminant effects at the level of communities are much less common in terrestrial systems. We consider the lack of information on responses of terrestrial communities to contaminants to be a significant research limitation in ecotoxicology.

3.2 CONVENTIONAL APPROACHES

Conventional approaches in biological monitoring begin with a species list (or some other taxonomic category) for the study site or sampling unit. The species list consists of species names and the numbers of individuals present for each. Depending on the taxonomic group, other units besides individuals might be used, such as species biomass or groundcover. Some lists may indicate simple presence or absence from the sample instead of the actual numbers of individuals. None of the methods retain information on the spatial relationship among individuals in the community other than the implicit understanding that all organisms came from the same sampling unit. An associated sampling site is defined operationally based on tractability and the assumption of homogeneity within the site (Pielou 1969). The species being enumerated might all be associated with a particular part of the habitat or microhabitat (e.g. a benthic community) or with a specific taxonomic group (e.g. tree canopy insects). Interpretation of the resulting indices must be done thoughtfully because the data will never reflect the entire ecological community.

Species diversity or heterogeneity indices include both evenness and richness. This blending may be seen as convenient or confounding depending on one's ultimate goal. Due to the computational ease for calculating these indices, tandem computation of species richness, evenness, and diversity seems the best way of extracting the most meaningful information. A few of the more common community indices are described below, with alpha diversity (see Chapter 2) being considered the most relevant for ecotoxicological investigations. The reader is referred to Pielou (1969), May (1976), Ludwig and Reynolds (1988), Magurran

(1988), Newman (1995), and Matthews, Matthews and Landis (1998) for more detail and theory associated with these metrics.

3.2.1 INDICATOR SPECIES CONCEPT

The impacts of degraded water quality on biological communities were first noted in the early 1900s by German biologists describing effects of organic enrichment on benthic fauna. The Saprobien system of classification (Kolkwitz and Marsson 1909) distinguished three categories of streams (polysaprobic, mesosaprobic, and oligosaprobic) based on the abundance of pollution-tolerant and pollution-sensitive species. The partially subjective index was based on well-established lists of species and their observed tolerances of conditions at various distances from a waste source. Primary among the factors considered is oxygen tolerance as it strongly influences the ability of a species to flourish in the different zones below the discharge. These early attempts to characterize water quality based on presence or absence of indicator species launched a significant but highly controversial period in biological monitoring. The use of indicator species, which are defined as species known to be sensitive or tolerant to a specific class of environmental conditions, has received considerable attention in the literature (Cairns and Pratt 1993).

Although their specific life history characteristics will vary, pollution-tolerant species generally include organisms with high intrinsic rates of increase, rapid colonization ability and/or morphological and physiological adaptations that allow them to withstand exposure to toxic chemicals or habitat alteration (see Chapter 6). In contrast, pollution-sensitive species are defined as those species that are consistently absent from systems with known physical or chemical disturbances. The classic example of indicator organisms in aquatic systems, which figured prominently in the development of the original Saprobien system, are the large numbers of pollution-tolerant chironomids (Diptera: Chironomidae) and oligochaete worms that commonly replace sensitive mayflies (Ephemeroptera) and stoneflies (Plecoptera) at sites with high levels of organic enrichment.

While the notion that presence or absence of a particular species could indicate the degree of environmental degradation has intuitive appeal, there are obvious limitations with this approach. The indicator species concept has received rather unfavorable reviews in the USA (Cairns 1974). One of the most obvious shortcomings of this approach is the difficulty of defining pollution tolerance for species without resorting to inherently tautological arguments (e.g. species are defined as pollution-sensitive because they are absent from polluted habitats). The second limitation, which is considerably more serious, is the need to distinguish the relative importance of chemical stressors from the multitude of other biotic and abiotic factors that influence the presence or absence of a species. This is especially problematic in aquatic systems because many of the species which are sensitive to chemical stressors are also sensitive to other natural or anthropogenic disturbances. The absence of a pollution-sensitive species from a contaminated site provides only weak support for the hypothesis that its absence is due to contamination. Similarly, the presence of pollution-tolerant species (e.g. chironomids and oligochaetes in aquatic systems) does not necessarily imply that a site is degraded. Roback (1974) summarized his opinion of the indicator species concept, which is probably shared by many stream ecologists, stating that '. . .the presence or absence of any species in a stream indicates no more or less than the bald fact of its presence or absence'.

Before dismissing the indicator species concept we should recognize its general contributions to biological monitoring and its applications outside of water quality assessments. Although the absence of a particular species tells little about environmental conditions, its presence may be much more informative. For example, in the Pacific Northwest the endangered spotted owl (*Strix occidentalis*) is a habitat-specialist known to be highly dependent on old growth forests. Because factors other than the availability of old growth forests can influence its distribution, the *absence* of spotted owls from an area is not especially informative. However, the presence of this old growth specialist provides useful information on habitat suitability. Similarly, the presence of a species known to be sensitive to a particular type of pollutant provides strong evidence that the chemical is either not present or not bioavailable. With careful application, the indicator species concept could be employed to locate potential reference sites or to document recovery following pollution abatement. Because of the ability of some species to either acclimate or adapt to chemical stressors (Wilson 1988; Mulvey and Diamond 1991; Newman 2001), it is important to consider that tolerance developed during exposure may allow sensitive organisms to persist in polluted habitats.

The hasty abandonment of the Saprobien system and the indicator species concept is at least partially responsible for the relatively slow progress in the field of biological monitoring. Cairns and Pratt (1993) note that the unwillingness of stream ecologists to accept the indicator species concept supported the dominant viewpoint that water quality monitoring programs could focus exclusively on physical and chemical measures. Despite the poor initial support, the indicator species concept and Saprobien system are credited with initiating interest in the development of numerical criteria (Davis 1995). Furthermore, the modern approach of using indicator communities to assess environmental perturbation was at least partially inspired by this early work.

3.3 BIOMONITORING AND COMMUNITY-LEVEL ASSESSMENTS

3.3.1 SPECIES ABUNDANCE MODELS

During the early history of ecology, field biologists were satisfied to characterize communities based on extensive species lists showing the presence or absence of individual taxa. There were few attempts to quantify species abundance distributions or to propose ecological explanations for these patterns. Frank Preston's (1948) seminal paper on the 'Commonness and rarity of species' was considered a significant turning point in the maturation of community ecology. Ecologists had long observed that some species in nature are quite rare and represented by relatively few individuals whereas other species are very abundant. Preston's contribution provided one of the first opportunities to quantify this relationship.

Species abundance models are a useful way to summarize data from community surveys. Models are fit to tabulated species abundances and model parameters become the summary statistics for the data set. However, more useful information can be extracted from these models (Pielou 1975), such as estimates of the total number of species in the community. Some variables, such as the parameter α of the log series model, are commonly employed diversity indices. The steepness of species abundance curves (Fig. 3.1 top panel) suggests the evenness with which individuals are distributed among species (Tokeshi 1993). As will be shown shortly, evenness increases in the following model sequence: geometric series $<$ log series $<$ discrete lognormal $<$ broken stick.

Although many models exist (Tokeshi 1993), abundance data are commonly fit to only four models: logarithmic series, geometric series, discrete lognormal, and broken stick. All have been interpreted in the context of resource competition, with the relative species abundance being used to imply the portion of resources or niche volume secured by a species. Whether competition is a reasonable foundation for such a model depends very much on the community, species assemblage, or taxonomic group being studied. It may be very appropriate for studying an ecological guild but quite inadequate for a collection of functionally divergent species. Although explanations based on realized niche and resource allocation 'are useful in suggesting possibilities underlying community organization' (Tokeshi 1993), interpretation based on competition theory should be done cautiously (Hughes 1986). Some researchers prefer to view species abundance models as statistical models because of this loose theoretical foundation. However, the cost of such freedom from theory is a severely restricted ability to assign ecological meaning to results.

The simplest and earliest model, the geometric series (Motomura 1932), is based on the niche preemption concept (Fig. 3.1). According to this model, one species takes k^{th} of the available niche space, leaving only $1 - k$ for the remaining species to share. A second species then takes k^{th} of the remaining $1 - k$ niche space. This niche preemption sequence continues until all species have secured their portion of the available niche space. Any variation from k among species is attributed to stochasticity.

There will be a few very abundant species in such a community, as might be expected during early stages of succession in which r-selected strategies dominate or for a community associated with a severe environment in which one or a few

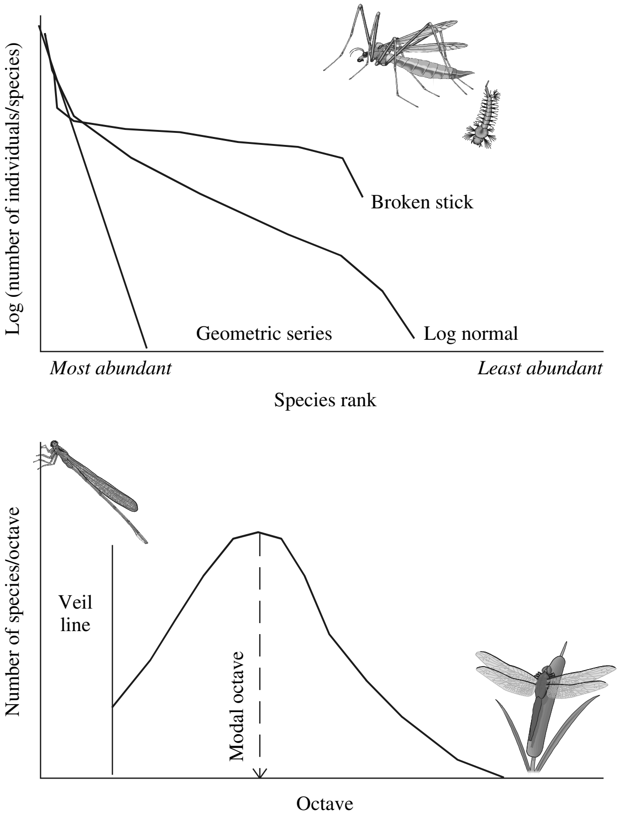

Fig. 3.1. Species abundance curves for summarizing community data. The top panel depicts three conventional models including the extremes (geometric series and broken stick) and most commonly used (lognormal) models. The bottom panel illustrates Preston's (1948) approach to analyzing species abundance data with a lognormal model. Notice that there is a veil line on the *x*-axis. For most such curves, there is some minimal count (e.g. one individual/species), below which abundance cannot be quantified. Much of the mathematics associated with Preston's analysis of the lognormal model is associated with estimating distributional parameters with such a left-truncated curve

factors determine species success (May 1976). The associated model is given in equation (3.1) (Magurran 1988).

$$N_i = kN\left[\frac{1}{1-(1-k)^S}\right][1-k]^{i-1} \tag{3.1}$$

A log series model is similar to the geometric series except that species arrive and occupy niche space randomly, not in the regular intervals as described for the geometric series. The result is a community with a few dominants and more rare species than the geometric model would predict. The curve for the log series would be intermediate between the geometric series and lognormal models in Fig. 3.1. The expected number of species with n individuals is $\alpha x^n/n$, with x being a sample size-dependent constant less than 1 and α being a community-dependent constant. The log series model is often described as the model most useful for 'samples from small, stressed, or pioneer communities' (Hughes 1986).

The discrete lognormal model fits most communities (Magurran 1988) and is often advocated as universally acceptable for species abundance modeling (May 1976). The competition theory behind it is that a species' success in occupying niche space is determined by many factors. The result is more intermediate abundance species and fewer rare species than for the geometric series model (Fig. 3.1). In contrast to the geometric series model in which r-selection strategists often dominate, this model might be more suggestive of equilibrium or K-selection strategies such as those occurring in climax or unstressed communities.

The lognormal model cannot be fit by simply calculating the central tendency and dispersion parameters because values for some observations to the left of the veil point are not known (Fig. 3.1, bottom panel). Preston (1948) speculated that lognormal distributions were truncated because of the difficulty sampling all rare species in a community and that the distribution would shift to the right with larger sample sizes. Preston developed the classic method for analyzing the truncated lognormal species abundance curve by first separating all species into abundance classes. The most convenient abundance categories were octaves, grouped by doubling in numbers such as 1 to 2, 2 to 4, 4 to 8, 8 to 16, 16 to 32 and so forth. The number of species in each octave was plotted to produce a graph similar to the bottom panel of Fig. 3.1. The octaves are often labeled relative to the modal octave, e.g. $R = 0$ denotes the modal octave, $R = -1$ denotes one octave to the left of the mode, and $R = 2$ denotes two octaves to the right of the mode. In samples containing large numbers of species, when the log abundance of species is plotted against the number of species in each category a normal distribution is obtained.

The original method of Preston (1948) or the more simplified approach of Newman (1995) can be used to estimate the distribution parameters and subsidiary information such as the estimated number of species in the community. The predicted number of species in octave $R(S_R)$ is estimated from the number of species in the modal octave (S_0) and the variance of the lognormal distribution σ^2.

Preston's lognormal distribution was found to be widely applicable for explaining the rank abundance of many taxonomic groups. Although Preston did not provide an ecological explanation for the generality of lognormal distributions in nature, other ecologists discussed the evolutionary implications. Using the broken stick model, MacArthur (1960) proposed that species abundance distributions resulted from interspecific competition and allocation of resources among species. According to this model, the niche space available to any species is allocated much as a length of stick would be if a stick were randomly snapped along its length to produce S pieces. In more formal terms, $S - 1$ points are randomly identified along the length of the stick and the stick is broken at these points. The length of each segment reflects the amount of niche space (inferred from species abundance) allocated to each species. In such a model, the niche space would be randomly distributed among the S species to produce a community with many moderately abundant species but relatively few rare or extremely abundant species (Fig. 3.1 bottom panel). As such, this model is most likely to describe an equilibrium assemblage of very similar species (e.g. a specific guild in a climax community).

Magurran (1988) provides estimators of the expected number of individuals (N_i) for the i^{th} most abundant species (equation (3.2)) and the expected number of species (S_n) for the n^{th} abundance class (equation (3.3)) based on the broken stick model.

$$S_n = S_0 \mathrm{e}^{-\left(\frac{1}{\sqrt{2\sigma^2}}\right)^2 R^2} \tag{3.2}$$

$$N_i = \frac{N}{S} \sum_{n=i}^{S} \frac{1}{n} \tag{3.3}$$

Which specific model best fits the data statistically can be determined by deferring to the advice of experts (e.g. May's preference for the lognormal model), or by applying conventional goodness-of-fit methods. Magurran (1988), Ludwig and Reynolds (1988), and Newman (1995) provide the details for formally assessing relative model goodness-of-fit. Regardless of how relative model goodness-of-fit is examined, one is ultimately faced with the difficult task of deciding which model best fits the ecological reality of the species assemblage being studied.

In general, attempts to seek underlying biological processes for lognormal distributions were unsuccessful. Recent analyses of lognormal distributions and MacArthur's broken stick model have revealed their statistical inevitability (Gotelli and Graves 1996). Despite the lack of an evolutionary explanation, comparisons of the distribution of individuals among species is a powerful tool in community ecology and ecotoxicology. Because of differences in sensitivity among species, shifts in the relative abundance of tolerant and sensitive species at polluted sites should be reflected in the shape of species abundance curves (Fig. 3.2). As the classic example, Patrick (1971) used the shapes of such curves to interpret shifts in diatom communities impacted by pollution. Because the shape of the lognormal distribution also reflects whether the contaminant is toxic or has a stimulatory influence (e.g. nutrient enrichment), the curves could be employed to distinguish between stressors. Thus, species abundance models extract more information than simple species lists, but are applied much less frequently than diversity, evenness, and richness metrics.

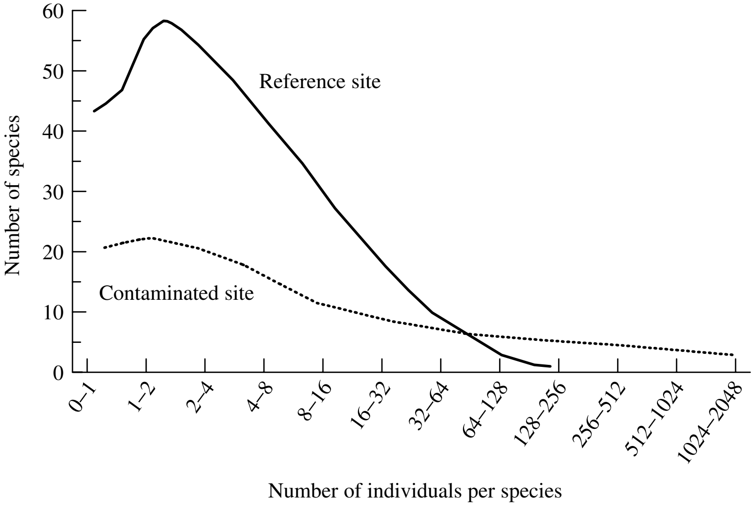

Fig. 3.2. The predicted rank abundance distribution of species collected from reference and polluted communities (Preston 1948). The figure shows the number of species within each abundance class. The community from the reference site approximates a lognormal distribution, whereas the community from the contaminated site is characterized by lower richness and increased abundance of tolerant species. This is a typical response of algal and benthic macroinvertebrate communities to organic pollution

3.3.2 THE USE OF SPECIES RICHNESS AND DIVERSITY TO CHARACTERIZE COMMUNITIES

3.3.2.1 Species Richness

As noted in Chapter 2, patterns of species richness across local, regional, and global scales have intrigued community ecologists for several decades. Community ecotoxicologists have routinely employed species richness as an indicator of ecological integrity. Rapport, Regier and Hutchinson (1985) include reduced species richness as one of five general indicators of the ‘ecosystem distress syndrome’ (Chapter 6). Among the scores of measures used by community ecotoxicologists to assess effects of contaminants, reduced species richness is probably the most consistent (and least controversial) response. Because of the perceived value of biodiversity to the lay public, measures of species richness also have high societal relevance.

Species richness is defined as the number of species present in a prescribed sampling unit. Richness (R) can be determined by sampling more and more individuals from a site and keeping a running tally of the number of species that appear (equations (3.4) and (3.5)). The results can be used to estimate the total number of species in the community. Plots of the cumulative number of species versus sampling effort (e.g. number of dredge hauls, km^2 searched, biomass sampled, or number of individuals captured) will show an initial rapid increase in the number of species followed by a more gradual increase until becoming asymptotic (Fig. 3.3). In most situations, this measure of species richness can be quite difficult to determine. In others, it might be undesirable to do such exhaustive sampling of a community if sampling was destructive or disruptive.

The number of species in a community can also be approximated with specific models (e.g. a lognormal model) or indices that assume specific models linking sample size (number of individuals in the sample or N) and species richness (equations (3.4) and (3.5)) (Ludwig and Reynolds 1988; Magurran 1988; Matthews, Matthews and Landis 1998). All of these methods rely on the law of frequencies (Fisher, Corbet and Williams 1943), which holds that a relationship exists between the number of species and number of individuals in any ecological community. However, the law of frequencies does not dictate a particular relationship between the numbers of species and individuals. Thus, Ludwig and Reynolds (1988) argue that, unless shown to be true, the assumption of a specific relationship between S and N in these models or metrics should be handled cautiously.

$$R_{Margal\acute{e}f} = \frac{S-1}{\ln N} \tag{3.4}$$

$$R_{Menhinick} = \frac{S}{\sqrt{N}} \tag{3.5}$$

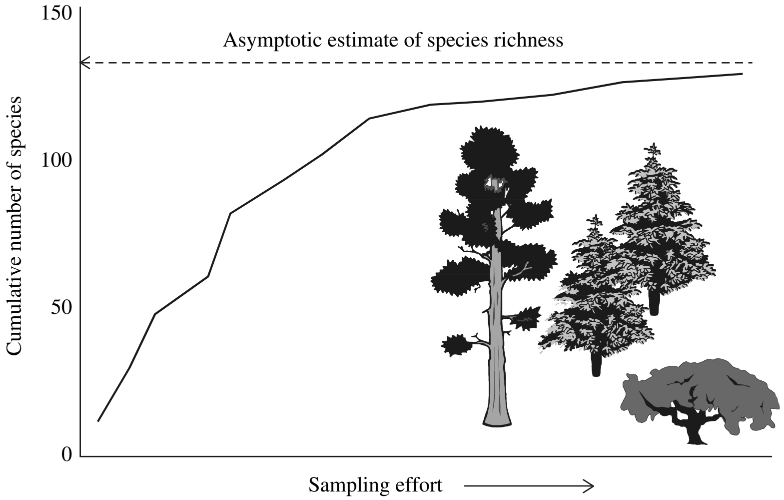

Fig. 3.3. Estimation of species richness for a community with a cumulative number of species versus sampling effort curve

Despite broad support for the use of species richness to assess biological integrity, estimating the number of species in the field is often problematic. Except in a few examples where all species in a habitat can be completely sampled (e.g. bird communities on small islands), we rarely know the total number of species in a community. Furthermore, species richness is highly dependent on area (Chapter 2) and increases asymptotically with sample size and the number of individuals collected (May 1973). Consequently, comparisons of the number of species among sites should be standardized for area and number of individuals (Vinson and Hawkins 1996). This is not a serious limitation in most biomonitoring studies because the same sampling effort will presumably be employed in both reference and impacted sites; however, it does complicate making comparisons with historic data or comparing results from different studies. One proposed solution to this problem is the use of a procedure known as rarefaction (Simberloff 1972), in which samples are selected randomly from the entire dataset to derive a quantitative relationship between number of species and total abundance. Rarefaction procedures estimate the expected number of species based on samples with standard sample sizes. The advantage of the rarefaction estimate is that samples of different sizes can be compared. The disadvantage is that information is lost when the actual sample size taken at a site is larger than the sample size for which the number of species is being estimated. The equation for estimating species richness by rarefaction is shown below.

$$\hat{S}_n = \sum_{i=1}^{S} 1 - \frac{\binom{N - N_i}{n}}{\binom{N}{n}} \tag{3.6}$$

where N = the number of individuals in the sample, N_i = the number of individuals of species i in the sample, S = the number of species in the sample, and n = the sample size (number of individuals) on which normalization is being carried out.

A second more pervasive problem is that measures of species richness do not account for differences in abundance among species. Theoretically, two locations could have very different total abundances and a very different distribution of individuals among species and still have the same species richness. Measures of species diversity, which account for both richness and the distribution of individuals among species, have been developed to resolve this problem. Although used routinely to compare communities in different locations, most diversity measures have received intense criticism from ecologists and ecotoxicologists. Diversity indices have been attacked based on theoretical, statistical, and conceptual arguments (Hurlbert 1971; Green 1979; Fausch *et al.* 1990). Despite the criticism, diversity measures continue to be widely used in biomonitoring studies and have appeared to multiply in the literature.

3.3.2.2 Species Diversity

Many ecologists, including ecotoxicologists, condense large species abundance data sets into diversity indices. There are two general types of diversity indices, those based on dominance and those derived from information theory. Both types include a species richness component and an evenness component of diversity; however, the relative importance of rare species differs between the two approaches. Simpson's index (1949), the most widely used measure of dominance, is given as:

$$\hat{\lambda} = \sum_{i=1}^{S} \frac{1}{p_i^2} \tag{3.7}$$

where λ is the measure of diversity and p_i is the proportion of the i$^{\text{th}}$ species in the sample. The value of λ ranges from 1 to S (where $S =$ species richness), with larger values representing greater diversity. Community evenness reflects the distribution of individuals among species. If all species in a community have the same relative abundance, the value of λ is maximized and equals species richness. In practice, equation (3.8) is often used to avoid bias associated with estimating p_i with N_i/N and from diversity estimation for the entire community based on a sample.

$$\hat{\lambda} = \sum_{i=1}^{S} \frac{N_i(N_i - 1)}{N(N - 1)} \tag{3.8}$$

Simpson's modified index as given in equation (3.8) is converted in practice to $1 - \lambda$ so that any increase in the index reflects an increase in diversity. This weighted mean of the species proportions is very sensitive to dominant species and relatively insensitive to rare species. Thus, the main criticism of Simpson's index is that rare species contribute relatively little to the index value.

Two common diversity indices based on information theory, the Shannon–Wiener and Brillouin indices, are more sensitive to rare species (Qinghong 1995) and, in our opinion, are more relevant to ecotoxicology. The distinction between the two indices is simply that the Shannon–Wiener index (equation (3.9)) estimates diversity for the community from which the sample was taken, whereas Brillouin's index (equation (3.10)) estimates diversity for the sample itself. The Shannon–Wiener index can be described as the uncertainty of predicting the species of a randomly selected individual from the community. This uncertainty increases as more species are present in the community and as the individuals are more evenly distributed among those species (Ludwig and Reynolds 1988). Although calculated here using natural logarithms, both diversity indices can be calculated with base 10 or 2. Therefore, it is important to note units in published diversity (and related evenness) indices prior to using them together.

$$H' = -\sum_{i=1}^{S} p_i \ln p_i \cong -\sum_{i=1}^{S} \frac{N_i}{N} \ln\left(\frac{N_i}{N}\right) \tag{3.9}$$

$$H = \frac{1}{N} \ln \frac{N!}{\prod_{i=1}^{S} N_i!} \tag{3.10}$$

In equations (3.9) and (3.10) the units of diversity are units of information per individual. If $\log_{10}$ or $\log_2$ were applied, the units would have been decits/individual or bits/individual, respectively. Like Simpson's index, Shannon–Wiener diversity is maximized (H_{MAX}) when all species are equally abundant in a sample.

3.3.2.3 Species Evenness

How equally the individuals in a community are distributed among the species can be measured with a variety of indices. The first two to be illustrated (Pielou 1969) are based on H' and H. They are simply H' or H divided by their estimated maxima, and consequently, the resulting evenness indices are those for the entire community (J') or for the sample itself (J). The maxima are used because they would be the values for H' and H if individuals were uniformly distributed among the available species.

$$J' = \frac{H'}{\ln S} \tag{3.11}$$

$$J = \frac{H}{H_{\text{MAX}}} \tag{3.12}$$

H_{MAX} is defined by the following formula:

$$H_{\text{MAX}} = \frac{1}{N} \ln \left[\frac{N!}{([N/S]!)^{S-r}(([N/S]+1)!)^{r}} \right]$$

where $[N/S] =$ the integer part of the quotient, N/S, and $r = N - S[N/S]$(Magurran 1988).

The third evenness index (Alatalo 1981) is insensitive to species richness and combines both Hill's and Shannon–Wiener's indices (equation (3.13)). It is a modification of Hill's index ($[1/\lambda]/[e^{H'}]$), a measure that quantifies the proportion of common species in the sample. In the modified Hill's index, $e^{H'}$ reflects the number of abundant species and $1/\lambda$ reflects the number of very abundant species. The modification consists only of subtracting the maxima (i.e. 1) from each of the estimates, $1/\lambda$ and $e^{H'}$.

$$E = \frac{\frac{1}{\hat{\lambda}} - 1}{e^{H'} - 1} \tag{3.13}$$

3.3.2.4 Limitations of Species Richness and Diversity Measures

The Simpson, Shannon–Wiener, and Brillouin indices are three examples from a long list of diversity measures that have been employed by community ecotoxicologists to assess effects of contaminants. Studies comparing performance and sensitivity of diversity measures have shown that each has specific limitations (Boyle *et al.* 1990). Thus, it is not possible to recommend an index that will be useful in all situations. Indices that are sensitive to dominant species will be more appropriate when stressors, such as organic enrichment, favor a particular group. In contrast, because rare species are often the first to be eliminated from polluted sites, it may be more appropriate to employ an index sensitive to rare species when assessing effects of toxic chemicals.

The dependence of the Shannon–Wiener diversity index on both species richness and evenness is considered a serious shortcoming by some researchers (Qinghong 1995). Because decreases in species richness can be offset by increases in evenness (or vice versa), a single value of H' can be derived from numerous combinations of richness and evenness values. For example, in Fig. 3.4 Shannon-Wiener diversity (H') is the same (1.61) in two hypothetical communities (B and

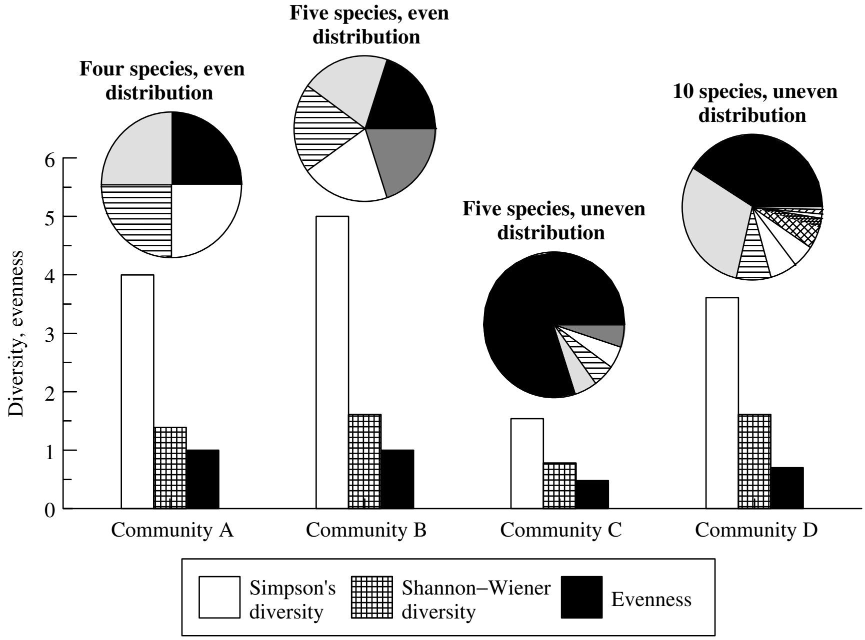

Fig. 3.4. The influence of species richness and evenness on Shannon–Wiener and Simpson's diversity in four communities. The pie diagrams show the relative abundance of each species in the community. Note that both measures of diversity increase as species richness and evenness increase

D), despite large differences in species richness and evenness. In practical terms, this means that changes in species diversity may go undetected even though large shifts in community composition have occurred. To address this problem, Qinghong (1995) proposed a simple model of species diversity that expresses changes in richness and evenness graphically (Fig. 3.5). Using this approach, differences between any two points (e.g. two sampling locations or two points in time) on a plot of diversity versus richness can be attributed to a change in either diversity, richness, or evenness.

The most serious criticism of simple community-level endpoints such as species richness and diversity is the loss of information that occurs when details of community composition are reduced to a single number. While species abundance plots such as those developed by Preston (1948) describe how individuals are distributed among species (Fig. 3.1), they do not provide information on community composition. Because sensitive species may be replaced by tolerant species at contaminated sites, it is conceivable that two communities could have a strikingly different composition but still have similar richness and diversity. An alternative approach which retains important information about community composition relevant to contaminants is the use of biotic indices. These indices (Section 3.3.3) are

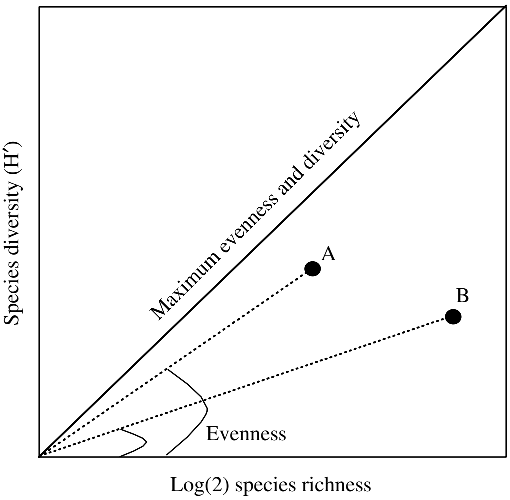

Fig. 3.5. Illustration showing the diversity monitoring (DIMO) model (Qinghong 1995), an alternative approach for presenting species richness, evenness, and Shannon–Wiener diversity in communities. The diagonal line is the maximum species diversity and evenness based on species richness within a community. The two points represent the species diversity and richness of two different communities (A and B). The angle of the vector for each point represents the evenness component of the Shannon–Wiener diversity index. In this hypothetical example, community B has greater species richness but lower species diversity than community A because of the lower evenness

designed to integrate estimates of relative abundance with measures of species-specific sensitivity, thus capturing in a single index the fraction of a community consisting of tolerant and sensitive organisms.

Community ecologists have recently begun to appreciate the importance of rare species (e.g. those species that occur at low densities or are infrequently encountered in a community), especially in terms of preservation of biological diversity. However, the importance of rare species in ecotoxicology and bioassessment has received little attention (Fore, Karr and Wisseman 1996; Cao, Williams and Williams 1998). Barbour and Gerritsen (1996) argue that it is unnecessary and would be fiscally prohibitive to include rare species in biological monitoring programs. For practical reasons and because of the assumption that rare species contribute relatively little to ecosystem function, a common practice in biological assessments is to remove rare species from data analyses. However, because rare species may account for a disproportionate number of the total species at undisturbed sites (Gotelli and Graves 1996), removing them from the analysis may decrease our ability to detect differences among locations. In addition, rare species are more prone to local extinction because of low population densities. Finally, recent studies conducted in aquatic systems indicate that censoring data to eliminate rare species may underestimate effects of anthropogenic perturbations. Cao, Williams and Williams (1998) showed that differences between reference and impacted sites were reduced if rare species were removed from the analyses (Fig. 3.6). These researchers also showed that the small sample sizes typical of most biomonitoring studies often miss rare species, resulting in greater underestimation of species richness at reference sites compared with polluted sites.

3.3.3 BIOTIC INDICES

Measures of total abundance, diversity, and species richness may not respond to some types of anthropogenic perturbations if sensitive species are simply replaced by tolerant species. Because sensitivity to contaminants often varies among species, the relative abundance of sensitive and tolerant taxa in a community could be employed to assess the degree of contamination. Biotic indices were developed early in the history of ecotoxicology with the intent of assessing the state of a community based on abundance of sensitive and tolerant species. Although Matthews, Matthews and Landis (1998) note the subjective nature of many tolerance rankings (Box 3.1) and the existence of different rankings for the same species used in different regions, they conclude that biotic indices are used effectively throughout Europe today.

Innumerable biotic indices exist (Matthews, Matthews and Landis 1998), and all have similar features. Biotic indices assign values to individual taxa based on their relative sensitivity or tolerance to a specific type of pollution. These values are often generated based on expert opinion of ecologists with knowledge of the communities being impacted. This approach allows more information and

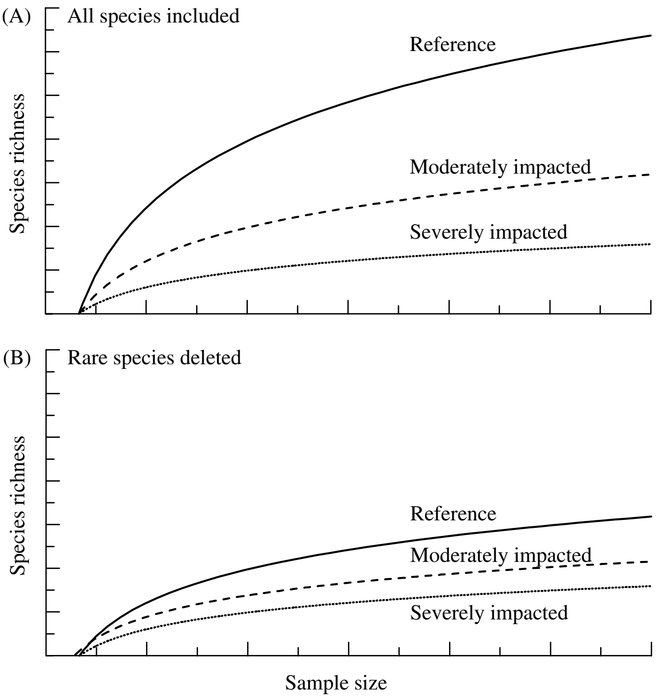

Fig. 3.6. The relationship between sample size and species richness at reference, moderately impacted, and severely impacted sites when all species are included (A) and when rare species are deleted (B). Because rare species often comprise a greater portion of communities at reference sites, the difference between reference and impacted sites diminishes when rare species are deleted. (Modified from Figure 2 in Cao, Williams and Williams 1998)

the most relevant information to be combined in comparison to the simple diversity, evenness, and richness indices discussed earlier. However, it also makes subjective the selection of particular community qualities and the assignment of scores or weights to these qualities. In addition, the indices are relative. A score from a site suspected of being impacted is meaningful only relative to the score expected for a non-impacted site. Finally, and as a consequence of the previous points, the indices tend to be useful in a limited context, and must be modified thoughtfully to be applied elsewhere.

Because biotic indices account for both species-specific sensitivity and relative abundance they are strongly influenced by pollution-induced changes in community composition. For example, it is well established that mayflies (Ephemeroptera), caddisflies (Trichoptera), and stoneflies (Plecoptera) are relatively sensitive to organic enrichment, whereas chironomids (Diptera) are generally tolerant. Indices such as Hilsenhoff's Biotic Index (Hilsenhoff 1987) take advantage of these differences in sensitivity and categorize sites based on the relative abundance of sensitive and tolerant species. Hilsenhoff's biotic index is given as:

$$\text{Biotic index} = \Sigma p_i / t_i \tag{3.14}$$

where p_i and t_i are the proportion abundance and tolerance values of the i^{th} species, respectively. Because most biotic indices use estimates of relative abundance, quantitative sampling is not necessary to calculate these measures. This feature is particularly useful for rapid bioassessment protocols (see Section 3.4) that often rely upon qualitative measures of community composition.

Because biotic indices are based on differences in species-specific sensitivity, their usefulness is often restricted to the particular region where tolerance values (t_i) were developed. Hilsenhoff's biotic index uses species-specific tolerance values from >2000 macroinvertebrate collections from polluted and unpolluted Wisconsin streams. Depending on the amount of variation in sensitivity among species within a family or higher taxonomic unit, pollution indices based on coarse levels of taxonomic resolution may be an effective solution to regional specificity. Chessman (1995) showed that family-level tolerance values were necessary for Australian streams because of the lack of taxonomic keys and the difficulty identifying immature life stages for some groups. A modified version of Hilsenhoff's biotic index based on family-level estimates of tolerance provided reasonable estimates of biological condition and was appropriate as an initial screening approach for water quality assessments (Hilsenhoff 1988).

Another criticism of pollution indices is that they are often specific to a particular class of contaminants (Slooff 1983; Chessman and McEvoy 1998). While Hilsenhoff's biotic index is especially well suited for assessing impacts of organic enrichment, the applicability of this index to other classes of contaminants (e.g. heavy metals, acidification, or pesticides) is uncertain. From a practical perspective, chemical-specific pollution indices may be of little value in systems affected by multiple chemical stressors. An alternative approach is to develop biotic indices that respond to more general classes of perturbations. Lenat (1993) published an extensive list of tolerance values for benthic macroinvertebrates in North Carolina (USA) streams. Unlike other pollution indices, Lenat's North Carolina Biotic Index (NCBI) is intended to provide a more general assessment of water quality, regardless of pollution type. Comparisons of species-specific tolerance values from Hilsenhoff's biotic index and the NCBI revealed many differences; however, mean tolerance values for major taxonomic groups were similar (Lenat 1993). These results are encouraging and suggest that sensitivity of some groups may be independent of the type of perturbation.

A key advantage of developing chemical-specific biotic indices is the potential to identify stressors based on biological measures. Chessman and McEvoy (1998) proposed a suite of biotic indices, each responding to a particular type of perturbation. A diagnostic index, based on family-level responses, was developed for several types of physical and chemical perturbations. Chessman and

McEvoy (1998) concluded that while diagnostic indices had promise, differences in sensitivity among species within a family hindered their performance. If chemical-specific biotic indices can be developed, these indices may be useful for quantifying the importance of individual chemicals in systems receiving multiple stressors.

Box 3.1 Experimental determination of species-specific sensitivity

Perhaps the most serious criticism of biotic indices concerns the subjective assignment of tolerance values to individual species (Herricks and Cairns 1982; Clements, Cherry and Van Hassel 1992; Matthews, Matthews and Landis 1998). While best professional judgment applied to survey data can provide legitimate estimates of species-specific sensitivity, these data should be supported by experimental evidence. In a review of biomonitoring approaches, Johnson, Wiederholm and Rosenberg (1993) recognized the need to integrate laboratory-derived tolerance values with field data. The subjectivity and tautological reasoning inherent in biotic indices could be avoided by validating tolerance values experimentally. Because of the opportunity to test responses of numerous species to the same chemical or mixture of chemicals simultaneously, community-level toxicity tests conducted in microcosms or

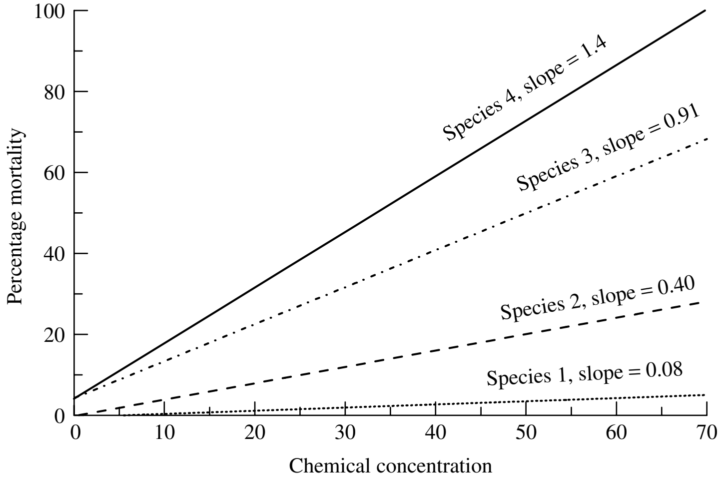

Fig. 3.7. Results of community-level toxicity tests comparing the hypothetical responses of four species to a contaminant. The slope of the relationship between percent mortality and concentration is an indicator of relative sensitivity to the chemical and can be used in the development of biotic indices. In this example, species 1 is relatively tolerant to the chemical whereas species 4 is highly sensitive

mesocosms are an efficient way to obtain species-specific estimates of sensitivity. Standard toxicological endpoints (e.g. LC50, EC50) could be used to estimate relative sensitivity among species in a mesocosm experiment. Alternatively, experimental designs that use regression analyses to establish concentration–response relationships can provide objective estimates of species-specific sensitivity for numerous taxa (Fig. 3.7). Estimates of relative sensitivity to chemicals derived experimentally could be integrated with field measures of relative abundance to produce pollution indices for different classes of contaminants. Clements, Cherry and Van Hassel (1992) used this approach to develop an index of community sensitivity for benthic macroinvertebrates in metal-polluted streams. Benthic macroinvertebrate communities collected from a reference site were exposed to heavy metals in stream microcosms. Experimentally-derived estimates of relative sensitivity were integrated into a biotic index (the index of metals impact), which was used to evaluate the degree of metal pollution downstream from the input of metals in a natural system.

In summary, while biotic indices have been employed extensively in Europe and other regions, they have received considerably less attention in the USA. These indices have been most successful when limited to a single class of stressors, especially organic enrichment. It should not be surprising when indices based on sensitivity to one chemical stressor fail to distinguish other types of perturbation. Bruns, Wiersma and Minshall (1992) rated several biological indicators based on their ecosystem conceptual basis, variability, uncertainty, ease of use, and cost-effectiveness. Litter decomposition and taxonomic richness received the highest ratings, whereas a biotic index received the lowest rating, primarily because it lacked information on responses of taxa to specific chemical toxicants. Finally, it is important to remember that the presence of tolerant taxa or the absence of sensitive taxa may result from numerous factors other than contaminants (Cairns and Pratt 1993). Biotic indices in isolation cannot demonstrate effects of pollution, only that a site is dominated by pollution-tolerant or pollution-sensitive organisms. However, biotic indices could be employed to evaluate potential reference sites in biomonitoring studies. A community dominated by species that are sensitive to a particular chemical provides reasonable evidence for the absence of that chemical.

3.4 DEVELOPMENT AND APPLICATION OF RAPID BIOASSESSMENT PROTOCOLS

One frequent criticism of community-level biomonitoring studies is the high cost of these approaches compared with physicochemical measures or single species toxicity tests. Because of the patchy spatial distribution of natural populations and the resulting high variability, large numbers of replicate samples are often necessary to detect differences between reference and contaminated sites. The time required for sample processing and species-level identification of taxonomically-difficult groups may also be prohibitive, particularly for agencies conducting large-scale monitoring programs. Niemi, Detenbeck and Perry (1993) compared the cost and explanatory value of physical, chemical, and biological measures of recovery rates in streams. Biological measures (e.g. density, primary production, leaf litter decomposition) were considerably more expensive because of the greater variability and the need to collect larger numbers of replicate samples. However, these authors acknowledged that because of their greater explanatory power, high cost should not preclude the use of biological variables in ecological assessments. We should also note that some studies have reported that costs of biological monitoring were competitive with other approaches for assessing water quality. An analysis conducted by the Ohio EPA showed that per sample costs of invertebrate and fish surveys were actually less than physical and chemical analyses of water quality (Karr 1993).

While there is evidence that biological assessments can be conducted cost-effectively, it is likely that the expense and logistical difficulties of conducting these surveys has limited our ability to assess the status of communities at larger spatial scales. Resolving the often conflicting goals of large-scale, spatially-extensive monitoring with the need for intensive, long-term biological assessments requires innovative techniques that will improve efficiency but not sacrifice data quality. Rapid assessment programs (RAPs) and their aquatic counterpart, rapid bioassessment protocols (RBPs), developed independently in the fields of conservation biology and biomonitoring to address these concerns. Both approaches attempt to streamline biological assessments by employing a variety of cost-saving but somewhat controversial procedures. RAPs have been used extensively in conservation biology, especially in tropical ecosystems, where researchers must quickly estimate biodiversity and prioritize sites for preservation without the luxury of exhaustive biological surveys. The validity of many of these programs is based on the assumption that diversity of one group of organisms can be used as an indicator of total biological diversity within a region. For example, conservation biologists have used surveys of well known flora and fauna (flowering plants, birds, and mammals) to estimate diversity of more difficult taxonomic groups (invertebrates). Using species diversity of one group to predict diversity of other groups has intuitive appeal and could significantly reduce costs of biological surveys (Blair 1999); however, the underlying assumption that diversity across broad taxonomic groups is regulated by the same ecological processes remains to be tested.

Innovations in rapid bioassessment procedures that streamline biological monitoring programs and reduce costs have accelerated the development of several large-scale monitoring programs in the United States, including the US EPA's

Environmental Monitoring and Assessment Program (EMAP) and the US Geological Survey's National Water-Quality Assessment (NAWQA) program (Resh, Norris and Barbour 1995). The long-term goals of these programs are to assess the status and trends of terrestrial and aquatic ecosystems using a combination of probabilistic sampling designs and large-scale (regional) analyses. Given the limited funds available for routine monitoring in the USA, it is unlikely that these programs could accomplish their objectives without the cost savings provided by RBPs. More importantly, the reduced collection and processing costs allow researchers to sample a larger number of sites or increase the frequency of sampling.

In aquatic ecosystems, RBPs reduce sample collection and processing costs by: (1) using qualitative sampling techniques; (2) subsampling and fixed count processing; (3) eliminating replication and pooling samples collected from individual sites; and (4) relaxing the level of taxonomic resolution (Plafkin *et al*. 1989; Resh and Jackson 1993). Each of these four cost-saving measures involve important trade-offs that must be considered when implementing biomonitoring programs, regardless of whether sampling is conducted within a single stream or at a regional level. Resh, Norris and Barbour (1995) acknowledged the widespread acceptance of these cost-saving measures, noting that in our haste to expand biomonitoring programs the consequences of reduced data quality have not been critically evaluated. In a review of RPBs, Hannaford and Resh (1995) reported that while RBPs may be appropriate for prioritizing sites, their ability to produce legally defensible data or their use for routine impact assessments remains questionable. Below we consider the limitations of each of the cost-saving measures used in RBPs.

3.4.1 APPLICATION OF QUALITATIVE SAMPLING TECHNIQUES

The abandonment of quantitative sampling techniques in many RBPs is an issue that requires serious consideration. Because of the time required to process quantitative samples, especially those collected from aquatic habitats, qualitative surveys of community composition have become increasingly common in biological assessments. Qualitative sampling techniques generally limit our ability to express data in terms of numbers of organisms per unit area or volume. Because interactions that structure communities are determined largely by absolute numbers of organisms and not their relative abundance, qualitative assessments do not provide insight into factors that regulate community composition. Furthermore, statistical analyses of biomonitoring results based on qualitative or quantitative data may lead to important differences. Figure 3.8 shows responses of several benthic macroinvertebrate metrics to heavy metals and compares statistical results based on qualitative (relative abundance) or quantitative (number per m^2) data. Analyses based on qualitative data were generally more variable and often unable to detect differences between metal-polluted and unpolluted sites.

To be fair, our appraisal of qualitative sampling employed in many RBPs neglects one major advantage of this approach. Because sample processing times

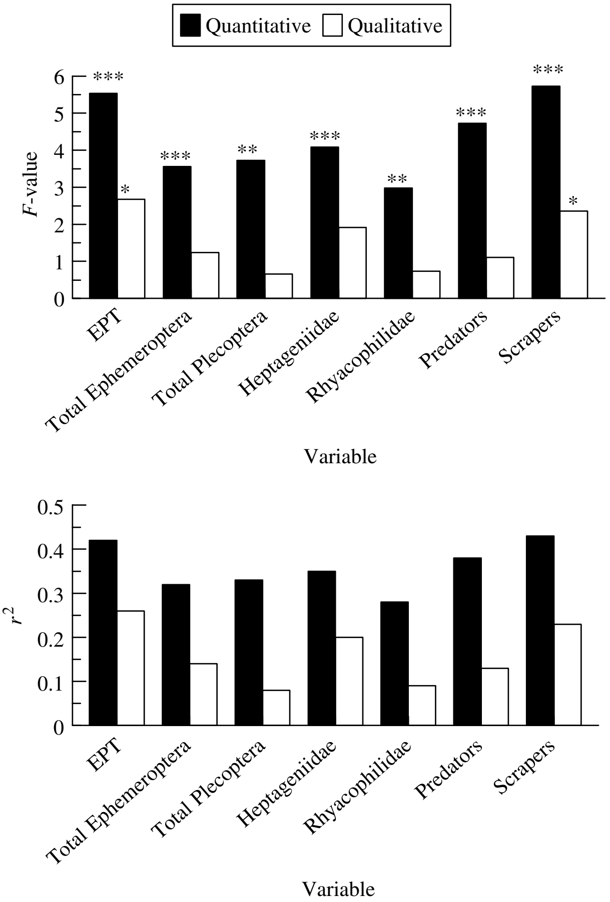

Fig. 3.8. Comparison of quantitative (number/m^2) and qualitative (relative abundance) measures of macroinvertebrate community responses to metals in Rocky Mountain streams. Data were obtained from one-way ANOVA testing for differences among reference, moderately polluted, and highly polluted streams. All measures based on quantitative data were highly significant (*$P < 0.05$; **$P < 0.001$; ***$P > 0.0001$), whereas only two measures based on qualitative data (EPT and scrapers) were significant. In all instances, F-values and the amount of variation explained were much greater when based on quantitative measures. (From Clements, unpublished data)

are greatly reduced using qualitative techniques, organisms can be collected from a larger and more diverse group of microhabitats. Sampling diverse habitats generally increases the total number of species collected compared with traditional quantitative techniques (e.g. 0.1 m^2 Surber sampler), which are often microhabitat-specific. Thus, species lists generated from qualitative sampling of diverse habitats will likely provide a more complete characterization of total species richness. Although quantitative techniques can be modified to sample different microhabitats, care must be taken to estimate relative habitat availability and to express the data accordingly.

3.4.2 SUBSAMPLING AND FIXED COUNT SAMPLE PROCESSING

The second major cost-saving measure in RBPs is the use of fixed-count sample processing (e.g. removal of 100, 200, or 300 individuals from a sample). Although fixed count processing is standard in most RBPs, few studies have critically examined this procedure or determined the optimal number of individuals that should be removed from a sample (Barbour and Gerritsen 1996; Courtemanch 1996; Vinson and Hawkins 1996; Somers, Reid and David 1998). Courtemanch (1996) argues that because of the relationship between total abundance and species richness, fixed-count processing of samples can result in inconsistent and erroneous estimates of species richness. In addition, fixed-count processing is biased against rare taxa (although fixed counts can be supplemented by including large, rare taxa). Barbour and Gerritsen (1996) defend the use of fixed-count subsampling on the basis of significantly reduced costs and, more importantly, a greater ability to detect differences among sites compared with analyses using entire samples. Surprisingly, some studies have reported that removing a larger number of animals from samples does not necessarily improve the performance of RBP metrics. Using data collected from lakes, Somers, Reid and David (1998) concluded that a two or three times increase in the number of organisms subsampled by fixed count processing did not improve the ability of metrics to distinguish among locations. Analysis of >2000 benthic macroinvertebrate samples collected from the USA showed that while fixed-count processing will significantly underestimate true species richness, this technique is quite robust with respect to distinguishing among locations (Vinson and Hawkins 1996). Furthermore, these authors conclude that fixed-count subsampling eliminates the need for using rarefaction techniques to estimate species richness when density varies greatly between locations.

3.4.3 POOLING SAMPLES

The third cost-saving measure common to many RBPs is the collection of a single, unreplicated sample from reference and polluted sites. The abandonment of replication has been criticized because it precludes estimating within-site variation and therefore limits statistical analyses (Resh, Norris and Harbour 1995). Although one could argue that since RBPs often integrate numerous metrics, each reflecting a unique component of ecological integrity, rigorous statistical analyses are less important. Indeed, summary metrics in RBPs are generally compared among sites without including estimates of variation. However, just like their constituent metrics, RBPs can vary among locations due to chance alone and therefore some analysis of variation would be useful.

From an experimental design perspective the uneasiness that some ecotoxicologists feel about the abandonment of replication in RBPs is irrelevant. Because samples collected from a single site are not true replicates, some argue that the use of inferential statistical analyses is not appropriate (Hurlbert 1984). One practical solution to the lack of replication in RBPs is to collect data from many reference and polluted sites within a region (Feldman and Connor 1992; Clements and Kiffney 1995). Using this approach, sites are placed into categories (e.g. reference or impacted) and estimates of variation within and between categories are compared. This approach is the basis for the use of regional reference conditions described in Section 3.5. Because of the patchy distribution of organisms at any one location, it is recommended that collecting several pooled samples from a site is better than one large sample of equal area (Vinson and Hawkins 1996).

3.4.4 RELAXED TAXONOMIC RESOLUTION

The appropriate level of taxonomic resolution is an important consideration in any biomonitoring study because of the difficulty and cost associated with identifying organisms to species. For many groups of organisms and in some regions, species-level identification is impossible because of the lack of sufficient taxonomic keys (e.g. many invertebrate groups in the tropics), difficulties with immature life stages (most aquatic insects), and large numbers of undescribed species (e.g. fungi, nematodes, and tropical beetles). Because of the difficulty in obtaining species-level identifications, some researchers have proposed abandoning traditional taxonomic approaches in favor of ‘recognizable taxonomic units’ (RTUs) for assessing biological diversity. RTUs are taxa that are readily distinguished based on simple morphological characteristics and are generally developed by individuals that lack formal training in taxonomy. Oliver and Beattie (1993) reported that estimates of biodiversity of spiders, ants, and mosses based on RTUs were similar to those based on traditional taxonomic analysis (Fig. 3.9). The correspondence for marine polychaetes was not as good, suggesting that applicability of RTUs for biomonitoring must be evaluated on a group by group basis. Although these non-taxonomic approaches can significantly reduce sample processing costs, the lack of taxonomic information may hinder comparisons among studies.

Taxonomic resolution is a serious issue that deserves special consideration when employing RBPs. Large savings in sample processing costs may be realized using relatively coarse (e.g. family level) taxonomic resolution (Lenat and Barbour 1994; Vanderklift, Ward and Jacoby 1996). The major assumption when employing relaxed taxonomic resolution is similar to that of studies using species-level identification, namely that these taxonomic units respond predictably to environmental gradients (Olsgard, Somerfield and Carr 1998). Several researchers have reported that relatively coarse levels of taxonomic resolution are sufficient to detect effects of pollution (Warwick 1993; Ferraro and Cole 1995;

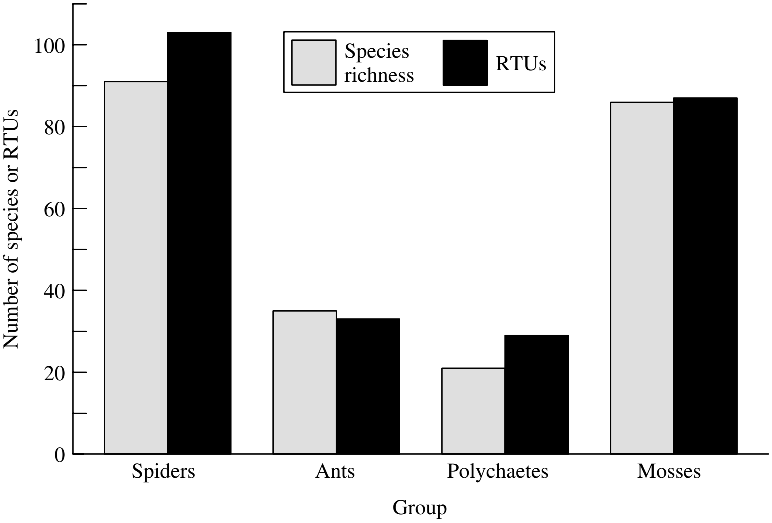

Fig. 3.9. Comparison of species richness and recognizable taxonomic units (RTUs) for spiders, ants, polychaetes, and mosses. Measures of species richness were determined by taxonomic experts, whereas RTUs were determined by technicians with minimal training in taxonomy. Results show that for most groups, actual species richness and RTUs were similar. The major exception was for marine polychaetes, which were split into more groups by non-experts. (Data from Table 1 in Oliver and Beattie 1993)

Vanderklift, Ward and Jacoby 1996; Olsgard, Somerfield and Carr 1998). For example, Bowman and Bailey (1997) concluded that patterns of community structure were similar when analyses were based on genus- or family-level identifications. Aggregate measures of phytoplankton community composition were actually more reliable indicators of eutrophication than species-level analyses in a whole-lake enrichment experiment (Cottingham and Carpenter 1998). Marchant, Barmuta and Chessman (1995) reported that analyses of benthic macroinvertebrate data collected over a large region were relatively robust to sampling techniques and taxonomic resolution. They showed that patterns of benthic communities measured using qualitative sampling techniques (presence/absence data) and family-level identification were similar to those using quantitative data and species-level identification. Ferarro and Cole (1995) compared the ability of different indices to detect differences between polluted and unpolluted locations when analyses were conducted at the level of genus, family, order, and phylum. Results showed that the level of taxonomic resolution was relatively unimportant for detecting pollution. The most likely explanation for these results is that taxonomically-related species often have similar ecological requirements and therefore similar sensitivities to contaminants (Warwick 1988).

As previously noted, conservation biologists have also investigated the consequences of relaxed taxonomic resolution on their ability to estimate biological diversity. Williams and Gaston (1994) found family-level richness was a highly significant predictor of species richness ($r^2 > 0.79$) for several groups, including ferns, butterflies, passerine birds, and bats. However, these researchers cautioned that the relationship between species richness and richness at higher levels of resolution could be influenced by the spatial scale of an investigation.

The appropriate level of taxonomic resolution will be determined by variation in sensitivity within groups, natural variation, and the spatial scale of the investigation (Box 3.2). When samples are collected over relatively large geographic areas, higher taxonomic aggregates (e.g. families, orders) may be necessary to characterize effects of stressors. Because relatively few species will occur at all sites across a large geographic region, it may be difficult to assess the effects of contamination using species-level data. In addition, abundances of individual species are more sensitive to natural environmental variability than aggregate indicators at coarse levels of taxonomic resolution (Warwick 1988). If all species within a group show similar responses to disturbance, then measures at coarse levels of taxonomic resolution will most likely be better indicators. Finally, the usefulness of genus- and family-level abundance data for discerning effects of contamination will also be influenced by the severity of the stressor. Olsgard, Somerfield and Carr (1998) reported better correlations between species' abundances and higher levels of taxonomic resolution at polluted sites compared with reference sites.

Box 3.2 The relationship between taxonomic resolution, sensitivity, and natural variation

The appropriate level of taxonomic resolution in biomonitoring studies represents a trade-off between natural background variability, sensitivity to the stressor, and, in the case of problematic groups such as chironomids, practical considerations. Ultimately, the level of taxonomic resolution may also depend on the spatial scale of the investigation. Family-level or higher identification may be appropriate over a regional scale; however, this coarse taxonomic resolution may not be sufficient to detect effects of disturbance within a single stream (Marchant, Barmuta and Chessman 1995). In addition, the practice of using qualitative sampling techniques typical of many RBPs may also influence the appropriate level of taxonomic resolution. Bowman and Bailey (1997) found that as taxa are aggregated, qualitative data are less useful for assessing differences in community composition. These researchers recommended that if trade-offs are necessary when employing RBPs, it is better to sacrifice taxonomic resolution than quantitative sampling.

Using data collected from 73 streams in the Southern Rocky Mountain ecoregion of Colorado (USA), Clements *et al.* (2000) reported that the effects of taxonomic aggregation on statistical differences between reference and impacted sites varied among groups. For the mayflies (Ephemeroptera), statistical differences between reference and metal-polluted sites were greatest at the level of family and order (Fig. 3.10A). Although mayflies in the genus

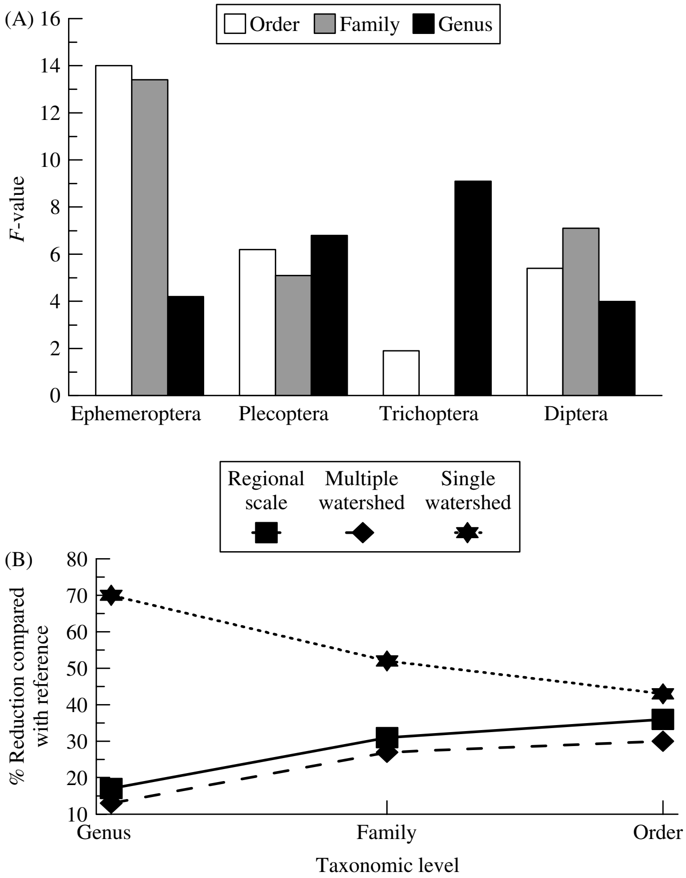

Fig. 3.10. (A) Influence of taxonomic resolution on statistical differences between polluted and unpolluted sites based on the magnitude of *F*-values from one-way ANOVA. Separation of polluted and unpolluted sites was greatest at coarse levels of taxonomic resolution for some groups (e.g. Ephemeroptera), whereas differences were greatest at the level of genus for others (e.g. Trichoptera). (B) The relationship between sensitivity and taxonomic resolution across different spatial scales. Sensitivity was defined as the percent reduction compared with a reference site. Within a single watershed, responses at the level of genus were most sensitive (e.g. showed a greater reduction compared with reference streams). At multiple watershed and regional scales, sensitivity increased with taxonomic aggregation

Rhithrogena sp. are sensitive to metals, high variability in abundance of *Rhithrogena* sp. among reference sites limited the ability to detect statistical differences. Aggregate taxonomic measures at the level of family and order were better indicators of pollution because most mayflies and almost all heptageniid mayflies in Rocky Mountain streams are sensitive to metals. In contrast to these results, total caddisfly abundance was a poor indicator of metal pollution. Unlike mayflies, the order Trichoptera includes taxa that are both highly tolerant (Brachycentridae and Hydropsychidae) and relatively sensitive (Rhyacophilidae) to heavy metal pollution. The relationship between taxonomic level and responses to stressors was also influenced by the spatial scale of the investigation. The percent reduction in abundance of mayflies was greatest at the level of genus in a single watershed study (Arkansas River, CO), but increased with taxonomic aggregation at larger spatial scales (Fig. 3.10B).

3.5 REGIONAL REFERENCE CONDITIONS

Ecologists have long recognized that patterns of vegetation vary naturally among landscapes and are influenced by regional climate, geology, and soil type (Clements 1916). Qualitative assessment of these patterns and compilation of ecoregion maps (Omernik 1987) improve our ability to define reference conditions. Much of the natural variability among reference sites can be reduced by restricting sites to a single ecoregion or subregion. Alternatively, variation among reference sites within a region can be explained using predictive models (Fausch, Karr and Yant 1984).

The traditional approach in most biomonitoring studies is to compare communities at disturbed sites to a single reference site. In lotic surveys of point source discharges, upstream reference sites are often compared with downstream impacted and recovery sites within the same watershed. In assessments of sediment contamination, communities are collected from locations along a gradient of pollution, generally within the same watershed. As noted above, replicates in these studies often consist of subsamples collected from a single location and are not considered true replicates (Hurlbert 1984). Within-site variance estimates are not useful for defining true reference conditions and therefore extrapolations to other locations are greatly limited. Multiple reference sites, even those within the same watershed, are more appropriate for assessing single point source discharges (Hughes 1985), especially in situations where locating ecologically similar watersheds is problematic. However, natural spatial variation also complicates assessment of point source discharges within the same habitat. For example, the river continuum concept predicts significant changes in the structure and function of streams from headwater sites to downstream sites (Vannote *et al.* 1980). The traditional upstream-reference versus downstream-impacted design employed in many stream surveys is confounded by natural changes in structure and function along a river continuum (Clements and Kiffney 1995). Community-level indicators that respond to both natural and anthropogenic variation will not be particularly useful for assessing disturbance unless these natural changes can be quantified.

Defining reference conditions and selecting appropriate reference sites are among the most difficult steps when designing biomonitoring studies. Unlike laboratory experiments where all variables except those of direct relevance to the experiment are controlled, field studies lack true controls and are often complicated by large amounts of natural variation. Reynoldson *et al.* (1997) defined the reference condition as 'the condition that is representative of a group of minimally disturbed sites organized by selected physical, chemical, and biological characteristics'. Hughes (1995) reviewed the strengths and limitations of six approaches for determining reference conditions (regional reference sites, historical and paleoecological data, laboratory experiments, quantitative models and best professional judgment) and concluded that multiple approaches are often required. Of these six approaches, the use of regional reference conditions holds the most promise. The regional reference approach involves selecting multiple sites within a single region to define expected conditions (Bailey *et al.* 1998). Establishment of regional reference conditions is a major improvement over traditional biomonitoring approaches that allows researchers to objectively characterize expected community composition and obtain legitimate estimates of natural variation.

3.6 INTEGRATED ASSESSMENTS OF BIOLOGICAL INTEGRITY

Physical and chemical measures of contaminant effects dominated the field of pollution assessment until the 1970s (Cairns and Pratt 1993). The historic emphasis on abiotic measures has gradually been replaced by an understanding that biological indicators of ecological integrity are equally important. Natural resource managers now realize that integrated assessments including chemical analyses, toxicity tests, and biological surveys are often necessary to discern impacts of contaminants (Fig. 3.11). The sediment quality triad (Chapman 1986) is an example of an integrated approach that combines chemical measures of contaminants, toxicology, and field assessments of communities to characterize the degree of sediment contamination. The strength of the sediment quality triad lies in the weight of evidence approach and in its ability to discern direct toxicological effects from natural variation in habitat characteristics (Chapman 1996). For example, results that show altered community composition but no detectable levels of chemical contamination and no toxicological effects suggest that factors other than contaminants (e.g. substrate composition, habitat quality) are responsible for these differences. Conversely, results that show chemical contamination and toxic effects in the laboratory but no changes in community composition

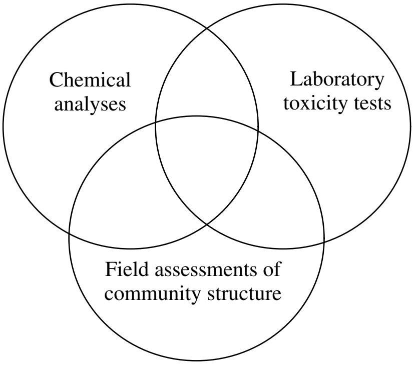

Fig. 3.11. Integration of chemical analyses, laboratory toxicity tests, and field assessments of community structure can provide the strongest evidence for a causal relationship between the presence of chemical stressors and ecological impairment. (Modified from Chapman 1986)

imply that the chemicals are not bioavailable in the field or that organisms have acclimated to these chemicals. Although the sediment quality triad was developed specifically to assess contamination in marine and freshwater ecosystems, the general integrated approach could be used in most biomonitoring programs. For example, toxicological effects of pesticides on surrogate species could be integrated with residue analysis and field assessments of community composition to estimate the subtle effects of pesticides on songbirds.

3.7 LIMITATIONS OF BIOMONITORING

Although integrated, weight of evidence approaches such as the sediment quality triad can suggest a relationship between stressors and ecological responses, they do not demonstrate causation. Descriptive approaches such as biomonitoring studies provide support for hypotheses rather than direct tests of hypotheses. Results of biomonitoring studies are often equivocal because of the lack of adequate controls, non-random assignment of treatments, and lack of replication (Hurlbert 1984). Suter (1993) discusses the ‘ecological fallacy’ of presuming that differences between polluted and unpolluted sites are a result of anthropogenic factors when alternative hypotheses (*sensu* Platt 1964) have not been tested experimentally. Several researchers have offered useful advice on how to strengthen causal relationships in descriptive studies (Hill 1965; Suter 1993; Beyers 1998; Newman 2001). The most often cited criteria for determining causation are derived from epidemiological studies of disease (Box. 3.3), where cause-and-effect relationships are elusive (e.g. dioxin exposure and cancer) and identifying these associations has major societal implications (e.g. smoking and lung cancer).

Box 3.3 The use of causal criteria in community-level assessments

Hill's (1965) nine criteria and modifications of these guidelines have been employed in ecological risk assessment studies to strengthen causal relationships between stressors and ecological responses (Suter 1993; Beyers 1998; Newman 2001). However, most of these adaptations have been developed for population-level studies and not directly applied to communities. Below, we review Hill's nine criteria for determining causation within the context of assessing effects of stressors on communities.

1 Strength of the association

The presence of a strong relationship between a stressor and alteration in community structure is one of the most important components for the formation of a logical argument of causation. The complete elimination of a sensitive species from a contaminated site or large shifts in the abundance of sensitive and tolerant species would be considered strong responses.

2 Consistency of the association

The responses of communities to the stressor should agree with those observed at other locations and by other researchers. The more diverse the situations where consistent responses are observed, the stronger the argument for causation. For example, is species richness of avian communities consistently reduced in areas sprayed with pesticides? Because the composition of communities will vary spatially and temporally, it may not be possible to satisfy this criterion by measuring effects on any single species. For example, responses of benthic communities to organic enrichment frequently result in increased abundance of certain groups; however it is unlikely that we could predict the response of any particular species. Consistent community-level responses to contamination will necessarily incorporate multiple measures.

3 Specificity

Because the specificity of responses to contaminants often decreases at higher levels of biological organization, requiring that the observed response is diagnostic of exposure will be problematic for most population-, community-, and ecosystem-level studies. Information on the relative sensitivity of dominant species to a particular chemical may allow researchers to predict specific community-level responses. However, most endpoints used in these studies (e.g. diversity, species richness) will likely show similar responses among contaminant classes.

4 Temporality

The requirement that exposure to the stressor must precede the responses is obvious for showing causation at any level of biological organization.

However, demonstrating this temporal association is difficult when pre-exposure data are unavailable. Paleoecological studies of communities are especially appropriate for demonstrating temporal associations between stressors and community responses. Species composition of certain groups of organisms preserved in sediments can provide a long-term record of community change that could be associated with the onset of contamination.

5 Plausibility

A credible mechanistic explanation for the observed response of communities to a stressor strengthens the case for a causal relationship. However, this criterion may also be problematic in community-level studies. Identifying specific mechanistic explanations for changes in community-level endpoints may require an understanding of responses at lower levels of biological organization. For example, reduced species diversity could result from either the loss of sensitive species and/or increased dominance by tolerant species. An understanding of species-specific responses is necessary to provide a mechanistic explanation for reduced species diversity at polluted sites.

6 Coherence

Are the observed changes in community composition in agreement with our understanding of the stressor and the characteristics of the particular community? Often, identifying coherent community-level responses requires an understanding of the structure and function of reference and impacted communities. We generally expect that most toxic chemicals will have negative effects on species in a community. Therefore, increased abundance of a particular species at a contaminated site is difficult to explain unless we can attribute this response to indirect effects, such as the removal of a potential competitor or predator.

7 Analogy

If similar classes of stressors elicit similar community responses, then the case for a causal relationship is strengthened. For example, despite different modes of toxic action, responses of benthic communities to heavy metals and acidification are generally similar. Note that this criterion is somewhat contrary with the requirement that responses to contaminants should also be diagnostic.

8 Ecological gradient

Studies that show a gradient of responses to contamination (e.g. concentration–response relationship) provide stronger evidence for causation than all-or-none responses. Although relatively common in biological assessments, comparing a single contaminated site with a single reference site is a weak experimental design since differences between sites cannot be attributed directly to contamination. Because of differences in sensitivity among species, it is likely that many community-level variables will show a continuous distribution along contaminant gradients. The key challenges are to develop experimental designs that allow these gradients to be quantified and to separate contaminant effects from other sources of variation along the gradient. Where possible, study sites should be located along a known gradient of contamination and a suite of community variables should be measured at each site.

9 Experimentation

The last and perhaps most important criterion to support a causal argument is direct experimental evidence. Changes in community composition resulting from experimental manipulation of stressors provide the most convincing evidence that the stressors are directly responsible for the observed responses. Unfortunately, this is probably the most difficult type of evidence to obtain in community studies and, as a result, there are relatively few examples of whole community manipulations with chemical stressors. Conducting manipulative experiments on intact communities in the field is challenging and, depending on the nature of the stressor, often logistically impractical. Microcosm and mesocosm experiments are a reasonable alternative to field manipulations, but they are limited in terms of their spatial and temporal scale (Chapter 4).

3.7.1 SUMMARY

Regardless of the strength and consistency of stressor–response relationships or the use of appropriate reference sites in a biomonitoring study, there is no substitute for experimentation to demonstrate causality. The transition from purely descriptive to manipulative approaches represents a major shift in scientific rigor and sophistication. It is the ability to test hypotheses with experiments that define the maturity of a science (Popper 1972), whether it is physics, ecology, or ecotoxicology. In Chapter 4 we will review the development of experimental approaches in community ecology and show how these approaches can be employed to support causal arguments in ecotoxicology.

REFERENCES

Alatalo RV (1981). Problems in the measurements of evenness in ecology. *Oikos* **37**: 199–204.

Bailey RC, Kennedy MG, Dervish MZ and Taylor RM (1998). Biological assessment of freshwater ecosystems using a reference condition approach: comparing predicted and actual benthic invertebrate communities in Yukon streams. *Freshw Biol* **39**: 765–774.

Barbour MT and Gerritsen J (1996). Subsampling of benthic samples: A defense of the fixed-count method. *J N Am Benthol Soc* **15**: 386–391.

Beyers DW (1998). Causal inference in environmental impact studies. *J N Am Benthol Soc* **17**: 367–373.

Blair RB (1999). Birds and butterflies along an urban gradient: surrogate taxa for assessing biodiversity? *Ecol Appl* **9**: 164–170.

Bowman MF and Bailey RC (1997). Does taxonomic resolution affect the multivariate description of the structure of freshwater benthic macroinvertebrate communities? *Can J Fish Aquat Sci* **54**: 1802–1807.

Boyle TP, Smillie GM, Anderson JC and Beeson DR (1990). A sensitivity analysis of nine diversity and seven similarity indices. *Water Pollut Cont Fed* **62**: 749–762.

Bruns DA, Wiersma GB and Minshall GW (1992). Evaluation of community and ecosystem monitoring parameters at a high-elevation, Rocky Mountain study site. *Environ Toxicol Chem* **11**: 459–472.

Cairns Jr J (1974). Indicator species vs. the concept of community structure as an index of pollution. *Water Res Bull* **10**: 338–347.

Cairns Jr J and Pratt JR (1993). A history of biological monitoring using benthic macroinvertebrates. In *Freshwater Biomonitoring and Benthic Macroinvertebrates*, ed. by Rosenberg DM and Resh VH, pp. 10–27. Chapman and Hall, New York, NY.

Cao Y, Williams DD and Williams NE (1998). How important are rare species in aquatic community ecology and bioassessment? *Limnol Oceanogr* **43**: 1403–1409.

Chapman PM (1986). Sediment quality criteria from the sediment quality triad: an example. *Environ Toxicol Chem* **5**: 957–964.

Chapman PM (1996). A test of sediment effects concentrations: DDT and PCB in the Southern California Bight. *Environ Toxicol Chem* **15**: 1197–1198.

Chessman BC (1995). Rapid assessment of rivers using macroinvertebrates: A procedure based on habitat-specific sampling, family level identification and a biotic index. *Aust J Ecol* **20**: 122–129.

Chessman BC and McEvoy PK (1998). Towards diagnostic biotic indices for river macroinvertebrates. *Hydrobiologia* **364**: 169–182.

Clements FE (1916). Plant Succession: analysis of the development of vegetation. Carnegie Institute of Washington Publication, No. 242. Washington, DC.

Clements WH and Kiffney PM (1995). The influence of elevation on benthic community responses to heavy metals in Rocky Mountain streams. *Can J Fisheries Aquat Sci* **52**: 1966–1977.

Clements WH, Cherry DS and Van Hassel JH (1992). Assessment of the impact of heavy metals on benthic communities at the Clinch River (Virginia): evaluation of an index of community sensitivity. *Can J Fish Aquat Sci* **49**: 1686–1694.

Clements WH, Carlisle DM, Lazorchak JM and Johnson PC (2000). Heavy metals structure benthic communities in Colorado mountain streams. *Ecol Appl* **10**: 626–638.

Cottingham KL and Carpenter SR (1998). Population, community, and ecosystem variates as ecological indicators: Phytoplankton responses to whole-lake enrichment. *Ecol Appl* **8**: 508–530.

Courtemanch DL (1996). Commentary on the subsampling procedures used for rapid bioassessments. *J N Am Benthol Soc* **15**: 381–385.

Davis WS (1995). Biological assessment and criteria: building on the past. In *Biological Assessment and Criteria: Tools for Water Resource Planning and Decision Making*, ed. by Davis WS and Simon TP, pp. 15–29. Lewis Publ., Boca Raton, FL.

Fausch KD, Karr JR and Yant PR (1984). Regional application of an index of biotic integrity based on stream fish communities. *Trans Am Fish Soc* **113**: 39–55.

Fausch KD, Lyons J, Karr JR and Angermeier PL (1990). Fish communities as indicators of environmental degradation. *Am Fish Soc Symp* **8**: 123–144.

Feldman RS and Connor EF (1992). The relationship between pH and community structure of invertebrates in streams of the Shenandoah National Park, Virginia, USA. *Freshw Biol* **27**: 261–276.

Ferraro SP and Cole FA (1995). Taxonomic level sufficient for assessing pollution impacts on the Southern California bight macrobenthos – Revisited. *Environ Toxicol Chem* **14**: 1031–1040.

Fisher RA, Corbet AS and Williams CB (1943). The relation between the number of species and the number of individuals in a random sample of an animal population. *J Anim Ecol* **12**: 42–58.

Fore LS, Karr JR and Wisseman RW (1996). Assessing invertebrate responses to human activities: Evaluating alternative approaches. *J N Am Benthol Soc* **15**: 212–231.

Gotelli NJ and Graves GR (1996). *Null Models in Ecology*. Smithsonian Institution Press, Washington, DC.

Green RH (1979). *Sampling Design and Statistical Methods for Environmental Biologists*. John Wiley and Sons, New York, NY.

Hannaford MJ and Resh VH (1995). Variability in macroinvertebrate rapid-bioassessment surveys and habitat assessments in a northern California stream. *J N Am Benthol Soc* **14**: 430–439.

Herricks EE and Cairns Jr J (1982). Biological monitoring. Part III – receiving system methodology based on community structure. *Water Res* **16**: 141–153.

Hill AB (1965). The environment and disease: association or causation. *Proc Royal Soc Med* **58**: 295–300.

Hilsenhoff WL (1987). An improved biotic index of organic pollution. *Great Lakes Entomol* **20**: 31–39.

Hilsenhoff WL (1988). Rapid field assessment of organic pollution with a family-level biotic index. *J N Am Benthol Soc* **7**: 65–68.

Hughes RG (1986). Theories and models of species abundance. *Am Nat* **128**: 879–899.

Hughes RM (1985). Use of watershed characteristics to select control streams for estimating effects of metal mining wastes on extensively disturbed streams. *Environ Manag* **9**: 253–262.

Hughes RM (1995). Defining acceptable biological status by comparing with reference conditions. In *Biological Assessment and Criteria: Tools for Water Resource Planning and Decision Making*, ed. by Davis WS and Simon TP, pp. 31–47. Lewis Publ., Boca Raton, FL.

Hurlbert SH (1971). The nonconcept of species diversity: a critique and alternative parameters. *Ecology* **52**: 577–586.

Hurlbert SH (1984). Pseudoreplication and the design of ecological field experiments. *Ecol Monogr* **54**: 187–211.

Johnson RK, Wiederholm T and Rosenberg DM (1993). Freshwater biomonitoring using individual organisms, populations, and species assemblages of benthic macroinvertebrates. In *Freshwater Biomonitoring and Benthic Macroinvertebrates*, ed. by Rosenberg DM and Resh VH, pp. 40–158. Chapman and Hall, New York, NY.

Karr JR (1993). Defining and assessing ecological integrity: beyond water quality. *Environ Toxicol Chem* **12**: 1521–1531.

Karr JR and Dudley DR (1981). Ecological perspective on water quality goals. *Environ Manag* **5**: 55–68.

Kolkwitz R and Marsson M (1909). Ökologie der tierischen Saprobien. *Int Rev Gesaten* **2**: 126–152.

Lenat DR (1993). A biotic index for the southeastern United States: derivation and a list of tolerance values, with criteria for assigning water quality ratings. *J N Amer Benthol Soc* **12**: 279–290.

Lenat DR and Barbour MT (1994). Using benthic macroinvertebrate community structure for rapid, cost-effective, water quality monitoring: rapid bioassessment. In *Biological Monitoring of Aquatic Systems*, ed. by Loeb SL and Spacie A, pp. 187–215. Lewis Publ., Boca Raton, FL.

Ludwig JA and Reynolds JF (1988). *Statistical Ecology. A Primer on Methods and Computing*. John Wiley and Sons, New York, NY.

MacArthur RH (1960). On the relative abundance of species. *Am Nat* **94**: 25–36.

Magurran AE (1988). *Ecological Diversity and its Management*. Princeton University Press. Princeton, NJ.

Marchant R, Barmuta LA and Chessman BC (1995). Influence of sample quantification and taxonomic resolution on the ordination of macroinvertebrate communities from running waters in Victoria, Australia. *Mar Freshw Res* **46**: 501–506.

Matthews RA, Matthews GB and Landis WG (1998). Application of community level toxicity testing to environmental risk assessment. In *Risk Assessment. Logic and Measurement*, ed. by Newman MC and Strojan CL, pp. 225–253. CRC Publishers, Inc, Boca Raton, FL.

May RM (1973). *Stability and Complexity in Model Ecosystems*. Princeton University Press, Princeton, NJ.

May RM (1976). *Theoretical Ecology: Principles and Applications*. W.B. Saunders Co, Philadelphia, PA.

Motomura I (1932). On the statistical treatment of communities. *Zool Mag Tokyo* **44**: 379–383.

Mulvey M and Diamond SA (1991). Genetic factors and tolerance acquisition in populations exposed to metals and metalloids. In *Ecotoxicology of Metals: Current Concepts and Applications*. ed. by Newman MC and McIntosh AW, Lewis Publishers, Chelsea, MI.

Newman MC (1995). *Quantitative Methods in Aquatic Ecotoxicology*. CRC Publishers, Inc, Boca Raton, FL.

Newman MC (2001). *Population Ecotoxicology*. John Wiley and Sons, Chichester, UK.

Niemi GJ, Detenbeck NE and Perry JA (1993). Comparative analysis of variables to measure recovery rates in streams. *Environ Toxicol Chem* **12**: 1541–1547.

Oliver I and Beattie AJ (1993). A possible method for the rapid assessment of biodiversity. *Conserv Biol* **7**: 562–568.

Olsgard F, Somerfield PJ and Carr MR (1998). Relationships between taxonomic resolution, macrobenthic community patterns and disturbance. *Mar Ecol Prog Ser* **172**: 25–36.

Omernik JM (1987). Ecoregions of the conterminous United States. *Ann Assoc Am Geogr* **77**: 118–125.

Patrick R (1971). Diatom communities. In *the Structure and Function of Freshwater Microbial Communities*, ed. by Cairns Jr J, pp. 151–164. Research Division Monograph 3, Virginia Polytechnic Institute and State University, Blacksburg, VA.

Pielou EC (1969). *An Introduction to Mathematical Ecology*. John Wiley and Sons, New York, NY.

Pielou EC (1975). *Ecological Diversity*. John Wiley and Sons, New York, NY.

Plafkin JL, Barbour MT, Porter KD, Gross SK and Hughes RM (1989). *Rapid Bioassessment Protocols for Use in Streams and Rivers: Benthic Macroinvertebrates and Fish. EPA 440/4-89-001*. Washington, DC, US EPA.

Platt JR (1964). Strong inference. *Science* **146**: 347–353.

Popper KR (1972). *The Logic of Scientific Discovery* (3rd edn). Hutchinson, London, UK.

Preston FW (1948). The commonness and rarity of species. *Ecology* **29**: 254–283.

Qinghong L (1995). A model for species diversity monitoring at community level and its applications. *Environ Monitor Assess* **34**: 271–287.

Rapport DJ, Regier HA and Hutchinson TC (1985). Ecosystem behavior under stress. *Am Nat* **125**: 617–640.

Resh VH and Jackson JK (1993). Rapid assessment approaches to biomonitoring using benthic macroinvertebrates. In *Freshwater Biomonitoring and Benthic Macroinvertebrates*, ed. by Rosenberg DM and Resh VH, pp. 195–223. Chapman and Hall, New York, NY.

Resh VH, Norris RH and Barbour MT (1995). Design and implementation of rapid assessment approaches for water resource monitoring using benthic macroinvertebrates. *Aust J Ecol* **20**: 108–121.

Reynoldson TB, Norris RH, Resh VH, Day KE and Rosenberg DM (1997). The reference condition: a comparison of multimetric and multivariate approaches to assess water-quality impairment using benthic macroinvertebrates. *J N Am Benthol Soc* **16**: 833–852.

Roback SS (1974). Insects (Arthropoda: Insecta). In *Pollution Ecology of Freshwater Invertebrates*, ed. by Hart Jr CW and Fuller SLH, pp. 313–376. Academic Press, New York, NY.

Simberloff DS (1972). Properties of rarefaction diversity measures. *Am Nat* **106**: 414–415.

Simpson EH (1949). Measurement of diversity. *Nature* **163**: 688.

Slooff W (1983). Benthic macroinvertebrates and water quality assessment: some toxicological considerations. *Aquat Toxicol* **4**: 73–82.

Somers KM, Reid RA and David SM (1998). Rapid biological assessments: how many animals are enough? *J N Am Benthol Soc* **17**: 348–358.

Suter II GW (1993). A critique of ecosystem health concepts and indexes. *Environ Toxicol Chem* **12**: 1533–1539.

Tokeshi M (1993). Species abundance patterns and community structure. *Adv Ecol Res* **24**: 112–186.

Vanderklift MA, Ward TJ and Jacoby CA (1996). Effect of reducing taxonomic resolution on ordinations to detect pollution-induced gradients in macrobenthic infaunal assemblages. *Mar Ecol Prog Ser* **136**: 137–145.

Vannote RL, Minshall GW, Cummins KW, Sedell JR and Cushing CE (1980). The river continuum concept. *Can J Fish Aquat Sci* **37**: 130–137.

Vinson MR and Hawkins CP (1996). Effects of sampling area and subsampling procedure on comparisons of taxa richness among streams. *J N Am Benthol Soc* **15**: 392–399.

Warwick RM (1988). The level of taxonomic discrimination required to detect pollution effects on marine benthic communities. *Mar Biol* **19**: 259–268.

Warwick RM (1993). Environmental impact studies on marine communities: pragmatical considerations. *Aust J Ecol* **18**: 63–80.

Williams PH and Gaston KJ (1994). Measuring more of biodiversity: can higher-taxon richness predict wholesale species richness? *Biolog Conserv* **67**: 211–217.

Wilson JB (1988). The cost of heavy-metal tolerance: an example. *Evolution* **42**: 408–413.

4 Experimental Approaches in Community Ecology and Ecotoxicology

Observational approaches may provide support for a causal relationship between stressors and community responses; however, descriptive studies alone cannot be used to show causation. While application of Koch's postulates, Hill's criteria, and other weight-of-evidence approaches may strengthen arguments for causal relationships (Suter 1993; Beyers 1998), to many researchers controlled experimental manipulations remain the only way rigorously to demonstrate causation in scientific investigations. The relationship between descriptive and experimental approaches in ecotoxicology can be depicted as continua along two axes that reflect the degree of experimental control, replication, and ecological relevance (Fig. 4.1). Experimental approaches, such as single species toxicity tests and microcosm experiments, provide rigorous control over confounding variables and are easily replicated, but lack ecological realism. Purely descriptive studies (e.g. routine biomonitoring) lack true replication and random assignment of treatments to experimental units. Because treatments are not assigned randomly, differences between reference and impacted sites in biomonitoring studies cannot be directly attributed to a particular stressor. Several alternative experimental designs have been proposed that address problems associated with the lack of replication and random assignment of treatments; however, Beyers (1998) argues that it is 'fundamentally wrong to apply inferential statistics to pseudoreplicated data to show that an observed effect was caused by an impact'. The widespread application of inferential statistics in published biomonitoring studies suggest that this opinion is not shared by many researchers or journal editors. As we will see, the use of inferential statistics is not an essential component of all experimental designs. In some instances sustained manipulations at a large spatial or temporal scale may provide adequate evidence to demonstrate causation.

4.1 EXPERIMENTAL APPROACHES IN BASIC COMMUNITY ECOLOGY

> *Anyone who has tried to perform a replicated experiment in community ecology knows that the replicates within a treatment have a perverse way of becoming different from each other, even when every effort is made to keep them identical.* (Wilson 1997)

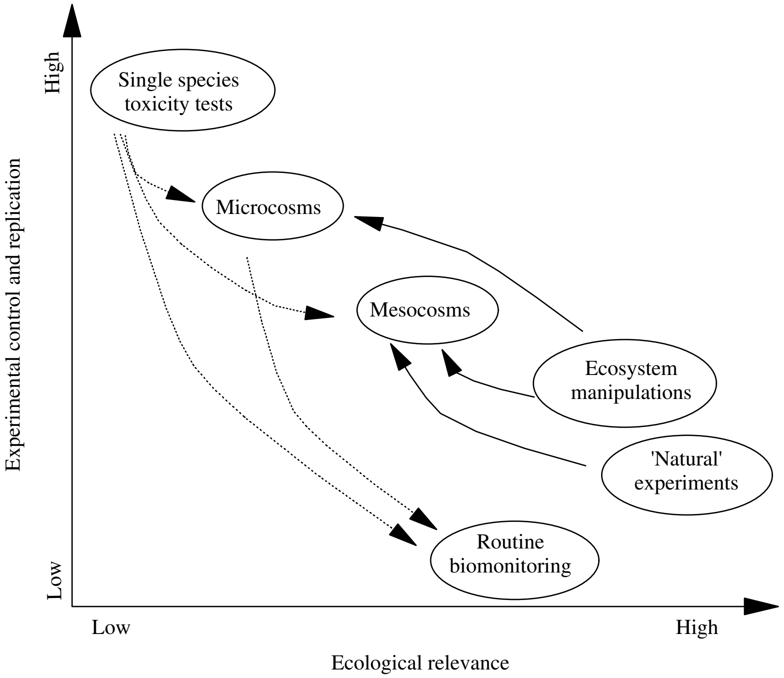

Fig. 4.1. The relationship between ecological relevance, experimental control, and replication in ecotoxicological assessments is represented as continua along two axes. Small-scale laboratory and microcosm experiments lack ecological realism but are easily replicated and provide tight control over experimental variables. Experiments conducted at larger spatiotemporal scales (e.g. ecosystem manipulations, natural experiments) have greater ecological relevance but lack rigorous control and are difficult to replicate. A research program that integrates experimental approaches at different scales is optimal for determining causation. For example, the relevance of single species toxicity tests and microcosm experiments can be validated by conducting studies at larger spatial and temporal scales (represented by the dashed lines). The underlying mechanisms responsible for changes observed in unreplicated, large-scale experimental systems can be examined in microcosm and mesocosm studies (represented by the solid lines)

4.1.1 THE TRANSITION FROM DESCRIPTIVE TO EXPERIMENTAL ECOLOGY

Observational approaches dominated the field of basic ecology during its early history, a period when ecology was primarily a concept-driven science instead of an experiment-driven science (Lubchenco and Real 1991). Descriptions of habitat requirements, feeding habits, and associations among populations formed the basis of most ecological research during this period. More recently, ecologists have recognized the importance of integrating purely descriptive and hypothesis-driven research by comparing patterns observed in natural communities to those predicted by theoretical studies (Werner 1998). Although this approach represented an important step in the transition of ecology to a more rigorous science, too often weak agreement between theory and observation was accepted as evidence for causal processes. The resulting harsh criticism of non-experimental studies in ecology created a backlash against descriptive research that is still evident today. The acrimonious debate over the role of descriptive approaches is at least partially responsible for the rigor with which ecological experiments are conducted today. The transition from a purely descriptive to an experimental science is generally regarded as evidence of maturation in most fields of scientific inquiry, and ecology is no exception. The ability to test hypotheses with controlled experiments defines science and separates true science from pseudoscience (Popper 1972). Sciences that have progressed rapidly (e.g. physics, molecular biology, chemistry) have employed a particular form of inquiry that involves posing multiple hypotheses and testing these hypotheses with experiments (Platt 1964; Newman 2001).

In a survey of the three major ecology journals *(Ecology, The American Naturalist, The Journal of Animal Ecology)*, Ives *et al.* (1996) reported a dramatic shift from laboratory studies to purely observational and descriptive studies that began in the 1960s (Fig. 4.2). Although it was well established that an

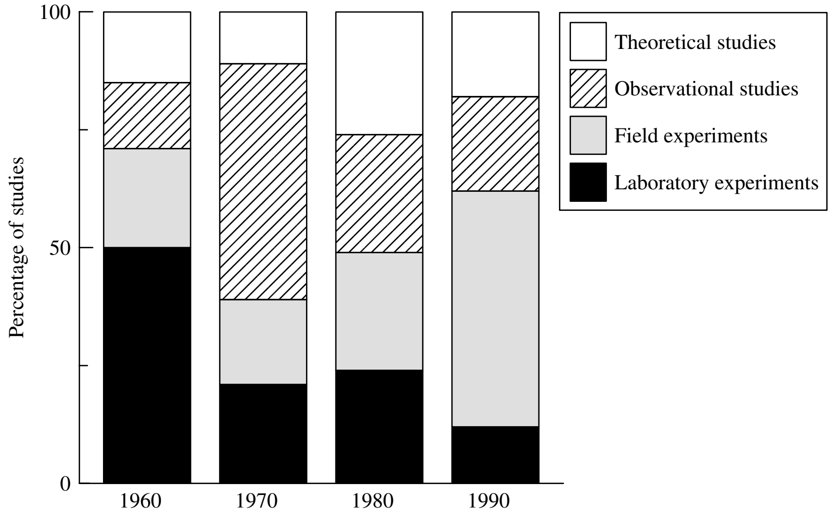

Fig. 4.2. Changes in the approaches that ecologists employ to study populations and communities over a 40-year period. The results are based on the number of publications in each of four categories. Data were derived from a search of articles published in several leading ecological journals (*Ecology, The American Naturalist, Journal of Animal Ecology*). (Modified from Figure 1 in Ives *et al.* 1996)

understanding of natural history was necessary to predict the distribution and abundance of organisms, ecologists realized the diminishing returns of purely descriptive studies and their inability to demonstrate causation. Thus, the late 1970s were characterized by another shift from descriptive and comparative approaches to field experiments (field cages and *in situ* manipulations). The role of experimental manipulations in the history of ecology is illustrated by the intense controversy over the importance of interspecific competition in regulating communities (Strong *et al*. 1984). Considerable research effort was devoted to showing that competition was a pervasive force in nature and that patterns of species abundances were a direct result of competition for limited resources. Comparisons of morphological characteristics and feeding habits of allopatric and sympatric populations supported the hypothesis that either competition or the 'ghost of competition past' (Connell 1980) was a primary factor regulating communities. However, much of the corroborative evidence collected to support these hypotheses was based on observational studies. Comparative studies lacked the risky predictions required of experimental approaches and were virtually impossible to falsify (Popper 1972). Upon closer examination, results of these comparative studies were attacked as statistical artifacts (Connor and Simberloff 1979).

This transition from descriptive to experimental approaches in ecology was hampered by the tremendous natural variability of ecological systems and the difficulty in isolating specific components for investigation (Lubchenco and Real 1991). Natural variability adds uniqueness to ecological systems and limits our ability to generalize among systems. The interdependence and interactions among specific components in ecological systems, which are often of considerable interest to ecologists, makes it difficult to isolate effects of any single factor. Interestingly, similar concerns over complexity and natural variability contribute to the skepticism that many laboratory toxicologists have expressed for community and ecosystem studies.

Despite the logistical difficulties of conducting experiments on complex ecological systems, researchers began to realize that experimental manipulation was the most direct approach for showing causation and for resolving some of the more significant controversies in ecology. Although small-scale experiments investigating the importance of competition and predation had been conducted in the laboratory (Gause 1934; Park 1948), field manipulations were generally considered impractical and logistically difficult. This all changed in the early 1960s. The pioneering experiments conducted by Connell (1961) investigating competition in the rocky intertidal zone are considered an important turning point in the history of ecology, providing the framework for field manipulations in a variety of other habitats. These conceptually simple but elegant experiments demonstrated that competition played an important role in structuring communities and that environmental factors can influence the outcome of species interactions. A critical period of self-evaluation followed as ecologists were introduced to the writings of Popper (1972) and Platt (1964), strong advocates of the need to falsify hypotheses and to test alternative hypotheses with experiments. Contemporary ecologists employ a variety of experimental procedures to advance our understanding of factors that limit the distribution and abundance of organisms in nature.

4.1.2 MANIPULATIVE EXPERIMENTS IN ROCKY INTERTIDAL COMMUNITIES

Since the early 1960s, the rocky intertidal habitat has been a rich source for many of the significant hypotheses in community ecology. Experiments conducted by Paine (1966, 1969) illustrated the effects of predators on local species diversity and introduced the concept of keystone species. Paine (1969) showed that intense predation by the starfish *Pisaster* maintained local species diversity by preventing a competitively superior species (the mussel *Mytilus*) from dominating all available space. Subsequent work by Sousa (1979) provided support for the intermediate disturbance hypothesis (see Chapter 6), which states that species diversity is influenced by competition and physical disturbance and that greatest diversity is observed at intermediate levels of disturbance (Connell 1978). Disproportionate effects of a particular species or the notion that species diversity may be enhanced under moderate levels of disturbance are significant ecological concepts that have major implications for community ecotoxicology. The relationship between natural and anthropogenic disturbance will be considered in Chapter 6.

It is no coincidence that several of the most significant contributions to the field of community ecology, namely the role of competition, the effects of predation on species diversity, the keystone species concept, and the intermediate disturbance hypothesis, were derived from experiments conducted in rocky intertidal habitats. The classic studies of Joseph Connell, Robert Paine, Paul Dayton, and Bruce Menge influenced a generation of ecologists and clearly demonstrated the effectiveness of field manipulations. Compared with other systems, rocky intertidal habitats are less complex and lend themselves to easy experimental manipulation. Removing competitors or excluding predators is relatively simple in these essentially two-dimensional systems, where most of the organisms are either sessile or very slow moving.

4.1.3 MANIPULATIVE STUDIES IN MORE COMPLEX COMMUNITIES

Conducting manipulative experiments in more complex systems and at larger spatial scales has proven to be logistically challenging. However, there are several excellent examples where researchers have tested important principles of community ecology using large-scale field manipulations. The most striking example of a large-scale experiment designed to test specific theoretical predictions was Dan

Simberloff's defaunation studies of mangrove islands in the Florida Keys (see Chapter 2). Simberloff and Wilson's (1969) demonstration of the dynamic equilibrium in number of species has important implications for conservation biology and restoration ecology. Interestingly, while these experiments were designed to test basic principles of island biogeography, removal of insects from the islands was accomplished by pesticide application. Thus, the results have relevance to community ecotoxicology from the perspective of studying recovery from chemical stress.

A second set of large-scale experiments conducted in the 1960s involved direct measurement of ecosystem dynamics in a New Hampshire watershed. The box and arrow diagrams developed by ecologists in the 1950s and 1960s to describe energy flow and nutrient cycling were generally abstract and remained untested hypotheses. Manipulation of a watershed in the Hubbard Brook Experimental Forest provided an opportunity to test these models and to measure the response to deforestation (Likens *et al.* 1970). The researchers observed large export of nutrients and particulate materials in the deforested stream compared with a reference watershed.

In addition to testing theoretical predictions of ecosystem responses to perturbation, these early studies set the stage for a series of whole ecosystem manipulations that measured effects of chemical stressors, including pesticides and acidification. These experiments also demonstrated that a powerful case can be made for causal relationships without true replication. Details of these experiments will be described in Section 4.4.1.

4.1.4 TYPES OF EXPERIMENTS IN BASIC COMMUNITY ECOLOGY

It is important to realize that all experimental approaches are not equal and that certain types of experimental systems may be more useful than others for investigating ecological responses to perturbations. Diamond (1986) distinguishes three types of experiments in ecological research: laboratory experiments, field experiments, and natural experiments (Table 4.1). He compares these experimental approaches in terms of control over independent variables, site matching (e.g. pre-treatment similarity among experimental units), ability to follow a trajectory, spatiotemporal scale, scope, ecological realism, and generality. Laboratory experiments rank high in terms of control of independent variables and site matching, but are unrealistic because of their limited scope, spatiotemporal scale, ecological realism, and generality. Field experiments are conducted outdoors and often involve manipulation of natural communities, such as the removal or addition of a predator or competitor. Connell's studies in the rocky intertidal zone and Simberloff's defaunation studies in the Florida Keys are examples of field experiments. Although field experiments have played an important role in the development and testing of ecological theory, Diamond (1986) is critical of these approaches. Compared with laboratory experiments, field experiments are more realistic and offer a greater range of possible manipulations.

Table 4.1. Comparison of the strengths and weaknesses of different types of experiments in community ecology. (After Diamond 1986)

Characteristic	Laboratory	Field	Natural trajectory	Natural snapshot
Regulation of independent variables	Highest	Medium to low	None	None
Site matching	Highest	Medium	Medium to low	Lowest
Ability to follow trajectory	Yes	Yes	Yes	No
Temporal scale	Lowest	Lowest	Highest	Highest
Spatial scale	Lowest	Low	Highest	Highest
Scope (range of manipulations)	Lowest	Medium to low	Medium to high	Highest
Realism	Low to none	High	Highest	Highest
Generality	None	Low	High	High

However, field experiments have less control and may be confounded by pretreatment differences among experimental units. According to Diamond, field experiments are usually conducted at a small spatiotemporal scale and lack generality.

Natural experiments differ from field experiments in that the researcher does not directly manipulate the variables of interest, but selects sites where the perturbation is already present or will be present. Comparisons of species abundance, habitat preferences, and morphological characteristics in allopatric and sympatric populations are considered natural experiments. Probably the best example of a natural experiment is the comparison of beak sizes among allopatric and sympatric populations of Galapagos finches. Assuming that beak size is an appropriate surrogate for resource use, the greater separation of beak sizes on sympatric islands compared with allopatric islands is considered evidence for interspecific competition. Because researchers may investigate results of processes that occur over very large areas (island archipelagoes) and over evolutionary time periods, natural experiments have the greatest spatial and temporal scales. Diamond further distinguishes between natural snapshot experiments, in which a researcher compares sites that differ in a particular characteristic (e.g. presence or absence of a predator) and natural trajectory experiments, where a researcher makes comparisons before and after a perturbation.

It is important to note that Diamond's enthusiasm for natural experiments is not shared by all researchers. Because treatment sites are not assigned by the investigator and because nothing is controlled or manipulated in natural experiments, differences between locations cannot be directly attributed to any particular cause. Lubchenco and Real (1991) consider these experiments a special case of observational studies and conclude that Diamond's 'natural experiment' is a misnomer that masks the true contributions of comparative ecological studies.

4.2 EXPERIMENTAL APPROACHES IN COMMUNITY ECOTOXICOLOGY

Development of experimental techniques in basic ecology was partially motivated by the recognition that comparative approaches are insufficient for demonstrating causation and understanding mechanisms. Manipulative experiments gained popularity in the 1960s as ecologists realized that agreement between mathematical predictions and field observations did not necessarily demonstrate the truth of these predictions. Although this same realization provided some motivation for the development of experimental approaches in community ecotoxicology, other factors also played an important role. Some ecotoxicologists questioned the validity of using single species laboratory experiments to predict responses of more complex systems in the field (Cairns 1983). In addition, some ecotoxicologists realized that the relative influence of biotic and abiotic factors on responses of communities to contaminants could only be assessed using experiments.

Like ecology, the field of community ecotoxicology is currently undergoing a transition from purely descriptive, observational approaches to more rigorous experimental techniques. However, this transition has occurred much more slowly in ecotoxicology, as experiments investigating community and ecosystem responses to contaminants are still relatively rare. Laboratory experiments, such as standardized 96-h toxicity tests, have been the workhorse of the regulated community for many years (Cairns 1983). The historical focus on simple laboratory experiments using single species has at least partially impeded implementation of community-level experimental approaches. The continued emphasis on these reductionist techniques for predicting ecological consequences of contaminants has been criticized (Cairns 1983, 1986; Odum 1984; Kimball and Levin 1985) and is surprising given the widespread support for integrated assessments (Adams *et al*. 1992; Karr 1993; Clements and Kiffney 1994; Joern and Hoagland 1996). In addition, recent studies have shown that single species tests may not predict community-level responses to contaminants because of indirect effects and higher-order interactions (Schindler 1987; Clements, Cherry and Cairns 1989; Pontasch, Niederlehner and Cairns 1989; Gonzalez and Frost 1994). If communities are more than random associations of non-interacting species, it follows that experimental approaches are required to understand the effects of contaminants on these interactions.

Currently there are no established protocols for investigating community responses to contaminants in experimental systems. Reviews of experimental approaches reveal an astonishing diversity of experimental conditions, communities, duration, spatiotemporal scale, experimental designs, and endpoints (Gillett 1989; Gearing 1989; Kennedy *et al*. 1995; Pontasch 1995; Shaw and Kennedy 1996). Most of these experimental studies have been conducted in aquatic systems (freshwater and marine). The limited number of studies conducted in terrestrial systems to investigate community responses to contaminants is considered a significant shortcoming in the field of ecotoxicology.

Ecotoxicologists have employed the same experimental approaches described in Table 4.1 to investigate the effects of contaminants on communities: laboratory experiments, field experiments, and natural experiments. Laboratory experiments using small-scale microcosms involve the exposure of natural or synthetic communities to specific chemicals. Larger experimental systems (mesocosms) are outdoors and generally have some interaction with the natural environment. Not surprisingly, field experiments (defined as the intentional addition of contaminants to natural systems) have received limited attention in ecotoxicology. However, this technique has become more common in the past few years. Researchers have also taken advantage of planned perturbations to assess the impacts of contaminants on communities. If data are collected before a particular chemical is released into the environment, the before–after control-impact (BACI) design (Stewart-Oaten, Murdoch and Parker 1986) is a powerful quasi-experimental approach that can be employed to assess community responses. Based on their experiences following the *Exxon Valdez* oil spill, Wiens and Parker (1995) provide an excellent overview of quasi-experimental approaches for assessing the impacts of unplanned perturbations. They note that experimental designs that treat the level of contamination as a continuous variable are generally more precise and offer the greatest opportunity to detect non-linear responses. Although relatively uncommon in community ecotoxicology, large-scale monitoring studies that compare communities with varying levels of perturbation are analogous to Diamond's (1986) natural experiments. Because treatments are not assigned randomly in comparative studies, these experimental designs also suffer from some of the same limitations as natural experiments.

4.3 MICROCOSMS AND MESOCOSMS

> *While direct projection from the small laboratory microecosystem to open nature may not be entirely valid, there is evidence that the same basic trends that are seen in the laboratory are characteristic of succession on land and in large bodies of water.* (Odum 1969)

> *Most of the crucial questions in applied ecology are not open to attack by microcosms.* (Carpenter 1996)

4.3.1 BACKGROUND AND DEFINITIONS

Because the application of microcosms and mesocosms to ecotoxicological research has been the subject of considerable controversy in recent years, it is important to place this research within the proper context. Model systems are effectively employed in a variety of fields, including engineering, architecture, and aviation. These scaled replicas are used to describe and evaluate performance of natural systems under a variety of experimental conditions. Similar to mathematical models, physical models make numerous simplifying assumptions to investigate the influence of specific variables. We contend that much of the criticism of model systems in ecotoxicological research is due to the failure of researchers explicitly to state these assumptions. To a certain extent, all experimental systems suffer from attempts to limit or control confounding variables (Drake, Huxel and Hewitt 1996). However, the strength of model systems lies in their ability to isolate key components and to investigate how these components respond to perturbation. Unlike field studies, microcosm and mesocosm experiments can provide clean tests of specific predictions of hypotheses (Daehler and Strong 1996). However, the degree of simplification necessary to obtain precise control often severs any connection to natural processes. This may or may not be a serious issue, depending on the specific goals of the study. If the primary objective of an experiment is to understand how a system works, then experiments should be as realistic as possible. However, if the primary objective is to obtain a mechanistic understanding of underlying processes, then realism may not be as significant (Peckarsky 1998). It is important to remember that microcosms and mesocosms do not attempt to duplicate all aspects of nature. In fact, given our incomplete understanding of the structure and function of ecosystems, it is naive to think that we could reproduce the complexities of nature. We agree with Lawton (1996) that the best way to understand the operation of a complex ecological system is to construct a model and determine if it functions as expected. Despite criticism by some researchers (Carpenter 1996), we feel that perturbations of model systems provide a powerful way to test basic and applied ecological hypotheses.

Recent reviews, essays, and special features have discussed the advantages and disadvantages of small-scale experiments in basic ecological research (Daehler and Strong 1996; Carpenter 1996; Schindler 1998; Resetarits and Bernardo 1998). Ives *et al.* (1996) characterized complexity, time scale, and scientific impact of microcosm and mesocosm experiments relative to other approaches employed in basic ecology (e.g. observational studies, field manipulations, theoretical studies). As expected, microcosm experiments generally included fewer species and were of shorter duration. However, there was relatively little difference in complexity and time scale between mesocosm experiments (field cages) and other approaches. The scientific impact of small-scale experiments was investigated by comparing the frequency of citations and prevalence in undergraduate ecology textbooks of microcosm and mesocosm experiments relative to other approaches. Ives *et al.* (1996) concluded that the type of study had a negligible role in determining scientific impact. In general, there were relatively few differences between small-scale experiments and other approaches employed in basic ecology.

Several chapters in the excellent book by Resetarits and Bernardo (1998) address the issues of spatiotemporal scale and trade-offs between control and realism in ecological experiments. The consistent theme in this volume is the necessary link between small-scale experiments and well planned observational studies. Resetarits and Fauth (1998) argue that the perceived trade-off between rigor and realism is partially a consequence of our lack of creativity in designing experiments. The importance of ecological realism in experimental design should be addressed in the same way scientists evaluate other research questions. That is, the criticism that model systems do not reflect processes in the natural world is simply a 'hypothesis to be tested' (Resetarits and Fauth 1998).

Currently, the most significant challenge in microcosm and mesocosm research is to identify those key features that must be carefully reproduced in order to simulate structure and function of natural systems. How much simplification is possible in model systems before we lose the connection with the natural system we are attempting to simulate? In a comparison of microcosm, mesocosm, and whole ecosystem experiments, Schindler (1998) contends that small-scale studies may provide highly replicable but spurious results about community and ecosystem processes. Perez (1995) recommends the use of sensitivity analysis, a simulation technique that allows researchers to evaluate the relative importance of numerous variables, to identify critical aspects of model systems. Variables that significantly influence function of the model system must be reproduced carefully, whereas unimportant variables may receive less attention.

Although model systems are not typically included in ecological risk assessment or used for establishing chemical criteria, the value of microcosms and mesocosms to assess effects of contaminants on communities has been recognized for many years (see reviews by Gillett 1989; Gearing 1989; Graney, Giesy and DiToro 1989). The emergence of model systems in ecotoxicological research represents an important transition from reductionist to holistic approaches (Odum 1984). Although the distinction between microcosms and mesocosms is not always obvious in the literature, microcosms are generally smaller in size and commonly located indoors. Microcosms are defined as controlled, laboratory systems which attempt to simulate a portion of the natural world. Odum (1984) defined mesocosms as 'bounded and partially enclosed outdoor experimental setups'. Because they are only partially enclosed, mesocosms generally have greater exchange with the natural environment. Despite these differences, one common feature of both microcosm and mesocosm experiments is that they can investigate the responses of numerous species simultaneously. Consequently, endpoints examined in microcosm and mesocosm experiments are not restricted to simple estimates of mortality and growth but generally include an array of structural and functional measures (community composition, species richness, primary productivity).

A special series of articles published in *Ecology* entitled 'Can we bottle nature?' (Daehler and Strong 1996) examined the role of microcosms in basic ecological research. Although the articles did not emphasize effects of contaminants, a general consensus that emerged was that small-scale experimental approaches should be used to solve problems in applied ecology. Most of the contributors agreed that while microcosm experiments can provide very 'clean' results with tight control of biotic and abiotic variables, microcosm research programs should be well integrated with field studies. Issues such as the simplicity of artificial communities and the lack of immigration and emigration can be addressed by comparing results of microcosm experiments with more traditional monitoring approaches conducted in the field. We agree with Carpenter (1996) that without the context of proper field studies, many microcosm experiments are 'irrelevant and diversionary'.

As noted above, microcosm experiments have played a major role in the development and testing of ecological theory (Drake, Huxel and Hewitt 1996). Many of the ideas proposed by early theoretical ecologists (e.g. the competitive exclusion principle) were tested in relatively simple experimental systems, and results provided insights for additional theoretical and empirical research. Unfortunately, microcosm and mesocosm research has not achieved a similar status in ecotoxicology. Although microcosms and mesocosms have been employed to assess impacts of contaminants on populations and communities, they have not played a major role in ecotoxicological research. Reviews of the major journals in aquatic and terrestrial toxicology reveal a surprisingly infrequent application of these tools. Notable exceptions include a few published symposia and special features that focused on microcosm and mesocosm experiments (*Environmental Toxicology and Chemistry*, 1992, 11(1); *Ecological Applications*, 1997, 7(4)).

4.3.2 DESIGN CONSIDERATIONS IN MICROCOSM AND MESOCOSM STUDIES

A valid criticism of microcosm and mesocosm research is that the emphasis placed on increasing reproducibility and decreasing variability has come at the expense of ecological relevance to natural systems. Thus, one of the most important considerations when conducting microcosm or mesocosm research is to understand how biotic and abiotic conditions in model systems compare with the natural system. Surprisingly, few studies report information collected from the specific field sites represented by these experimental systems. In a review of aquatic microcosms, Gearing (1989) noted that only 9% of 339 published articles collected field data to verify that communities in microcosms were similar to those in natural systems. The most likely explanation for the failure to report ecological conditions is that many of these experiments were conducted simply to test the effects of a particular chemical. Relatively few microcosm or mesocosm experiments were designed to validate data from a specific field site. Nonetheless, information on the similarity or dissimilarity of the experimental systems and natural systems is necessary when evaluating the efficacy and ecological realism of microcosms.

4.3.2.1 Source of Organisms

The source of organisms is a major design issue when conducting microcosm and mesocosm experiments. One common approach is to add synthetic assemblages of organisms, generally obtained from laboratory cultures, to the experimental system at known densities. This technique ensures that replicates have similar initial community composition before the experimental units are assigned to treatments. In addition to providing a standardized technique for assessing effects of contaminants, variance is greatly reduced by controlling initial community composition. Freda Taub and others (Taub 1989, 1997; Matthews, Landis and Matthews 1996; Landis, Matthews and Matthews 1997) have successfully employed this approach to investigate the effects of contaminants on microbial and planktonic assemblages. Taub's standardized aquatic microcosm (SAM) is now an American Society for Testing and Materials (ASTM) protocol (ASTM 1995), representing a major advance in the application of community-level endpoints in a regulatory framework. The same opportunities for comparisons among chemicals and among species which are cited as a major advantage of single species toxicity tests are also realized using a SAM. However, because of the synthetic composition of these communities, this standardized approach has been criticized because it lacks ecological relevance to natural systems (Perez 1995). As with most decisions in the development of model systems, trade-offs are often necessary between standardization and increased ecological realism.

The alternative methods for establishing organisms in microcosms and mesocosms are to add natural communities or to allow the system to colonize naturally. Both methods should result in communities that are initially similar to those in the natural system, thus improving ecological realism of the experiment. Samples of a known area or volume collected from the environment can be added to obtain realistic abundances of organisms. Perez *et al*. (1991) collected discrete samples of seawater and sediment cores containing indigenous organisms to investigate fate and effects of Kepone in microcosms. Experiments conducted with naturally-derived microbial communities have investigated effects of herbicides and other chemicals on structural and functional endpoints (Niederlehner *et al*. 1990; Pratt *et al*. 1997; Pratt and Barreiro 1998). Colonized substrates obtained from reference systems are placed in replicate microcosms containing initially uncolonized 'islands'. Using principles derived from the theory of island biogeography (MacArthur and Wilson 1963), colonization rate of these islands over time is compared in control and contaminated microcosms (Cairns, Hart and Henebry 1980). Clements, Cherry and Cairns (1989) developed a similar collection technique to expose natural communities of benthic macroinvertebrates to contaminants in stream microcosms. Substrate-filled trays were colonized in a natural stream and then transferred to replicate microcosms. The communities added to the streams were similar among replicates and, more importantly, similar to those in the natural system.

Natural colonization of microcosms and mesocosms is probably the best way to ensure that communities resemble natural systems. This approach is most appropriate in larger mesocosm experiments that have some exchange with the local environment. However, because initial densities are not controlled by the investigator, variability among replicates may be problematic. For example, Jenkins and

Buikema (1998) showed that zooplankton communities established in 12 similar pond mesocosms were markedly different after 1 year of colonization. In addition to differences in structural characteristics among the ponds, secondary productivity and community-level respiration rates also varied. Differences in structural and functional characteristics prior to the start of a mesocosm experiment will greatly complicate our ability to measure responses to contaminants. Unlike standard toxicity tests, initial abundances will not be known precisely and therefore data cannot be expressed using conventional toxicological endpoints (e.g. percent mortality). Initial community composition can be compared with controls at the end of the experiment to obtain some estimate of variability. However, more commonly results are simply compared across treatments.

4.3.2.2 Spatiotemporal Scale

The limited spatiotemporal scale of microcosms and mesocosms is considered one of their most serious weaknesses. Few studies have tested the hypothesis that experiments conducted at one scale are appropriate for predicting responses at a different scale. This question is central to the debate over the usefulness of model systems and clearly an important research need in ecotoxicology. Although increasing the size of a mesocosm may eliminate some potential artifacts, this does not make the study an ecosystem experiment (Schindler 1998). The relatively small spatial scale of microcosms greatly restricts the numbers and types of organisms that can be included. If larger or longer-lived organisms such as top predators are an essential component of the natural system (e.g. in systems regulated by top-down predators) or have a disproportionate influence on its structure (e.g. a keystone species), results of microcosm experiments that exclude these species may not be valid. However, because relatively few natural communities are controlled by top predators or keystone species, failure to include large, wide-ranging taxa in model systems may not be a serious issue. The fact remains that we do not know if the exclusion of certain species from microcosm experiments will influence results because of our poor understanding of these scaling issues.

A more serious issue related to the small spatial scale of microcosms and some mesocosms are container artifacts. Accumulation of biotic and abiotic materials on the container walls can complicate assessments of exposure, especially if contaminants are removed from the system either by bioaccumulation or adsorption. Periodic scraping of fouling material from the container walls is one solution to this problem. However, in a closed system this can result in pulses of organic enrichment unless the material is removed from the container. Because of surface area to volume relationships, container effects generally diminish with increased size of the microcosm.

Perez *et al.* (1991) provided one of the few detailed analyses of the effects of spatial scale on community responses to contaminants. Intact water column and benthic communities were exposed to Kepone in 9-, 35- and 140-l containers. Results showed that fate and effects of Kepone on aquatic communities were size dependent. Phytoplankton density was actually greater in treated microcosms compared with controls due to reductions in abundance of grazing zooplankton; however, this effect was limited to small microcosms (Fig. 4.3). Similarly, the concentration of Kepone in surface sediments and the potential exposure to benthic organisms increased with microcosm size due to greater mixing and bioturbation in larger microcosms. Based on these results, Perez *et al.* (1991) concluded that small microcosms would underestimate the effects of Kepone on aquatic communities. The dependency of community responses on container size has obvious implications for ecological assessments using microcosms and mesocosms.

Finally, the relatively short temporal duration of most microcosm and mesocosm experiments limits the realism of these systems. The logistical difficulties of maintaining laboratory or large mesocosm experiments often prohibit long-term

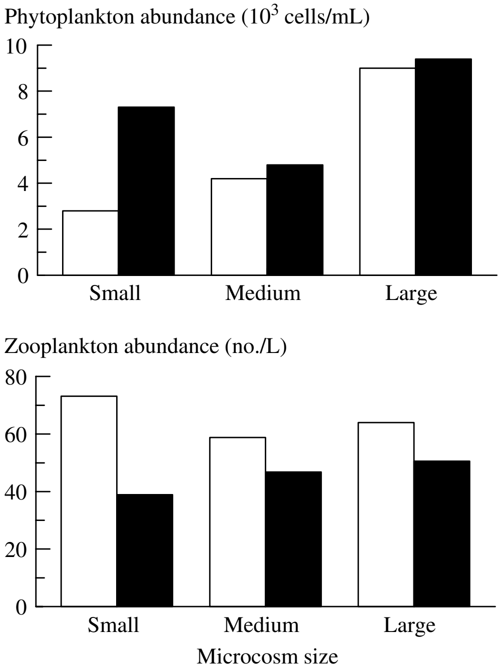

Fig. 4.3. Response of phytoplankton and zooplankton communities to Kepone (solid histograms) in small, medium, and large microcosms. Effects of Kepone on zooplankton abundance were greater in small microcosms. Reduced abundance of zooplankton and lower grazing pressure resulted in an increase in abundance of phytoplankton in small microcosms. (Modified from Perez *et al.* 1991)

studies. More importantly, because environmental conditions in model systems deviate from natural systems over time, most experiments are conducted over relatively short time periods (generally <6 months). In model systems where recruitment or immigration are absent, population abundances of most species will decrease and community composition may significantly deviate from the initial conditions. While comparison across treatments partially alleviates this problem, separating these temporal changes in communities from those due to contaminants will complicate assessment of effects.

4.3.2.3 The Influence of Seasonal Variation on Community Responses

The time of year when microcosm or mesocosm experiments are conducted can influence the relative toxicity of contaminants and responses of communities. Because physical and chemical conditions that modify toxicity and bioavailability (temperature, pH, dissolved organic carbon) may vary seasonally (Perez *et al*. 1991), it is important to document this information when conducting mesocosm studies. Experimental results of mesocosm studies will also be influenced by seasonal variation in community composition. Winner, Owen and Moore (1990) used a mesocosm study to demonstrate that seasonal variation in sensitivity of planktonic communities to copper resulted from seasonal changes in dissolved organic carbon (DOC) and community composition. Although this temporal variation may complicate interpretation of experimental results, it also provides opportunities to test specific hypotheses concerning the role of seasonality. By conducting experiments at different times of year with presumably different communities and different physicochemical conditions, we can obtain a better understanding of how these factors influence responses in the field.

4.3.3 STATISTICAL ANALYSES OF MICROCOSM AND MESOCOSM EXPERIMENTS

The major advantage of model systems over field experiments and ecosystem manipulations is the ability randomly to assign and replicate treatments, thus allowing researchers to analyze results using inferential statistics. Depending on the specific objectives of the study, a wide range of experimental designs have been employed in microcosm and mesocosm studies. An excellent overview of design considerations describing how to evaluate different experimental designs for community-level tests is provided by Smith (1995). Assuming that a finite number of experimental units is available, one of the first decisions is how to allocate experimental units among treatments and replicates. The necessary number of replicates will depend on the sampling variability, desired precision (e.g. how much change is considered ecologically relevant), and the selected α-value. Several algorithms are available to estimate power of an experiment and the necessary number of replicate samples based on these considerations (Green 1979). Because sampling variability and the number of replicates will differ among endpoints, estimates of sample size should be based on the most variable endpoint.

There has been considerable discussion in the literature concerning the relative merits of ANOVA and regression approaches for analyzing results of microcosm and mesocosm experiments (Liber *et al*. 1992). There is little difference in the statistical analyses used in ANOVA and regression designs. However, because the allocation of treatments and replicates among experimental units must occur prior to the start of the experiment, researchers must decide in advance which design to employ. Again, this decision will depend on the specific goals of the investigation. If the primary objective is to estimate a 'safe' concentration of a particular chemical (e.g. the no observed effect concentration, NOEC), an ANOVA approach is most appropriate. The number of treatment levels will be determined after estimating the number of replicates required. For example, if only 12 experimental units are available and preliminary power calculations indicate that three replicates are necessary to detect significant differences, four levels of treatment are possible. Unbalanced designs (unequal number of replicates in each treatment) are possible using ANOVA, but these are uncommon in community-level experiments (Smith 1995). More complex factorial designs are also useful in community experiments where researchers assess the relative importance of multiple stressors. For example, if we are interested in understanding the interaction of temperature and acidification, the same 12 mesocosms could be used in a 2 × 2 factorial design (three replicates each) with two levels of temperature (low, high) and two levels of acidification (control, acid dosed). In addition to estimating the relative importance of temperature and acidification (the main effects), this design allows us to test for potential synergistic or antagonistic interactions between these stressors.

If the goal of the experiment is to establish a relationship between the concentration of the chemical and community-level response, then regression analysis is more appropriate than ANOVA. In a regression approach, we are less interested in a specific chemical concentration than in the slope of the concentration–response relationship. In the above example, each of the 12 experimental units could receive a different treatment (without replication) to establish this relationship. This approach would allow us to estimate the specific concentration that elicits a particular community response. For example, we may be interested in knowing the concentration that results in a 20% reduction in species richness. In addition, by comparing the slopes of the regression lines for several community-level endpoints, we could estimate their relative sensitivity to the particular chemical.

4.3.4 GENERAL APPLICATIONS OF MICROCOSMS AND MESOCOSMS

> *Microcosms, in theory, should be one of the most valuable tools available to ecotoxicology.* (Gearing 1989)

The original focus of most microcosm and mesocosm research was to predict transport and fate of contaminants under controlled conditions. Various processes involved in the movement of contaminants through biotic and abiotic compartments, including volatilization, microbial degradation, biotransformation, and food chain transfer, are readily quantified using microcosms and mesocosms. More recent applications of microcosms and mesocosms in community ecotoxicology emphasize assessment of ecological effects. Experimental systems have been used to support regulatory decisions regarding safe concentrations of pesticides (Giddings *et al*. 1996), establish concentration–response relationships in community-level experiments (Kiffney and Clements 1996), validate single species toxicity tests (Pontasch, Niederlehner and Cairns 1989), compare sensitivity of different endpoints (Carlisle and Clements 1999), validate field responses (Niederlehner *et al*. 1990), and evaluate interactions among multiple factors (Barreiro and Pratt 1994; Pratt and Barreiro 1998). Because community-level responses to contaminants may vary among locations, mesocosms also provide an efficient way to compare effects among different communities.

4.3.4.1 The Use of Mesocosms for Pesticide Registration

Mesocosm testing has been employed to measure effects of chemicals and estimate safe concentrations. Using an experimental design in which target concentrations bracket lowest observed effect concentrations (LOEC), researchers can determine if levels considered safe based on single species toxicity tests are actually protective at the community and ecosystem level. Although this type of experimental design has been criticized, most studies conducted in pond mesocosms were designed to estimate ecological effects at a specific test concentration. The most controversial application of mesocosms in ecotoxicology was their use in a regulatory framework. The US EPA's tiered approach for hazard assessment, the predecessor of contemporary ecological risk assessment, used a sequential series of tests to evaluate the risk of pesticides. Tier 4 tests, the most complex and ecologically relevant, involved field experiments that measured population, community, and ecosystem-level effects. A large number of studies published in the 1980s were designed to meet guidelines developed by the US EPA for pesticide registration (Touart 1988; Touart and Maciorowski 1997). An excellent series of papers on the use of mesocosms for pesticide registration was published as a special issue of *Environmental Toxicology and Chemistry* (vol. 11, no. 1) in 1992. Although most of the studies examined fate and effects of pyrethroid insecticides (Heinis and Knuth 1992; Fairchild *et al*. 1992; Lozano *et al*. 1992; Webber *et al*. 1992), appropriate experimental designs were also discussed (Liber *et al*. 1992). A unifying theme for these studies, and indeed a primary motivation for conducting mesocosm research, is the opportunity to investigate direct and indirect effects simultaneously.

EPA's requirements for pesticide registration using mesocosm testing were rescinded in 1992. Not surprisingly, this decision created an outcry among ecotoxicologists who noted the paucity of ecological information in most risk assessments (Pratt *et al*. 1997). Institutions that had invested heavily in construction of mesocosm facilities in the USA were scrambling to identify other uses for these tests systems. This decision, which was defended on the grounds that the likelihood of false negative results based on single species tests did not justify the greater expense of multispecies experiments, was considered a major step backward by ecotoxicologists (Taub 1997).

The primary reasons for dropping mesocosm testing requirements were the problems obtaining reproducible results, variable data, and difficulties interpreting results. In addition, there was the belief that mesocosm experiments were not providing additional information beyond what was available based on single species laboratory tests. It is not surprising that data collected from mesocosm experiments were variable and complex. Indeed variability is a defining characteristic of most ecological systems and an understanding of this variability can greatly improve our ability to predict responses in nature. Simberloff (1980) characterizes ecologists' frustration with natural variability and their attempts to understand ecological responses based on purely deterministic processes as 'physics envy'. He further states that 'what the physicist considers noise is music to the ears of the ecologist'.

We feel that EPA's decision to abandon mesocosm testing represents a missed opportunity to increase our understanding of how natural systems respond to chemical stressors. Armed with an appreciation of natural variability of ecological systems and a greater commitment to more sophisticated data analysis procedures (e.g. multivariate techniques and non-linear regression), a national mesocosm testing program could make a major contribution to the field of ecotoxicology. As long as regulatory agencies continue to rely on simplistic laboratory procedures for estimating field effects, ecological risk assessment will remain a reactive rather than a predictive science (Fairchild *et al*. 1992; Chapman 1995; Perez 1995).

4.3.4.2 Development of Concentration–Response Relationships

Another important application of microcosm and mesocosm research is to establish concentration–response relationships between contaminants and community-level endpoints (Fig. 4.4). If treatments are selected to represent a range of potential responses, researchers can estimate the level of impact expected to occur at a particular chemical concentration (e.g. the concentration that results in 20% reduction in species richness). Therefore, instead of extrapolating results of single species toxicity tests to community-level responses, the direct effect of a chemical on these responses could be quantified in a mesocosm experiment. Figure 4.4 shows that the estimated community-level lowest observed effects concentration

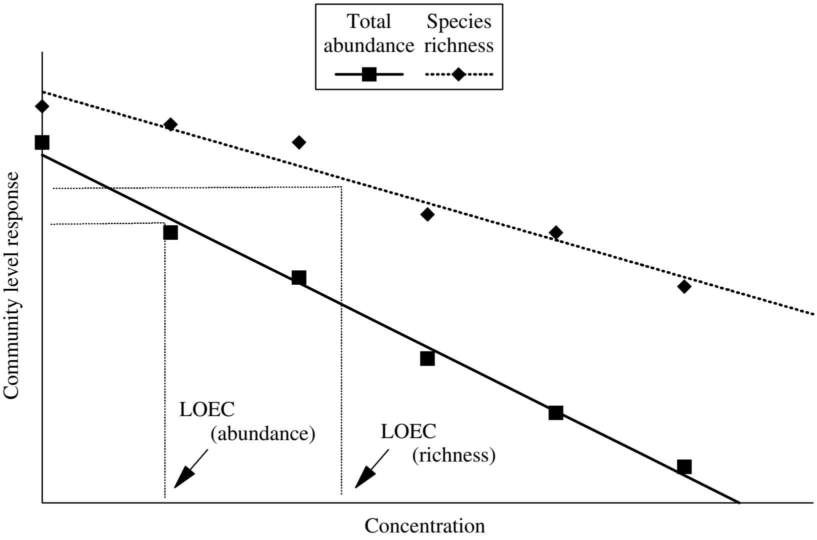

Fig. 4.4. Hypothetical community-level responses to contaminants in microcosm or mesocosm experiments. The figure shows experimentally-derived lowest observed effect concentrations (LOEC) for total abundance and species richness. LOEC values were based on an estimated 20% reduction in treated systems compared with controls. In this example, species richness was less sensitive to the contaminant than total abundance

(LOEC) is less for total abundance than for species richness. If these experimental results are correct, we would expect this particular chemical to have greater effects on abundance than species richness in the field. Because most microcosm and mesocosm experiments involve exposure of numerous species simultaneously, regression approaches can be used to estimate species-specific sensitivity to a particular contaminant. As described in Chapter 3 (Box 3.1), the slopes of concentration–response relationships for individual taxa provide an objective estimate of tolerance and can be used to develop biotic indices. These population and community responses observed in mesocosms could then be verified using routine field biomonitoring.

4.3.4.3 Investigation of Stressor Interactions

Perhaps the most important contribution of microcosm and mesocosm research, which cannot be easily investigated in ecosystem manipulations or natural experiments, is the opportunity to measure interactions among stressors. Using a relatively simple factorial design, researchers can investigate effects of two different stressors simultaneously and estimate the potential interaction between stressors (Genter *et al*. 1988; Genter 1995; Courtney and Clements 2000). Genter (1995) used stream microcosms to quantify interactive effects of acidification and aluminum on periphyton communities and to measure the indirect effects of heavy metals on grazing by snails (Genter *et al*. 1988). Conducting studies where direct and interactive effects of multiple stressors are investigated simultaneously requires a degree of control that is generally not possible in field studies. The opportunity to examine interactions among multiple stressors in microcosm experiments and to develop mechanistic explanations for these interactions will greatly improve our ability to predict responses in natural systems.

4.3.4.4 Influence of Environmental and Ecological Factors on Community Responses

One of the most consistent limitations of ecological data collected from field studies is the high amount of unexplained variability in natural communities. The same concentration of a particular chemical may have large effects on one community but negligible effects on another. Microcosm and mesocosm experiments can be designed to compare differences in responses among communities and to quantify the influence of environmental conditions on these responses. In addition, controlled experiments may elucidate mechanisms which show how environmental factors influence community responses. Simple factorial designs could be employed to compare the impacts of a stressor on communities collected during different seasons or obtained from different locations. Barreiro and Pratt (1994) used microcosms to demonstrate that effects of herbicides on periphyton communities were influenced by levels of nutrients and trophic status. Results showed that communities established under low nutrient conditions were more susceptible to chemical stress and required longer time to recover. Similar results were reported by Steinman *et al*. (1992) in which resilience of periphyton communities to chlorine stress increased with the rate of nutrient cycling. Experiments conducted with protozoan communities examined the influence of community maturity on contaminant responses (Cairns, Hart and Henebry 1980). These studies showed that effects of copper on colonization rate was greater in immature communities compared with mature communities.

Microcosm and mesocosm experiments are the most effective way to evaluate the influence of community composition on stressor responses. Sallenave, Day and Kreutzweiser (1994) reported that downstream transport of PCBs was greater in experimental streams with grazers or shredders than in streams without these two functional groups. Kiffney and Clements (1996) compared responses of benthic macroinvertebrate communities collected from low and high elevation streams to heavy metals in stream microcosms. Because low and high elevation communities were exposed to the same concentration of metals, the experiment provided an opportunity to estimate differences in sensitivity between locations. Results showed that headwater communities were more sensitive to heavy metals than communities from a low elevation stream (Fig. 4.5). These differences in sensitivity between locations suggest that criterion values protective of low elevation communities may not be protective of those from high elevations (Kiffney

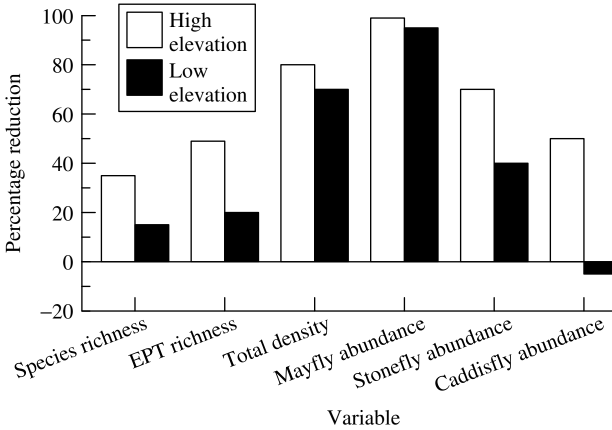

Fig. 4.5. Comparison of the effects of contaminants on communities from different locations. The figure shows the responses of benthic macroinvertebrate communities to heavy metals in stream microcosms. Communities collected from low and high elevation sites were exposed to the same concentration of heavy metals. The responses were based on the percent reduction of benthic metrics in treated microcosms compared with control microcosms. For all metrics the effects of metals were greater on the community from the high elevation site. (Modified from Figures 2 and 3 in Kiffney and Clements 1996)

and Clements 1996). Interestingly, this pattern was reversed for diatom assemblages. Medley and Clements (1998) observed reduced effects of heavy metals on diatoms from headwater communities compared with those from lower elevations. Because headwater streams were naturally dominated by early successional species (*Achnanthes minutissima*), which are also tolerant of metals, communities showed little response to metals in experimental streams.

4.3.4.5 Species Interactions

Microcosms and mesocosms can also be employed to measure the effects of contaminants on species interactions such as competition or predation. Manipulation of predator density and contaminant concentration in a 2 × 2 factorial design allows researchers to determine if the susceptibility of prey species to predation is influenced by exposure to a chemical stressor (Clements 1999). An interaction between stressor level and susceptibility to predation is the cause for many concerns about potential indirect effects of contaminants. Studies describing effects of contaminants on species interactions were reviewed in Chapter 2.

4.3.4.6 Applications in Terrestrial Systems

Microcosm and mesocosm research conducted at the community level has overwhelmingly focused on aquatic systems. Gillett's (1989) review of terrestrial microcosm and mesocosm experiments emphasized chemical fate and ecological effects of contaminants on populations. Relatively few studies cited in this review examined community-level responses. Nonetheless, there are important opportunities for microcosm and mesocosm experiments in terrestrial community ecotoxicology. In particular, soil microcosms offer a unique system to study structural and functional features of natural communities. Because of the small size and short generation times of many soil organisms, entire communities can be studied under realistic conditions in the laboratory. Verhoef (1996) compared ecosystem processes, such as CO_2 production and nutrient availability, in microcosms, mesocosms, and field studies. Although there were differences in functional attributes among systems, the magnitude and relative ranking of response variables were similar. These results suggest that spatial scale may be a less serious concern in soil microcosms.

The Ecotron facility in Ascot, UK is a large-scale, terrestrial mesocosm system where researchers have investigated a variety of community processes across several trophic levels (Lawton 1996). The facility consists of 16 environmental chambers with precise control over light, temperature, humidity, and rainfall. Research conducted in this facility has investigated: species interactions; the relationship between species diversity and ecosystem processes; and impact of CO_2 on population, community, and ecosystem dynamics. Although Ecotron has not been employed in ecotoxicological research, this type of facility would be ideal for investigating direct and indirect effects of chemical stressors on terrestrial communities.

Larger mesocosms have been employed to measure the effects of pesticides on terrestrial communities. Suttman and Barrett (1979) used a series of field enclosures to test Odum's (1969) hypothesis that effects of stress are greater on immature communities compared with mature communities. Field enclosures established in immature (monocultures of oats) and mature (late successional fields) systems were treated with the pesticide carbaryl and responses of plant and arthropod communities were compared with those in control plots. Although results supported the hypothesis that insecticide effects were greater in the immature system, the period of recovery was greater in the mature community. More recently, Sheffield and Lochmiller (2001) used 0.1-ha (32 × 32 m) enclosures to examine the effects of the organophosphate insecticide diazinon on community structure and species interactions. Applications of 1.0 × and 8.0 × the recommended field application rate of diazinon resulted in significant reproductive effects on small mammals, with considerable variation observed among species (Fig. 4.6). Consumption of dead and dying insects was considered the most important route of exposure. Because of the significant reduction in arthropod density, it is possible that some of the observed reproductive effects resulted from lower prey abundance in treated plots. We agree with the authors that field studies using mesocosms that simultaneously investigate population and community-level responses are critical for evaluating indirect effects of pesticides.

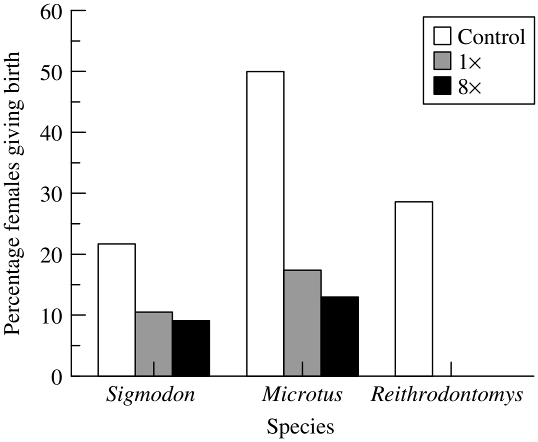

Fig. 4.6. Effects of the insecticide diazinon at 1× and 8× the recommended application rate on a small mammal community in outdoor enclosures. Results showed significant effects on reproduction at low levels of exposure and considerable variability among species. Because of the large reduction in insect abundance in the mesocosms, some of the effects on reproduction may have resulted from reduced prey availability. (Data from Table 4 in Sheffield and Lochmiller 2001)

4.3.5 SUMMARY

Because microcosm and mesocosm experiments attempt to bridge the gap between single species toxicity tests and full-scale ecosystem studies, they receive criticism for being too simplistic and too complex. Ecologists consider model systems to be unrealistic simplifications of nature, whereas toxicologists are reluctant to consider community-level testing because results are complex and difficult to interpret. Despite their shortcomings, the use of microcosms and mesocosms could contribute significantly to our understanding of the effects of contaminants on communities. The degree of control over independent variables allows researchers to isolate specific components and investigate the mechanisms responsible for changes in community composition. Microcosm and mesocosm approaches represent a link between standardized, single species toxicity tests and more expensive, logistically difficult field experiments. However, questions of spatiotemporal scale remain largely unanswered and must be addressed if model systems are to play an important role in ecotoxicological research. As noted above, the significance of spatiotemporal scale in microcosm and mesocosm research is a hypothesis that remains to be tested. Just as researchers design studies to test the effects of a particular chemical, experiments should also be conducted to test responses at different spatiotemporal scales. When mesocosm experiments and field collections are conducted simultaneously, model systems can be used to support results of non-experimental, descriptive studies and make a stronger argument for causal relationships.

4.4 WHOLE ECOSYSTEM MANIPULATIONS

> *...accurate ecosystem management decisions cannot be made with confidence unless ecosystem scales are studied.* (Schindler 1998)

Although microcosm and mesocosm studies have contributed to our understanding of community responses to contaminants and other forms of anthropogenic disturbance, critics argue that results of small-scale experiments reveal little about the natural world (Carpenter 1996). For example, because of the difficulty including top predators, results of mesocosm experiments should be viewed cautiously when predicting effects in systems where top-down effects are important. In addition, spatial and temporal scaling issues are a concern in most microcosm and mesocosm research. Container effects in small model systems may change environmental conditions, alter exposure regimes, and limit the duration of microcosm and mesocosm experiments.

One solution to the limited spatiotemporal scale and lack of ecological realism of model ecosystems is the direct application of contaminants in the field. Barrett (1968) treated a 0.4-ha (approximately 1.0 acre) fenced enclosure with the insecticide carbaryl and compared responses with those observed in a single control plot. Total biomass of arthropods was reduced by 95% in the treated plot, and patterns of recovery varied among taxa. The most significant response in the small mammal community was a dramatic shift in relative abundance of two species resulting from differential effects of carbaryl on reproduction. Barrett (1968) concluded that while direct toxicity of carbaryl was greatly reduced within a few days, long-term effects on structure and function persisted. Effects of disturbance on a forest ecosystem at a large spatial scale were investigated by Woodwell (1970). This classic experiment examined chronic effects of gamma radiation on structure and function of oak-pine forests at the Brookhaven National Laboratory, New York. Results showed a distinct alteration in community structure that diminished with distance from the radiation source. One of the first large-scale manipulations conducted in a riparian ecosystem examined the effects of clear-cutting and herbicide applications on nutrient budgets in the Hubbard Brook Experimental Forest, New Hampshire (Likens *et al*. 1970). Results showed that disturbed watersheds exported large amounts of particulate matter and inorganic material.

These early experiments revealed the usefulness of whole ecosystem manipulations for assessing effects of contaminants on terrestrial communities. More importantly, they demonstrated that community responses to anthropogenic stressors were predictable and similar to natural disturbances. For example, patterns observed in response to chronic radiation were remarkably consistent with those observed following exposure of plant communities to salt spray, fire, and other natural disturbances (Woodwell 1970). The similarity of responses to natural and anthropogenic stressors illustrated in these early studies has been a consistent theme in subsequent whole ecosystem manipulations (Rapport, Regier and Hutchinson 1985) and will be described in Chapter 6.

4.4.1 EXAMPLES OF ECOSYSTEM MANIPULATIONS: AQUATIC COMMUNITIES

With their emphasis on ecological theory and principles of recovery, these early experiments set the stage for more focused studies of ecosystem-level responses to contaminants. Although numerous ecosystem-level manipulations have been conducted since the early 1970s (see review by Perry and Troelstrup 1988), two research programs deserve special attention because of their significant contributions to our understanding of how natural communities respond to chemical stressors. First, David Schindler's experiments conducted in the Experimental Lakes Area (Ontario, Canada) measured structural and functional responses of lakes to a variety of anthropogenic stressors, including nutrients, acidification, and heavy metals (Schindler 1988). Subsequent whole lake manipulations conducted by researchers in other parts of North America verified the importance of this experimental approach. Next, Bruce Wallace's team at the University of Georgia has conducted a long-term study of watershed responses at Coweeta Hydrologic Laboratory (North Carolina, USA). Although these experiments were primarily limited to insecticides, results highlighted the importance of measuring direct and indirect effects of contaminants on ecological processes.

4.4.1.1 Experimental Lakes Area (ELA)

The Experimental Lakes Area (ELA) consists of 46 natural, relatively undisturbed lakes located in northwestern Ontario. The lakes have been designated specifically for ecosystem-level research and have been used to investigate the effects of anthropogenic stressors on biotic and abiotic characteristics. The initial motivation for these manipulations was to increase fish productivity (Schindler 1988), but early experiments at the ELA also clarified important misconceptions about the causes of eutrophication in lentic ecosystems. Previously, many researchers believed that carbon was the primary limiting factor in lakes, and that reducing input of other nutrients (N and P) would have little beneficial effect. The striking results of phosphorus addition experiments in Lake 227, visually displayed on the cover of *Science* in 1974 (Schindler 1974), demonstrated unequivocally that phosphorus was a major cause of eutrophication.

One of the more insightful observations from the ELA studies was that although these experiments were initiated with a set of explicit and testable hypotheses, researchers were consistently met with surprises (Schindler 1988). This statement is both a testimony to the importance of ecosystem manipulations and an admission of our relatively poor understanding of ecosystem processes. Many of these surprises were a result of indirect effects of contaminants on species interactions. Schindler states that 'in every aquatic experiment which we have done, the whole ecosystem response has involved complicated interactions between a number of species in the biotic community'. The most striking example of this statement, with obvious relevance to community ecotoxicology, is from whole lake acidification experiments. Effects of acidification on lentic communities resulted from a complex interaction of direct toxicity, reproductive failure, increased parasitism, and starvation due to loss of prey species (Schindler 1987).

Another significant finding from the long history of ecosystem manipulations at ELA was the relative insensitivity of functional measures (e.g. decomposition, nutrient cycling, primary productivity) compared with structural measures (e.g. species richness, community composition). Despite an initial emphasis on ecosystem processes, most studies found that functional measures were slower to respond and generally responded only to high levels of stress compared to structural measures (Schindler 1987). The general insensitivity of functional measures has been a consistent observation in ecosystem experiments (Howarth 1991), and has important implications for the selection of endpoints in contaminant research. Because of the insensitivity of functional measures, Schindler (1988) suggests that future studies should emphasize taxonomy and community ecology, possibly at the expense of more 'fashionable' measures such as ecosystem metabolism and nutrient cycling.

4.4.1.2 Coweeta Hydrologic Laboratory

Experiments conducted by Bruce Wallace and colleagues at Coweeta Hydrologic Laboratory investigated effects of the pesticide methoxychlor on benthic communities in small headwater streams. Interestingly, the initial motivation for these experiments was not to assess effects of pesticides but rather to determine the functional role of benthic macroinvertebrates. The application of methoxychlor was simply the most direct method for eliminating large numbers of macroinvertebrates from the stream. Catastrophic macroinvertebrate drift, approximately 1000 × greater than pre-treatment levels, occurred immediately following application of methoxychlor (Wallace, Webster and Cuffney 1982; Cuffney, Wallace and Webster 1984). The resulting alterations in benthic community composition included a dramatic reduction in abundance of aquatic insects, especially shredders, and subsequent replacement by non-insects (oligochaetes).

Although documenting changes in community composition and differences in sensitivity among macroinvertebrate groups was important, the most significant contribution of Wallace's experiments was the establishment of a relationship between structural and functional characteristics of headwater streams. In contrast to results reported from ELA experiments, Wallace and colleagues found that functional measures were relatively sensitive to chemical stress. Application of methoxychlor resulted in significant alteration in detritus dynamics in the treated stream (Fig. 4.7). The rate of leaf decomposition and the dry mass of

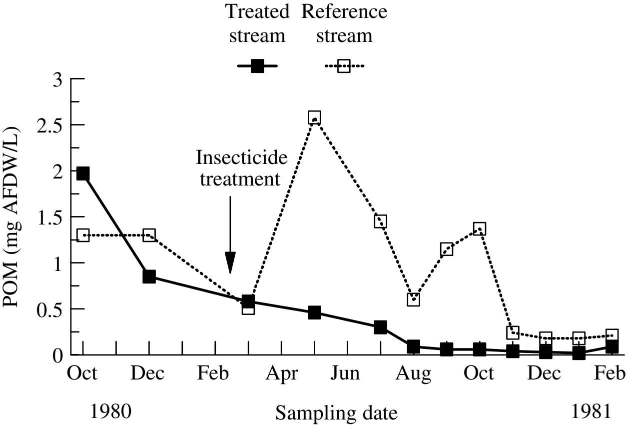

Fig. 4.7. Export of particulate organic material (POM) in reference and treated streams in Coweeta Hydrologic Laboratory (North Carolina, USA). The treated stream was dosed with the insecticide methoxychlor in February 1980. The reduction in export of POM in the treated stream was hypothesized to result from the elimination of shredders, organisms that feed on coarse leaf detritus and convert this material to smaller particles. (Modified from Figure 1 in Wallace, Webster and Cuffney 1982)

suspended particulate organic matter (POM) was significantly lower in treated streams compared with controls. These alterations were directly attributable to loss of shredders, as there was relatively little influence of pesticide treatment on microbial communities (Wallace, Webster and Cuffney 1982). More importantly, these results suggest that indirect effects of pesticides on organic matter processing and export of particulate material may exceed direct toxic effects (Wallace *et al*. 1989).

Because these manipulations were conducted over a relatively long time period, the findings also have important implications for the study of recovery from chemical stressors. Analysis of data collected several years after pesticide application showed that abundance data were not sufficient to evaluate recovery (Whiles and Wallace 1992). Total abundance of benthic macroinvertebrates was generally similar between treated and control streams within the first year following pesticide application. However, differences in ecosystem processes and taxonomic composition persisted for several years after treatment. Factors that influenced the rate of recovery in systems subjected to anthropogenic disturbance are considered in Chapter 6.

4.4.1.3 Summary

The ELA and Coweeta Hydrologic Laboratory are unique sites that were specifically established for manipulative, ecosystem-level research. Because of the expense and logistical difficulties associated with conducting these manipulations, it is unlikely that other large areas will be set aside exclusively for the purpose of assessing ecosystem responses to anthropogenic stressors. Thus, an important question is the relevance of these studies to understanding responses of other ecosystems and to other stressors. The answer to this question is quite encouraging. Indeed, the general patterns reported in Schindler's whole lake manipulations at ELA and Wallace's pesticide experiments at Coweeta are consistent with responses observed in numerous ecosystem studies, both descriptive and experimental. The similarity of responses among stressors and ecosystem types provides support for the 'ecosystem distress syndrome' proposed by Rapport, Regier and Hutchinson (1985) and described in Chapter 6.

4.4.2 EXAMPLES OF ECOSYSTEM MANIPULATIONS: AVIAN AND MAMMALIAN COMMUNITIES

Large-scale, experimental assessments of chemical effects on birds and mammals at the community level are uncommon in ecotoxicology. Like most applied research in wildlife biology, the primary emphasis in terrestrial ecotoxicology is at the level of populations. However, numerous studies have investigated impacts of other anthropogenic disturbances, particularly those related to forestry practices and other land use changes, on bird and mammal communities. Assuming that community-level responses to these disturbance are analogous to chemical stressors, results of large-scale experiments investigating effects of land use changes and other manipulations may provide some insight into how bird and mammal communities would be affected by chemicals. Chambers, McComb and Tappeiner (1999) measured community-level effects of silvicultural treatments on bird communities in the Pacific Northwest. This study is especially noteworthy because of the large spatial scale (treatment stands ranged from 5.5 to 17.8 ha) and because of the level of replication ($n = 7{-}11$). Results showed that total bird abundance declined along a disturbance gradient; however, species richness appeared to increase in treatments with intermediate levels of disturbance (Fig. 4.8). As expected, these differences resulted from species-specific responses to silvicultural treatments. Abundance of habitat generalists increased, whereas species with restricted geographical ranges decreased in response to disturbance.

A large-scale natural experiment compared responses of bird communities in boreal forests to harvesting and fire treatments over a 28-year period (Hobson and Schieck 1999). In addition to the large spatiotemporal scale, this study is especially relevant to our discussion of experimental approaches because of the unique 2×3 factorial design (two disturbance types, three time periods following disturbance) used to detect treatment effects and recovery times. Researchers observed an increase in bird abundance 14 and 28 years after disturbance; however, patterns of recovery differed between disturbance types, primarily because of differences in community composition immediately after treatment. Although

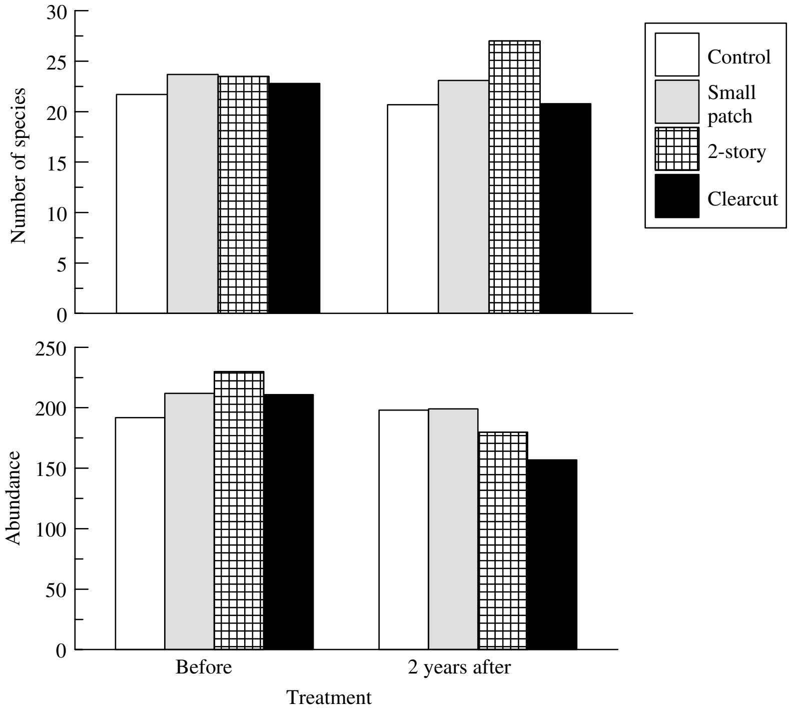

Fig. 4.8. Community-level effects of disturbance on bird communities in the Pacific Northwest. The figure compares species richness and abundance across four levels of silviculture treatments. Total bird abundance declined along a disturbance gradient; however, species richness increased in treatments with intermediate levels of disturbance (2-storey cut). (Data from Table 3 in Chambers, McComb and Tappeiner 1999)

bird communities slightly converged after 14 years, differences in community composition persisted 28 years following disturbance. These results suggest that responses of bird communities to disturbance may persist for relatively long periods and that patterns of recovery may be disturbance specific. In addition to studies of effects of land use changes, a few large-scale field experiments have measured the effects of contaminants on bird and mammal communities. Schauber, Edge and Wolff (1997) tested the hypothesis that differences in diet and vegetation influenced susceptibility of small mammals (deer mice, voles) to organophosphorus pesticides. Using a 3 × 2 factorial design (pesticide level × vegetation structure), organisms were exposed to pesticides in 24 relatively large (0.2 ha) enclosures. Results showed that variation in vegetation structure and timing of rainfall can affect susceptibility of small mammals to pesticides. In contrast to expectations, differences in diet between the insectivorous deer mice and herbivorous voles had little influence on toxicity of insecticides (Schauber, Edge and Wolff 1997). A similar large-scale experiment investigated the direct and indirect effects of organophosphate pesticides on growth and survival of passerines (Brewer's Sparrow, Sage Thrasher) (Howe *et al.* 1996). Application of malathion to a 520-ha treatment area significantly reduced abundance of insects, the primary prey of birds. Although this study focused on individual and population-level responses, the results are relevant to community ecotoxicology because of the emphasis on indirect effects. Despite a significant reduction in prey abundance, there were only moderate effects on nestling growth and survival. The authors speculated that the large reduction in prey abundance was not biologically significant because food in the shrub-steppe community is superabundant during the breeding season.

The resilience of grassland songbirds to dramatic reductions in prey abundance was also observed in a large-scale experimental study conducted in Alberta, Canada (Martin *et al.* 2000). Study plots (56 ha) were randomly assigned to three treatments (control, carbamate exposure, and pyrethroid exposure). Despite a 90% reduction in grasshopper abundance in treated plots, there were no significant effects on nest success, number fledged, or body weight of chestnut-collared longspur nestlings (*Calcarius ornatus*), the dominant species in the area. Although birds in the pyrethroid-exposed plots foraged at greater distances from the nest, there was no difference in biomass of prey delivered to nestlings among treatments. These results are in contrast to those reported by Martin *et al.* (1998) in which depredation rates were higher and hatching success lower on pyrethroid-treated plots. Finally, Patnode and White (1991) measured effects of pesticides on productivity of several songbird species (mockingbirds, brown thrashers, and northern cardinals) in a Georgia pecan grove. Although the focus of the research was on population-level effects (e.g. survival and nestling growth), there were species-specific differences that could result in alterations in community structure.

4.4.3 LIMITATIONS OF WHOLE ECOSYSTEM EXPERIMENTS

In their review of whole ecosystem manipulations, Perry and Troelstrup (1988) discuss several limitations of these experiments. In particular, the difficulty replicating treatments, high costs, and limited types of contaminants that may be investigated are important considerations. On the surface, the lack of replication may appear to be a major shortcoming of whole ecosystem experiments. Indeed, control, randomization, and replication are generally considered the major components of a legitimate experiment. Carpenter (1989) estimated that approximately 10 replicate lakes would be necessary to detect effects of contaminants on primary production because of high natural variability in these systems. It is unlikely that any research program can afford the luxury of this level of replication. Even in situations such as the ELA where a large number of lakes are available for manipulation, it is difficult to locate true replicates (Schindler 1998). Consequently, some researchers argue that sustained, long-term manipulations using unreplicated paired ecosystems is the best approach for assessing ecosystem responses (Carpenter 1989; Schindler 1998). Carpenter *et al.* (1998) make a strong case for evaluating 'alternative explanations' in ecosystem experiments instead of the traditional emphasis on testing null hypotheses. Researchers should identify an explanation that is most plausible based on data from the manipulation and other relevant information. Carpenter *et al.* (1998) also argue that imposing different treatments on different ecosystems may be more informative than 'wasting' precious resources on replicates for testing null hypotheses. This idea is the basis for a revolutionary approach advocated by some researchers who feel that ecologists have become too preoccupied with statistical significance at the expense of gaining mechanistic understanding of ecological processes (Box 4.1).

Box 4.1 An alternative approach to traditional hypothesis testing

> *The statistical null hypothesis testing paradigm has become so catholic and ritualized as to seemingly impede clear thinking and alternative analysis approaches* (Anderson *et al.* 2001)

Statistical approaches in which null hypotheses are compared with alternatives are widely used in ecological and ecotoxicological research. Finding a statistically significant difference between treatment groups often improves the likelihood of publishing results, thus tempting researchers to employ iterative data mining and 'fishing trips' to locate P-values (Anderson *et al.* 2001). Because researchers often confuse statistical significance with underlying processes of interest, data analysis has become synonymous with finding statistically significant differences. These exploratory approaches have recently been criticized because of their inherent subjectivity and reliance on *post hoc* techniques. In particular, model selection procedures, such as stepwise multiple regression, which identify 'best' models based on maximizing R^2 values, have a high probability of identifying spurious results. Their criticism goes beyond the well-known problems of distinguishing statistical significance from biological significance and correcting for experiment-wise error rates. Anderson *et al.* (2001) argue that while chasing P-values, researchers often lose sight of the critical thinking processes that should precede any data analysis. Rejecting weak or sterile null hypotheses that researchers know are false (e.g. there is no difference in growth between exposed and unexposed groups) is not wrong, but arbitrary and uninformative (Burhnam and Anderson 2001).

Recognizing that we construct models to separate important processes from underlying noise and that we never know which model is best (e.g. closest to truth), objective approaches are necessary to distinguish among competing alternatives. The proposed solution to the unquestioning reliance on hypothesis testing is the application of an information-theoretic approach as the basis for making inferences in scientific investigations (Burnham and Anderson 1998). The information-theoretic approach is an extension of classical likelihood methods that emphasize *a priori* thinking and provide a formal ranking of statistical models. The approach uses Kullback–Leibler (K-L) information (Kullback and Leibler 1951) as a measure of the distance between a model and reality, and then ranks a set of competing models from best to worst using the likelihood of each model. Formally, K-L distance between conceptual truth and a model is given as $I(f, g)$, which is defined as is the information that is lost when model g is used to estimate truth f. A significant breakthrough in the development of the information-theoretic approach occurred when Akaike found a formal relationship between K-L distance and maximum likelihood (Akaike 1992). Akaike's Information Criterion (AIC) can be used to estimate the expected value of K-L and provides a relative measure of the proximity of the model to the best model.

Although the focus of the K-L information approach is primarily on model selection, the issues addressed are relevant to all inferential methods. At the very least, researchers are reminded of the importance of *a priori* analyses and the need to distinguish between results derived from iterative processes of data mining and those obtained by an objective attempt to separate noise from underlying structure.

The cost of ecosystem manipulations will limit their widespread use in ecotoxicology. However, the expense may be justified in some instances because well-designed experiments generate extensive data on responses at different levels of organization. Ecosystem experiments often involve multiple investigators and promote cost-effective, interdisciplinary research (Perry and Troelstrup 1988). Interactions among investigators resulting from this collaboration may compensate for the greater expense of ecosystem experiments.

Finally, ecosystem experiments are limited by the types of manipulations that may be performed in natural systems. For example, experimental introduction of highly persistent compounds, such as PCBs and dioxins, would not (and should not) be allowed in most natural systems. Integration of smaller scale studies (microcosms) with ecosystem experiments and taking advantage of unexpected environmental perturbations (Wiens and Parker 1995) will be essential to understand effects of these persistent, highly toxic compounds.

Despite their limitations, whole ecosystem manipulations have revealed unique responses to anthropogenic disturbances that could not have been measured by microcosm and mesocosm studies. Although it is unlikely that whole ecosystem manipulations will be employed on a routine basis, large-scale experiments are the most direct method for demonstrating causation in natural systems. Kimball and Levin (1985) argue for the establishment of research programs that integrate microcosm experiments and whole ecosystem manipulations to predict effects of chemicals. Because certain ecological processes are scale dependent, large-scale studies may be the only way to characterize responses to stressors. Finally, ecotoxicologists must become more creative in designing and implementing large-scale experimental studies. Taking advantage of planned (e.g. the intentional application of pesticides to control insect outbreaks) or unplanned (e.g. the *Exxon Valdez* oil spill) manipulations could be used to measure stressor effects at the scale of whole ecosystems.

4.5 WHAT IS THE APPROPRIATE EXPERIMENTAL APPROACH FOR COMMUNITY ECOTOXICOLOGY?

4.5.1 QUESTIONS OF SPATIOTEMPORAL SCALE

Perhaps the most serious criticism of most experimental approaches employed in community ecotoxicology is the limited spatiotemporal scale of these investigations. Carpenter (1996) argues that the statistical advantages and high degree of control of microcosm and mesocosm experiments do not compensate for their lack of ecological realism. Ironically, this has been the basis for criticism of laboratory toxicity tests for almost 20 years (Cairns 1983), where the underlying assumption is that results of single species toxicity tests can be extrapolated to more complex ecological systems. Some researchers are highly skeptical of extrapolation across spatial and temporal scales (Schindler 1998), and these same concerns should apply to more complex ecotoxicological experiments. The small size and short duration typical of most microcosm experiments will limit our ability to study some potentially important processes. Conducting experiments at different spatial and temporal scales and across different levels of biological organization will at least partially address these concerns. If the response to a particular stressor is scale dependent, then conducting experiments at different spatial scales may allow quantification of this effect (Perez *et al*. 1991). Conducting experiments at different scales may also reveal mechanistic explanations for observed responses to contaminants. For example, a mesocosm experiment could show that abundance of a grazing invertebrate increased after treatment with a particular chemical. Experiments conducted at a smaller spatial scale (e.g. microcosms) would be necessary to show if this unexpected response resulted from increased abundance of primary producers, reduced competition with other grazers, or release from predation by a higher trophic level. Single species toxicity tests could be used to document differences in sensitivity among these potentially interacting species.

4.5.2 INTEGRATING DESCRIPTIVE AND EXPERIMENTAL APPROACHES

There are important limitations of all experimental approaches employed in community ecotoxicology, regardless of the spatial or temporal scale of these investigations (Diamond 1986). Indirect effects of contaminants, stressor interactions, and potential artifacts introduced by the experimental system will complicate interpretation of experimental studies. Even complex factorial designs that investigate stressor interactions are limited in the number of variables that can be manipulated. Because the goal of many experiments is to demonstrate the importance of a single factor (e.g. the effects of a specific chemical or the abundance of a particular predator), the connection between the experiment and the natural system is often lost. Furthermore, while a well-designed experiment with sufficient power can demonstrate the statistical significance of a single factor, the importance of this factor relative to other unmanipulated variables remains unknown without supporting comparative data.

There is legitimate concern that the harsh criticisms directed at descriptive ecology in the 1970s may have resulted in premature abandonment of useful comparative approaches. Consequently, ecologists are often unable to address problems at relevant spatial scales where experimental manipulations are impractical (Power, Dietrich and Sullivan 1998). The perception that experimentation and observation are opposing methodologies underlies a fundamental misconception about the importance of descriptive studies in ecological research. There is much to be learned by comparing patterns observed in nature with those predicted from theory, and a successful research program should combine theory, observations, and experiments. Werner (1998) describes the advantages of a research program that integrates experimental techniques with theoretical and comparative approaches for understanding basic ecological patterns. He makes a strong case for the importance of comparative components in a research program and argues that experiments lacking an obvious connection to observed patterns in nature may be irrelevant. Similar arguments can be made for research programs in ecotoxicology.

4.6 CONCLUSIONS

Experimental studies to evaluate the effects of stressors on communities may be conducted at a variety of spatial and temporal scales. The most effective experimental approach in community ecotoxicology will be determined by the specific objectives of the research, cost, and logistical considerations. Dogmatic statements regarding the superiority of one experimental approach over another disregard the obvious fact that researchers have different goals in mind when designing and conducting experiments. If a researcher is primarily interested in studying interactions among stressors or quantifying the effects of abiotic variables on community responses to contaminants, a factorial experimental design is probably necessary. It is unlikely that a factorial experimental design will be practical at a large spatial scale (e.g. an entire ecosystem), and therefore microcosms or mesocosms are most appropriate. Similarly, microcosm and mesocosm experiments are required when investigating the toxicity of chemicals that cannot be intentionally released into the natural environment. Although small-scale laboratory experiments and mesocosm studies provide the greatest degree of control over independent and confounding variables, they lack realism and have limited temporal and spatial scales. If researchers are interested in comparing the consequences of long-term (e.g. >1 year) exposure to a chemical or following the trajectory of a community response, a natural experiment is most appropriate. Although natural experiments have a high degree of ecological realism and offer greater opportunity to generalize to other systems, they often sacrifice control and replication. Finally, whole ecosystem manipulations are especially useful in situations where researchers wish to measure functional responses (e.g. primary productivity, nutrient cycling) of entire systems or where large, highly mobile species are believed to play an important role in community dynamics.

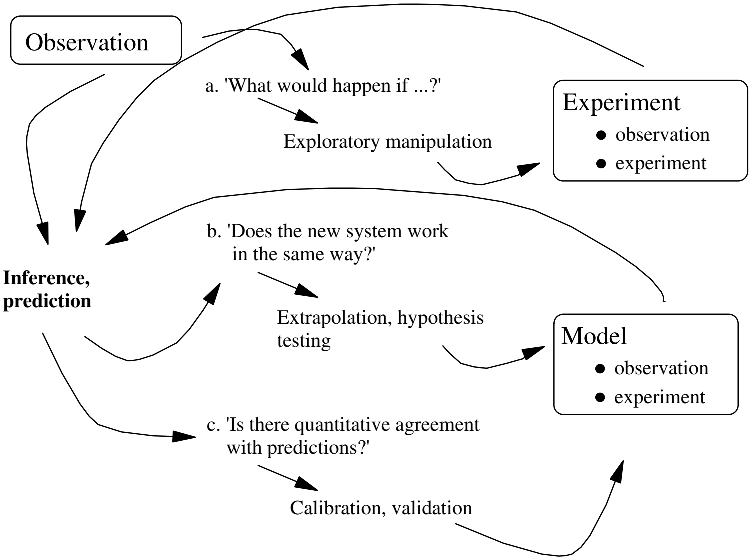

Fig. 4.9. Integrating descriptive, experimental, and modeling approaches in an ecological research program. Initial observations in nature stimulate research questions that can be addressed by exploratory manipulations. Both observational and experimental studies allow researchers to make inferences and predictions about the system, which can be formalized into a conceptual model. The model is validated by comparing model predictions with observations in nature. (Modified from Figure 6-1 in Power, Dietrich and Sullivan 1998)

Ecological and ecotoxicological experiments are conducted for a variety of reasons. Most commonly, researchers are interested in establishing relationships among biotic and abiotic variables or measuring the effects of a particular stressor on ecologically important endpoints. Experiments may be conducted to test ecological and ecotoxicological theory, or simply to satisfy scientific curiosity. Regardless of whether experiments are conducted to test model predictions or to determine the relative importance of hypothesized causal factors, the key issues are generality and extrapolation. Ecotoxicological experiments should not be conducted without an appreciation of natural history or in isolation from underlying ecological theory. Experiments that lack grounding in natural history and theory may provide inconsistent, incomprehensible, and misleading results. Power, Dietrich and Sullivan (1998) advocate a nested experimental, observational, and modeling approach designed to address three basic questions: (1) 'What would happen if . . .?' (2) 'Does this new system work the same way?' and (3) 'Is there quantitative agreement with predictions?' (Fig. 4.9). We advocate a similar integration of these three approaches for community ecotoxicology. Observations of broad spatial patterns and a quantitative analysis of these patterns should precede design and implementation of experiments. While experiments in ecotoxicology necessarily focus on a few factors (e.g. the concentration of a contaminant), understanding the importance of these factors relative to other variables is significantly enhanced by a research program that includes a descriptive component.

REFERENCES

Adams SM, Crumby WD, Greeley Jr MS, Ryon MG and Schilling EM (1992). Relationships between physiological and fish population responses in a contaminated stream. *Environ Toxicol Chem* **11**: 1549–1557.

Akaike H (1992). Information theory and the extension of the maximum likelihood principle. In *Breakthroughs in Statistics*, ed. by Kotz S and Johnson NL, pp. 610–624. Springer-Verlag, London, UK.

Anderson DR, Burnham KP, Gould WR and Cherry S (2001). Concerns about finding effects that are actually spurious. *Biometrics* **29**: 311–316.

ASTM (1995). E 1366-91 ASTM standard practice for standardized aquatic microcosm: fresh water. In 1995 Annual Book of ASTM Standards. Volume 11.05, pp. 1048–1082. American Society for Testing and Materials, Philadelphia, PA.

Barreiro R and Pratt JR (1994). Interaction of toxicants and communities: the role of nutrients. *Environ Toxicol Chem* **13**: 361–368.

Barrett GW (1968). The effects of an acute insecticide stress on a semi-enclosed grassland ecosystem. *Ecology* **49**: 1019–1035.

Beyers DW (1998). Causal inference in environmental impact studies. *J N Am Benthol Soc* **17**: 367–373.

Burnham KP and Anderson DR (1998). *Model Selection and Inference: a Practical Information-Theoretic Approach*. Springer-Verlag, New York, NY.

Burnham KP and Anderson DR (2001). Kullback–Leibler information as a basis for strong inference in ecological studies. *Wildl Res* **28**: 111–119.

Cairns Jr J (1983). Are single species toxicity tests alone adequate for estimating environmental hazard? *Hydrobiologia* **100**: 47–57.

Cairns Jr J (1986). The myth of the most sensitive species. *BioScience* **36**: 670–672.

Cairns Jr J, Hart KM and Henebry MS (1980). The effects of a sublethal dose of copper sulfate on the colonization rate of freshwater protozoan communities. *Am Midl Nat* **104**: 93–101.

Carlisle DM and Clements WH (1999). Sensitivity and variability of metrics used in biological assessments of running waters. *Environ Toxicol Chem* **18**: 285–291.

Carpenter SR (1989). Replication and treatment strength in whole-lake experiments. *Ecology* **70**: 453–463.

Carpenter SR (1996). Microcosm experiments have limited relevance for community and ecosystem ecology. *Ecology* **77**: 677–680.

Carpenter SR, Cole JT, Essington TE, Hodgson JR, Houser JN, Kitchell JF and Pace ML (1998). Evaluating alternative explanations in ecosystem experiments. *Ecosystems* **1**: 335–344.

Chambers CL, McComb WC and Tappeiner II JC (1999). Breeding bird responses to three silvicultural treatments in the Oregon Coast Range. *Ecol Appl* **9**: 171–185.

Chapman PM (1995). Extrapolating laboratory toxicity results to the field. *Environ Toxicol Chem* **14**: 927–930.

Clements WH (1999). Metal tolerance and predator–prey interactions in benthic macroinvertebrate stream communities. *Ecol Appl* **9**: 1073–1084.

Clements WH and Kiffney PM (1994). Assessing contaminant effects at higher levels of biological organization. *Environ Toxicol Chem* **13**: 357–359.

Clements WH, Cherry DS and Cairns Jr J (1989). The influence of copper exposure on predator–prey interactions in aquatic insect communities. *Freshw Biol* **21**: 483–488.

Connell JH (1961). The influence of interspecific competition and other factors on the distribution of the barnacle. *Chthamalus stellatus*. *Ecology* **42**: 710–723.

Connell JH (1978). Diversity in tropical rain forests and coral reefs. *Science* **199**: 1302–1310.

Connell JH (1980). Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* **35**: 131–138.

Connor EF and Simberloff DS (1979). The assembly of species communities: chance of competition? *Ecology* **60**: 1132–1140.

Courtney LA and Clements WH (2000). Sensitivity to acidic pH in benthic invertebrate assemblages with different histories of exposure to metals. *J N Am Benthol Soc* **19**: 112–127.

Cuffney TF, Wallace JB and Webster JR (1984). Pesticide manipulation of a headwater stream: invertebrate responses and their significance for ecosystem processes. *Freshw Invert Biol* **3**: 153–171.

Daehler CC and Strong DR (1996). Can you bottle nature? The roles of microcosms in ecological research. *Ecology* **77**: 663–664.

Diamond J (1986). Overview: laboratory experiments, field experiments, and natural experiments. In *Community Ecology*, ed. by Diamond J and Case TJ, pp. 3–22. Harper and Row, Publ., New York, NY.

Drake JA, Huxel GR and Hewitt CL (1996). Microcosms as models for generating and testing community theory. *Ecology* **77**: 670–677.

Fairchild JF, La Point TW, Zajicek JL, Nelson JK, Dwyer FJ and Lovely PA (1992). Population-, community- and ecosystem-level responses of aquatic mesocosms to pulsed doses of a pyrethroid insecticide. *Environ Toxicol Chem* **11**: 115–129.

Gause GF (1934). *The Struggle for Existence*. Williams and Wilkins, Baltimore, MD.

Gearing JN (1989). The role of aquatic microcosms in ecotoxicologic research as illustrated by large marine systems. In *Ecotoxicology: Problems and Approaches*, ed. by

Levin SA, Harwell MA, Kelly JR and Kimball KD, pp. 409–470. Springer-Verlag Inc., New York, NY.

Genter RB (1995). Benthic algal populations respond to aluminum, acid, and aluminum–acid mixtures in artificial streams. *Hydrobiologia* **306**: 7–19.

Genter RB, Colwell FS, Pratt JR, Cherry DS and Cairns Jr J (1988). Changes in epilithic communities due to individual and combined treatments of zinc and snail grazing in stream mesocosms. *Toxicol Indust Health* **4**: 185–201.

Giddings JM, Biever RC, Annunziato MF and Hosmer AJ (1996). Effects of diazinon on large outdoor pond microcosms. *Environ Toxicol Chem* **15**: 618–629.

Gillett JW (1989). The role of terrestrial microcosms and mesocosms in ecotoxicologic research. In *Ecotoxicology: Problems and Approaches*, ed. by Levin SA, Harwell MA, Kelly JR and Kimball KD, pp. 41–67. Springer-Verlag, New York, NY.

Gonzalez MJ and Frost TM (1994). Comparisons of laboratory bioassays and a whole-lake experiment: rotifer responses to experimental acidification. *Ecol Appl* **4**: 69–80.

Graney RL, Giesy Jr JP and DiToro D (1989). Mesocosm experimental design strategies: advantages and disadvantages in ecological risk assessment. In *Using Mesocosms to Assess the Aquatic Ecological Risk of Pesticides: Theory and Practice*, ed. by Voshell Jr JR, pp. 74–88. Entomological Society of America, Lanahm, MD.

Green RH (1979). *Sampling Design and Statistical Methods for Environmental Biologists*. John Wiley and Sons, New York, NY.

Heinis LJ and Knuth ML (1992). The mixing, distribution and persistence of esfenvalerate within littoral enclosures. *Environ Toxicol Chem* **11**: 11–25.

Hobson KA and Schieck J (1999). Changes in bird communities in boreal mixedwood forest: harvest and wildfire effects over 30 years. *Ecol Appl* **9**: 849–863.

Howarth RW (1991). Comparative responses of aquatic ecosystems to toxic chemical stress. In *Comparative Analyses of Ecosystems: Patterns, Mechanisms, and Theories*, ed. by Cole J, Lovett G and Findlay S, pp. 169–195. Springer-Verlag, New York, NY.

Howe FP, Knight RL, McEwen LC and George TL (1996). Direct and indirect effects of insecticide applications on growth and survival of nestling passerines. *Ecol Appl* **6**: 1314–1324.

Ives AR, Foufopoulos J, Klopfer ED, Klug JL and Palmer TM (1996). Bottle or big-scale studies: How do we do ecology? *Ecology* **77**: 681–685.

Jenkins DG and Buikema Jr AL (1998). Do similar communities develop in similar sites? A test with zooplankton structure and function. *Ecol Monogr* **68**: 421–443.

Joern A and Hoagland KD (1996). In defense of whole-community bioassays for risk assessment. *Environ Toxicol Chem* **15**: 407–409.

Karr JR (1993). Defining and assessing ecological integrity: beyond water quality. *Environ Toxicol Chem* **12**: 1521–1531.

Kennedy JH, Johnson ZB, Wise PD and Johnson PC (1995). Model aquatic ecosystems in ecotoxicology research: considerations of design, implementation, and analysis. In *Handbook of Ecotoxicology*, ed. by Hoffman DJ, Rattner BA, Burton Jr GA and Cairns Jr J, pp. 117–162. CRC Press, Inc., Boca Raton, FL.

Kiffney PM and Clements WH (1996). Effects of metals on stream macroinvertebrate assemblages from different altitudes. *Ecol Appl* **6**: 472–481.

Kimball KD and Levin SA (1985). Limitations of laboratory bioassays: the need for ecosystem-level testing. *BioScience* **35**: 165–171.

Kullback S and Leibler RA (1951). On information and sufficiency. *Ann Math Stat* **22**: 79–86.

Landis WG, Matthews RA and Matthews GB (1997). Design and analysis of multispecies toxicity tests for pesticide registration. *Ecol Appl* **7**: 1111–1116.

Lawton JH (1996). The Ecotron facility at Silwood Park: The value of ‘big bottle’ experiments. *Ecology* **77**: 665–669.

Liber K, Kaushik NK, Solomon KR and Carey JH (1992). Experimental designs for aquatic mesocosm studies: a comparison of the 'ANOVA' and 'regression' design for assessing the impact of tetrachlorophenol on zooplankton populations in limnocorrals. *Environ Toxicol Chem* **11**: 61–77.

Likens GE, Bormann FH, Johnson NM, Fisher DW and Pierce RS (1970). Effects of forest cutting and herbicide treatment on nutrient budgets in the Hubbard Brook Watershed-ecosystem. *Ecol Monogr* **40**: 23–47.

Lozano SJ, O'Halloran SL, Sargent KW and Brazner JC (1992). Effects of esfenvalerate on aquatic organisms in littoral enclosures. *Environ Toxicol Chem* **11**: 35–47.

Lubchenco J and Real LA (1991). Manipulative experiments as tests of ecological theory. In *Foundations of Ecology*, ed. by Real LA and Brown JH, pp. 715–733. Chicago University Press, Chicago, IL.

MacArthur RH and Wilson EO (1963). An equilibrium theory of insular zoogeography. *Evolution* **17**: 373–387.

Martin PA, Johnson DL, Forsyth DJ and Hill BD (1998). Indirect effects of the pyrethroid insecticide deltamethrin on reproductive success of chestnut-collared longspurs. *Ecotoxicology* **7**: 89–97.

Martin PA, Johnson DL, Forsyth DJ and Hill BD (2000). Effects of two grasshopper control insecticides on food resources and reproductive success of two species of songbirds. *Environ Toxicol Chem* **19**: 2987–2996.

Matthews RA, Landis WG and Matthews GB (1996). The community conditioning hypothesis and its application to environmental toxicology. *Environ Toxicol Chem* **15**: 597–603.

Medley CN and Clements WH (1998). Responses of diatom communities to heavy metals in streams: The influence of longitudinal variation. *Ecol Appl* **8**: 631–644.

Newman MC (2001). *Population Ecotoxicology*. John Wiley and Sons, Ltd, Chichester, UK.

Niederlehner BR, Pontasch KW, Pratt JR and Cairns Jr J (1990). Field evaluation of predictions of environmental effects from a multispecies-microcosm toxicity test. *Arch Environ Contam Toxicol* **19**: 62–71.

Odum EP (1969). The strategy of ecosystem development. *Ecology* **164**: 262–270.

Odum EP (1984). The mesocosm. *BioScience* **34**: 558–562.

Paine RT (1966). Food web complexity and species diversity. *Am Nat* **100**: 65–75.

Paine RT (1969). A note on trophic complexity and community stability. *Am Nat* **103**: 91–93.

Patnode KA and White DH (1991). Effects of pesticides on songbird productivity in conjunction with pecan cultivation in southern Georgia: a multiple-exposure experimental design. *Environ Toxicol Chem* **10**: 1479–1486.

Park T (1948). Experimental studies of interspecies competition. I. Competition between populations of the flour beetles, *Tribolium confusum* Duvall and *Tribolium castaneum* Herbst. *Ecol Monogr* **18**: 267–307.

Peckarsky BL (1998). The dual role of experiments in complex and dynamic natural systems. In *Experimental Ecology: Issues and Perspectives*, ed. by Resetarits Jr WJ and Bernardo J, pp. 311–324. Oxford University Press, Inc., New York, NY.

Perez KT (1995). Role and significance of scale to ecotoxicology. In *Ecological Toxicity Testing: Scale, Complexity, and Relevance*, ed. by Cairns Jr J and Niederlehner BR, pp. 49–72. CRC Press, Inc., Boca Raton, FL.

Perez KT, Morrison GE, Davey EW, Lackie NF, Soper AE, Blasco RJ, Winslow DL, Johnson RL, Murphy PG and Heltshe JF (1991). Influence of size on fate and ecological effects of kepone in physical models. *Ecol Appl* **1**: 237–248.

Perry JA and Troelstrup Jr NH (1988). Whole ecosystem manipulation: a productive avenue for test system research? *Environ Toxicol Chem* **7**: 941–951.

Platt JR (1964). Strong inference. *Science* **146**: 347–353.

Pontasch KW (1995). The use of stream microcosms in multispecies testing. In *Ecological Toxicity Testing: Scale, Complexity, and Relevance*, ed. by Cairns Jr J and Niederlehner BR, pp. 169–191. CRC Press, Inc., Boca Raton, FL.

Pontasch KW, Niederlehner BR and Cairns Jr J (1989). Comparisons of single-species, microcosm and field responses to a complex effluent. *Environ Toxicol Chem* **8**: 521–532.

Popper KR (1972). *The Logic of Scientific Discovery* (3rd edn). Hutchinson, London, UK.

Power ME, Dietrich WE and Sullivan KO (1998). Experimentation, observation, and inference in river and watershed investigations. In *Experimental Ecology: Issues and Perspectives*, ed. by Resetarits Jr WJ and Bernardo J, pp. 113–132. Oxford University Press, Inc., New York, NY.

Pratt JR and Barreiro R (1998). Influence of trophic status on the toxic effects of a herbicide: a microcosm study. *Arch Environ Contam Toxicol* **35**: 404–411.

Pratt JR, Melendez AE, Barreiro R and Bowers NJ (1997). Predicting the ecological effects of herbicides. *Ecol Appl* **7**: 1117–1124.

Rapport DJ, Regier HA and Hutchinson TC (1985). Ecosystem behavior under stress. *Am Nat* **125**: 617–640.

Resetarits Jr WJ and Bernardo J (1998). *Experimental Ecology: Issues and Perspectives*. Oxford University Press, Inc., New York, NY.

Resetarits Jr WJ and Fauth JE (1998). From cattle tanks to Carolina bays: the utility of model systems for understanding natural communities. In *Experimental Ecology: Issues and Perspectives*, ed. by Resetarits Jr WH and Bernardo J, pp. 133–151. Oxford University Press, Inc., New York, NY.

Sallenave RM, Day KE and Kreutzweiser DP (1994). The role of grazers and shredders in the retention and downstream transport of a PCB in lotic environments. *Environ Toxicol Chem* **13**: 1843–1847.

Schauber EM, Edge WD and Wolff JO (1997). Insecticide effects on small mammals: influence of vegetation structure and diet. *Ecol Appl* **7**: 143–157.

Schindler DW (1974). Eutrophication and recovery in experimental lakes: implications for management. *Science* **184**: 897–899.

Schindler DW (1987). Detecting ecosystem responses to anthropogenic stress. *Can J Fish Aquat Sci* **44** (Suppl 1): 6–25.

Schindler DW (1988). Effects of acid rain on freshwater ecosystems. *Science* **239**: 149–157.

Schindler DW (1998). Replication versus realism: The need for ecosystem-scale experiments. *Ecosystems* **1**: 323–334.

Shaw JL and Kennedy JH (1996). The use of aquatic field mesocosm studies in risk assessment. *Environ Toxicol Chem* **15**: 605–607.

Sheffield SR and Lochmiller RL (2001). Effects of field exposure to diazinon on small mammals inhabiting a semienclosed prairie grassland ecosystem. I. Ecological and reproductive effects. *Environ Toxicol Chem* **20**: 284–296.

Simberloff DS (1980). A succession of paradigms in ecology: essentialism to materialism and probabilism. *Synthese* **43**: 3–39.

Simberloff DS and Wilson EO (1969). Experimental zoogeography of islands: The colonization of empty islands. *Ecology* **50**: 278–296.

Smith EP (1995). Design and analysis of multispecies experiments. In *Ecological Toxicity Testing: Scale, Complexity, and Relevance*, ed. by Cairns Jr J and Niederlehner BR, pp. 73–95. CRC Press, Inc., Boca Raton, FL.

Sousa WP (1979). Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology* **60**: 1225–1239.

Steinman AD, Mulholland PJ, Palumbo A, DeAngelis D and Flum T (1992). Lotic ecosystem response to a chlorine disturbance. *Ecol Appl* **2**: 341–355.

Stewart-Oaten A, Murdoch WW and Parker KR (1986). Environmental impact assessment: ‘pseudoreplication’ in time? *Ecology* **67**: 929–940.

Strong DR, Simberloff D, Abele LG and Thistle AB (1984). *Ecological Communities: Conceptual Issues and Evidence*. Princeton University Press, Princeton, NJ.

Suter II GW (1993). A critique of ecosystem health concepts and indexes. *Environ Toxicol Chem* **12**: 1533–1539.

Suttman CE and Barrett GW (1979). Effects of sevin on arthropods in an agricultural and an old field plant community. *Ecology* **60**: 628–641.

Taub FB (1989). Standardized Aquatic Microcosms: tools for assessing the ecological effects of chemicals and genetically engineered microorganisms. *Environ Sci Technol* **23**: 1064–1066.

Taub FB (1997). Are ecological studies relevant to pesticide registration decisions? *Ecol Appl* **7**: 1083–1085.

Touart LW (1988). *Aquatic Mesocosm Tests to Support Pesticide Registrations. EPA 540-09-88-035*. US Environmental Protection Agency, Washington, DC.

Touart LW and Maciorowski AF (1997). Information needs for pesticide registration in the United States. *Ecol Appl* **7**: 1086–1093.

Verhoef HA (1996). The role of soil microcosms in the study of ecosystem processes. *Ecology* **77**: 685–690.

Wallace JB, Lugthart GJ, Cuffney TF and Schurr GA (1989). The impact of repeated insecticidal treatments on drift and benthos of a headwater stream. *Hydrobiologia* **179**: 135–147.

Wallace JB, Webster JR and Cuffney TF (1982). Stream detritus dynamics: regulation by invertebrate consumers. *Oecologia* **53**: 197–200.

Webber EC, Deutsch WG, Bayne DR and Seesock WC (1992). Ecosystem-level testing of a synthetic pyrethroid insecticide in aquatic mesocosms. *Environ Toxicol Chem* **11**: 87–105.

Werner EE (1998). Ecological experiments and a research program in community ecology. In *Experimental Ecology: Issues and Perspectives*, ed. by Resetarits Jr WJ and Bernardo J, pp. 3–26. Oxford University Press, Inc., New York, NY.

Whiles MR and Wallace JB (1992). First-year benthic recovery of a headwater stream following a 3-year insecticide-induced disturbance. *Freshw Biol* **28**: 81–91.

Wiens JA and Parker KR (1995). Analyzing the effects of accidental environmental impacts: approaches and assumptions. *Ecol Appl* **5**: 1069–1083.

Wilson DS (1997). Biological communities as functionally organized units. *Ecol Appl* **78**: 2018–2024.

Winner RW, Owen HA and Moore MV (1990). Seasonal variability in the sensitivity of freshwater lentic communities to a chronic copper stress. *Aquat Toxicol* **17**: 75–92.

Woodwell GM (1970). Effects of pollution on the structure and physiology of ecosystems. *Science* **168**: 429–433.

5 Application of Multimetric and Multivariate Approaches in Community Ecotoxicology

The most distinct and beautiful statement of any truth must take at last the mathematical form. Henry David Thoreau (Walls 1999)

5.1 INTRODUCTION

Methods to assess the effects of contaminants and other anthropogenic stressors on communities range from computationally-simple indices such as species richness to complex, computer-dependent algorithms such as multivariate analyses. The simplest community indices use species presence/absence or abundance data to show how individuals in the community are distributed among species. The advantages of these indices are their intuitive meaning and their ability to reduce complex data to a single number. Only slightly more involved but retaining more information, species abundance curves described in Chapter 3 characterize the distribution of individuals among the species by fitting abundance data to specified distributions. Estimated distributional parameters from species abundance models provide a parsimonious description of the community. Slightly more involved composite measures require additional knowledge about community qualities (e.g. the trophic status of a species) to produce indices developed specifically to gauge diminished community integrity due to anthropogenic stressors. Currently, the most popular of these composite indices is Karr's (1981) index of biological integrity (IBI). These composite indices require more ecological knowledge of the community than measures of species richness or species abundance models, but have the advantage of being focused primarily on human effects on communities or species assemblages. More convenient, but perhaps applying less ecology than warranted, distributions of individual species effect metrics (e.g. distributions of 96-h LC50 values) are used to predict 'safe concentrations' that presumably protect all but a specified, low percentage of the species making up the community. Even more computationally intense methods, such as multivariate analyses, aim to reduce the number of data dimensions to an interpretable low number, and to quantify similarities or differences among sampling units. These last methods tend to generate interpretive parsimony at the expense of methodological simplicity and straightforward terminology;

therefore, considerable caution is needed to avoid errors during their application. However, the value of these methods in identifying clear explanations from complex datasets makes worthwhile any effort spent wading through obtuse computer manuals or dealing with the associated jargon.

Jargon, not argument, is your best ally in keeping him from the Church. (Lewis 1942)

5.1.1 COMPARISON OF MULTIMETRIC AND MULTIVARIATE APPROACHES

Multimetric and multivariate approaches are applied to community data with the intent of rendering the associated complex array of information to a more parsimonious form. Because ecological assessments of biological integrity generally require analysis of numerous biotic and abiotic variables, sophisticated statistical approaches are often necessary to examine the complex relationships between species assemblages and multiple environmental factors. Multivariate approaches reduce complex, multidimensional data to two or three dimensions, thus allowing researchers to identify key environmental variables responsible for patterns of species abundance. In contrast, multimetric indices integrate a diverse suite of measures, often across several levels of biological organization, to assess biological integrity. It is appropriate to consider these two approaches together because the data necessary to calculate a multimetric index or to conduct multivariate analyses are often the same (e.g. abundance, richness, composition).

In their comparison of multivariate and multimetric approaches, Reynoldson *et al*. (1997) concluded that multivariate approaches provided greater accuracy and precision for assessing reference conditions in streams. Despite their growing popularity in Canada and Europe, multivariate approaches have received considerably less attention in the USA (Resh, Norris and Barbour 1995). Multivariate analyses have been criticized because of their inherent statistical complexity and because results are often difficult to interpret (Gerritsen 1995; Fore Karr and Wisseman 1996). Although strict reliance on complex statistical algorithms may obscure important biological results, multivariate approaches are an essential set of tools for biological assessments of water quality. We agree with the recommendations of Reynoldson *et al*. (1997) that multivariate and multimetric approaches are complementary and should be used in conjunction. For example, the variables used in multivariate analyses such as principal components could include species richness, abundance of sensitive groups, or other measures typically included in a multimetric index. Alternatively, a multimetric index similar to Karr's IBI could be developed using results of multivariate analyses. Loading coefficients from canonical discriminant analyses, principal component analyses, and other multivariate procedures identify variables that are most important for separation of groups (generally locations, sampling stations). Variables shown to be responsible for separation of reference and impacted stations could be combined in a multimetric index.

5.2 MULTIMETRIC INDICES

> *A principal objective of the 1972 Federal Water Pollution Control Act and its 1977 and 1987 amendments is to restore and maintain the biological integrity of the nation's waters.* (Miller *et al*. 1988)

One of the most significant advances in the field of biological assessments over the past 20 years is the development and application of multimetric approaches for measuring ecological integrity. Because no single measure of impairment will respond to all classes of contaminants, and because some individual metrics may show unexpected changes (e.g. increased species richness at polluted sites), multimetric indices are an effective tool for measuring effects of stressors (Karr 1981; Plafkin *et al*. 1989; Fausch *et al*. 1990; Kerans and Karr 1994). The individual metrics in a multimetric index reflect different characteristics of life history, community structure, and functional organization. In general, as the number of metrics increases (up to some reasonable number), the ability to separate contaminant effects from natural variation increases (Karr 1993) (Fig. 5.1). In addition, because individual metrics respond differently to different classes of contaminants, multimetric approaches are useful for assessing a diverse suite

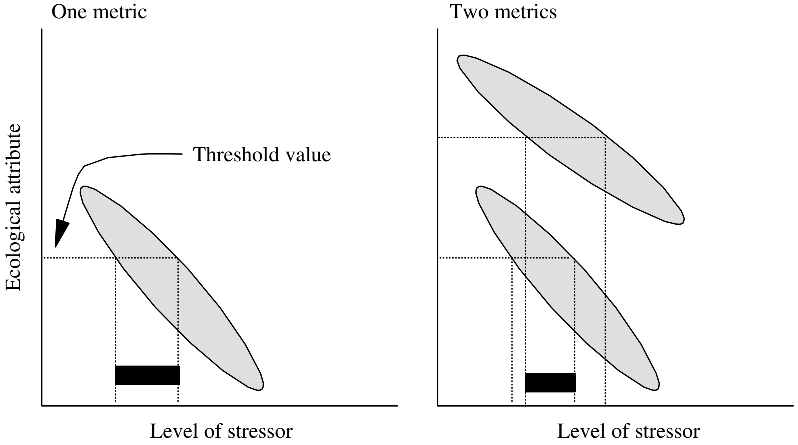

Fig. 5.1. Hypothetical relationship between stressor levels and ecological attributes characterized using one or two metrics. The threshold value of the ecological attribute is defined as the response that is considered to be biologically significant. For example, a researcher may conclude that a 20% reduction in abundance of a sensitive species is a biologically significant response. The responses of the individual metrics are represented as clouds of points and the level of the stressor known to affect the ecological attribute is represented by the black bar. Note that addition of a second metric provides a more refined measure of the stressor level that causes a biologically significant response. (Modified from Figure 1 in Karr 1993)

of stressors and measuring impacts in systems receiving multiple stressors. The individual metrics included in a multimetric index may vary among perturbations, but should reflect important structural and functional characteristics of the system. In general, deviation of individual metrics from expected values at reference sites is estimated and a final value that includes the sum of all individual metrics is calculated.

Karr's (1981) IBI is the most widely used multimetric index for assessing the health of aquatic communities. The IBI was developed in response to the federally-legislated mandate to 'restore and maintain the chemical, physical, and biological integrity' of US waters (Clean Water Act 1977, PL 95-217, also 1987 PL 100-4). Originally employed in Midwestern streams in the USA, the IBI is based on 12 attributes of fish assemblages in three general categories: species richness and composition, trophic composition, and fish abundance and condition. The individual metrics are assigned scores (1, 3, 5) based on their similarity to expected values in undisturbed or least impacted streams. Expected values for the individual metrics are obtained by sampling a large number of known reference sites in a region. Alternatively, expected values can be derived from surveys of reference and impacted sites and using the 'best' values from these samples (Simon and Lyons 1995). Because expected values for species richness and total abundance vary with stream size, these metrics must be adjusted to reflect watershed area and other regional conditions. The scores of the 12 metrics are summed to yield a total IBI score for a site (which ranges from 12 to 60), with larger values indicating healthy fish assemblages. The IBI is sensitive to a diverse array of physical and chemical stressors, including industrial and municipal effluents, agricultural inputs, habitat loss, and introduction of exotic species.

The IBI works especially well for characterizing fish communities because environmental requirements and historic distributions of this group are well known. This greatly facilitates establishment of expected values for individual metrics. The structural and functional metrics included in the IBI are biologically relevant, and each individual metric responds to known gradients of degradation (Fausch *et al*. 1990). The general approach outlined in the IBI has been modified for other ecosystems (e.g. lakes, estuaries) and applied to other taxonomic groups (e.g. benthic macroinvertebrates, diatoms). Although the specific metrics vary among these applications, comparison of measured values to expected values and integration of a suite of metrics into a single index are consistent among approaches. A multimetric index for benthic macroinvertebrate communities was used to distinguish polluted from reference sites in rivers of the Tennessee Valley (Kerans and Karr 1994). The benthic IBI (B-IBI) was found to be highly effective because benthic macroinvertebrates generally respond to chemical and physical degradation in a predictable fashion. The IBI now enjoys such popularity that the term, index of biological integrity, has come to be applied to any new composite or multimetric index.

Calculating multimetric indices involves comparing individual metrics measured at an impacted site to the expected values for the region (Fig. 5.2A). As described above, because some metrics (e.g. species richness) are greatly influenced by stream order and watershed area, these expected values must be adjusted to reflect natural variation (Fig. 5.2B). Assuming that community responses to other landscape variables are predictable, a logical extension

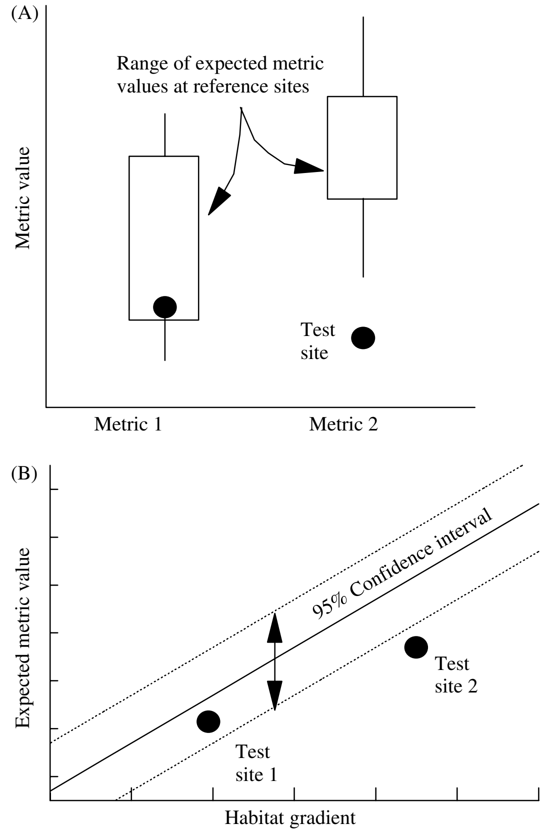

Fig. 5.2. Multimetric and multivariate approaches for comparing test sites with expected values at reference sites. (A) Two metric values at a test site (indicated by solid circles) are compared with expected values. Values are within the expected range for metric 1, but below the range of expected values for metric 2. (B) Metric values are adjusted to reflect expected changes in habitat characteristics along a gradient. Although the metric value at test site 2 is greater than at test site 1, it is less than the expected value and would indicate impact. (C) Multivariate analysis of expected metric values based on regional differences in habitat characteristics. Test sites 1 and 2 are within the expected values whereas test site 3 falls outside the 95% confidence ellipsoid

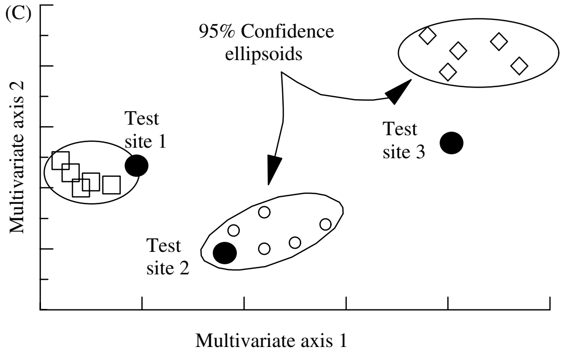

Fig. 5.2. (*continued*)

of this approach is to create models to account for natural variation across broad geographical areas. Bailey *et al.* (1998) found that simple geographic characteristics (distance from source, catchment area, elevation) and year sampled accounted for >50% of the variation among reference sites. The performance of several bioassessment metrics was significantly improved when a predictive model that included this geographic variation was employed to identify impacted sites. The conventional approach of comparing metric values at impacted sites with expected values at reference sites has now advanced to the point where we can characterize habitat variation within subregions using more sophisticated multivariate statistics (Fig. 5.2C). The application of multivariate techniques for assessing reference conditions is described below.

5.2.1 MULTIMETRIC APPROACHES FOR TERRESTRIAL COMMUNITIES

Although multimetric indices such as the IBI have been limited primarily to aquatic ecosystems, the general approach could be modified for terrestrial communities. Because of their sensitivity and rapid response to environmental stressors, terrestrial arthropods would be especially useful for assessing biological integrity (Kremen *et al.* 1993). Nelson and Epstein (1998) investigated the responses of lepidopterans to habitat modifications and concluded that butterfly communities integrate important structural and functional characteristics of terrestrial ecosystems. Kremen (1992) evaluated the indicator properties of butterfly communities and reported that this group was quite responsive to anthropogenic disturbance. Bird communities also offer opportunities for development of integrated measures of ecological integrity. The abundance, distribution, and habitat requirements of birds are generally well known, especially in North America. National monitoring programs, such as the Christmas Bird Counts conducted by the Audubon Society and Breeding Bird Surveys, have provided spatially-extensive, long-term data on bird assemblages. Finally, responses of bird populations to some environmental stressors, especially pesticides and habitat alterations, have been well documented. However, given the logistical difficulties of sampling bird communities, developing a suite of ecologically relevant indicators for this group will be a challenge. In particular, surveys must be corrected to account for differences in detectability among species and among locations (Chambers, McComb and Tappeiner 1999). One promising alternative is to predict effects of anthropogenic stressors on bird communities based on characteristics of surrogate taxonomic groups. Blair (1999) reported a strong relationship between species richness of birds and butterflies along a gradient of urban development (Fig. 5.3). Because butterfly surveys are relatively easy to conduct, Blair suggested that species richness of butterflies could be used as a surrogate for monitoring bird communities.

5.2.2 LIMITATIONS OF MULTIMETRIC APPROACHES

One major advantage of multimetric approaches is that they integrate several ecologically relevant responses into a single measure, a characteristic that appeals to many water resource managers. However, some researchers are skeptical of multimetric indices and argue that a better approach is to assess an array of ecosystem responses which provide a direct linkage between cause and effect (Suter 1993). Detailed critiques of multimetric indices as well as a discussion of their limitations have been published previously (Fausch *et al.* 1990; Suter 1993; Simon and Lyons 1995). Only a summary of the major limitations will be presented here.

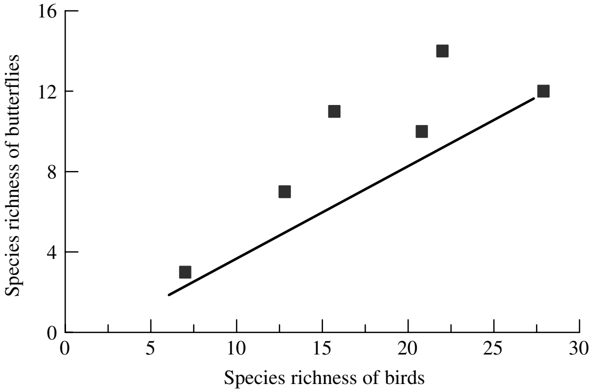

Fig. 5.3. The relationship between species richness of birds and butterflies at six sites along a gradient of urban development. Obtaining quantitative data for certain taxonomic groups, such as birds and small mammals is often expensive and logistically challenging. The close relationship between these measures suggests that butterflies, which are relatively easy to monitor, can be used as a surrogate to predict the response of birds to stressors. (Modified from Figure 1 in Blair 1999)

First, multimetric indices are data intensive. Regardless of the specific system or taxonomic group, development and application of multimetric approaches require a thorough understanding of the ecology and habitat requirements of species as well as their tolerances for environmental stressors. For some taxonomic groups and in some systems these data will not be available. Second, most multimetric approaches cannot be employed to identify specific causes of environmental impacts. This criticism reflects two mutually exclusive goals of many biological monitoring programs. While chemical-specific, diagnostic indicators may allow researchers to identify a single source of perturbation, more general measures such as the IBI are required to characterize the integrity of systems receiving multiple stressors. It is possible that the responses of individual metrics in a multimetric index could offer some insight into the specific source of contamination. For example, a multimetric index for benthic macroinvertebrates might include metrics for abundance and species richness of mayflies, stoneflies, and caddisflies. All three groups are generally sensitive to organic enrichment; however, many caddisflies and some stoneflies are tolerant of heavy metals (Clements, Cherry and Cairns 1988; Clements and Kiffney 1995). Analysis of the responses of component metrics may allow researchers to quantify the relative importance of individual stressors in systems affected by multiple perturbations. Third, multimetric indices may not respond to some types of perturbation because changes in one metric may be offset by changes in another metric. Again, the obvious solution to this problem is to report not only the integrated scores but also the responses of component metrics. Finally, multimetric indices based on attributes of community composition will be less effective in areas with low species richness or naturally impoverished assemblages. Fausch *et al*. (1990) note that the low species richness of fish assemblages in western coldwater streams requires that many of the community-level metrics be replaced by life history and population-level responses.

5.3 MULTIVARIATE APPROACHES

Multivariate datasets are broadly defined here as those in which more than two dependent or independent variables are collected for each sampling unit. These variables typically include community characteristics (e.g. species abundances) that change or might be influenced together in complex ways. A wide range of multivariate statistical methods has been used to analyze these types of data. In contrast to the methods described to this point, multivariate analyses are not based on ecological concepts but are statistical constructs that reduce complex datasets to potentially meaningful patterns involving a few variables. Some, such as ordination methods, combine species abundance information for many sites or sampling units into functions that capture a portion of the total variance in the data. A small number of uncorrelated, linear combinations of the species abundances might be identified. Ecotoxicological meaning can be assigned to the positions of sampling units (e.g. sites) along these linear functions. Alternatively, the researcher may simply use the results to describe trends among sampling units. Other methods, such as cluster analysis, separate samples into groups in the hope of identifying some ecological or toxicological pattern that may emerge to explain the groupings. Another type of analysis might be applied to species abundance data to identify which qualities weigh most heavily in discriminating among known groups. Regardless of the applied method, the overarching idea is that multivariate analysis of the measured variables can reveal hidden or unmeasured qualities.

As with most parametric analyses, transformation of species abundance data is often advisable before applying a multivariate method. Transformation might be done to reduce the influence of one variable relative to others in the linear combinations of variables. One variable might have a much wider range of values and, in the absence of transformation, would have a disproportionately heavy influence on the data variance. In such a case, each variable (e.g. species' abundances at all sampling sites) may be standardized to a mean of 0 and standard deviation of 1. If a skewed distribution were to occur with the species abundance distributions, some transformation such as the square root or another power of abundance might be employed prior to standardization and multivariate analysis. This is often necessary when a few species are very abundant at some sites.

5.3.1 SIMILARITY INDICES

Although generally not included in the treatment of multivariate analyses, similarity indices also reduce complex, multi-species data for the purpose of comparing communities among locations or over time. Similarity indices quantify the correspondence between two communities based on either presence–absence or abundance data. These indices are especially useful for comparing communities from regional reference sites with impacted sites. Alternatively, similarity indices are appropriate in studies of well-defined pollution gradients where similarity to reference conditions is expected to increase with distance from a pollution source. The simplest and most frequently used similarity index based on presence–absence data is the Jaccard Index:

$$J = j/(a + b - j) \tag{5.1}$$

where a = the number of species in community a, b = the number of species in community b, and j = the number of species common to both sites.

Because Jaccard's index does not account for differences in abundance between locations, rare species and abundant species are weighted equally. Thus, it is likely that the Jaccard index will be relatively insensitive to low or moderate levels of contamination. More sophisticated similarity indices, such as the Morisita–Horn measure, compare the relative abundance of taxa between two communities. The Morisita–Horn index is given as:

$$MH = 2\Sigma(an_i \times bn_i)/(\mathrm{d}a + \mathrm{d}b)aN \times bN \tag{5.2}$$

where an_i = the number of individuals of the i^th^ species at site a, bn_i = the number of individuals of the i^{th} species at site b, aN = the total number of individuals at site a, and bN = the total number of individuals at site b. The terms da and db in the equation (5.2) are calculated as:

$$\mathrm{d}a = \Sigma an_i^2/aN^2, \quad \mathrm{d}b = \Sigma bn_i^2/bN^2$$

The Morisita–Horn measure of similarity is favored by some researchers because it is relatively insensitive to sample size and species richness (Wolda 1981; Magurran 1988).

Dissimilarity among locations or between time points can also be used to evaluate responses to environmental stressors. Philippi, Dixon and Taylor (1998) quantified spatial and temporal responses to perturbations by comparing the pairwise dissimilarity between sites with the average dissimilarity among replicate samples. These researchers noted that measures of dissimilarity (or similarity) can be employed to evaluate changes in community composition during recovery (Fig. 5.4). If remediation was effective, the relative *dissimilarity* between reference and impacted sites would be expected to decrease over time.

While similarity indices provide a simple way to compare community composition, there are potential problems with these measures. Boyle *et al.* (1990) evaluated the ability of similarity indices to discriminate effects of simulated perturbations based on initial community structure, sensitivity to community change, stability in response to reduced richness and abundance, and consistency. These researchers concluded that some similarity indices were misleading because results were strongly influenced by initial community composition and the nature of the perturbation. Although similarity indices are useful when

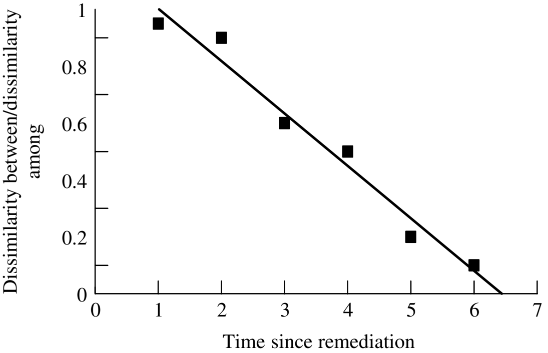

Fig. 5.4. Hypothetical changes in community similarity between reference and impacted sites as a function of time since remediation was initiated. The relationship shows that the index of dissimilarity (expressed as the ratio of dissimilarity between sites to the average dissimilarity among sites) is reduced over time as a result of remediation

comparing communities from two locations, more sophisticated techniques are necessary to compare multiple sites. Cluster analysis, a logical extension of similarity indices, is applicable for comparing communities from several locations or for comparing the similarity of a single site to a group of sites. Cluster analysis employs a variety of similarity measures based on either presence–absence or abundance data. These data are often expressed using a dendrogram, with the most similar sites combined into a single cluster. Additional sites are included based on their similarity to the existing clusters. Several different clustering algorithms have been developed, and relatively simple software packages are available for most analyses. Details of the different clustering techniques and the justification for deciding how different sites and clusters should be joined have been published (Gauch 1982). These methods will be described below.

5.3.2 ORDINATION

Ordination is a process in which a large set of variables is reduced to a few variables with the intent of enhancing conceptual parsimony and tractability. With ordination analysis of community abundance data, the measured variables (e.g. abundance of each species for each sampling unit) are used to identify hidden patterns or unmeasured factors explaining the data structure. Mathematical constructs are sought that help interpret correlations among variables. There are five steps to ordination analysis, regardless of the specific method applied (Comrey 1973). (1) The relevant data are generated and selected for analysis. As noted above, the data might require transformation prior to use. (2) The correlation matrix for the variables is calculated. (3) Factors (mathematical functions) are extracted. (4) The factors might be rotated to enhance interpretation. (5) The factors are then interpreted. Ideally, plots of the sampling unit positions along the first few of the mathematical constructs reveal explanatory, or at least consistent, themes.

As an example, linear functions can be defined such as

$$\mathit{Function}\ 1 = b_1X_1 + b_2X_2 + b_3X_3 + b_4X_4 + \cdots \text{ etc.} \tag{5.3}$$

where X_i = the normalized ln (abundance + 1) for each species sampled at the site. A first function is constructed that incorporates as much of the variance in the data as possible, and the process is repeated for additional functions with the remaining variance. Residual correlations after extraction of the first factor are used to produce a second, uncorrelated function that explains as much of the remaining variance as possible. The process is repeated to produce a series of functions. Ideally, most of the variance will be explained in the first few functions. A score for each sampling unit can be calculated for placement along each function. Plots for all sampling units using the formulated functions as axes should reveal an interpretable pattern. In this process, a matrix of many species abundances is reduced to a few sampling unit positions on a two- or three-dimensional plot. For example, the entire species abundance dataset for a site might be reduced to one point in a two- or three-dimensional plot. The X, Y, and perhaps, Z dimensions are constructs that can be given physical meaning such as the influences of soil type (function 1), heavy metal contamination, (function 2), and agricultural activity (function 3) (Fig. 5.5). Insight from additional information on soils, agricultural history, and soil metal concentrations might be used to interpret the distribution of the sampled plant communities along these

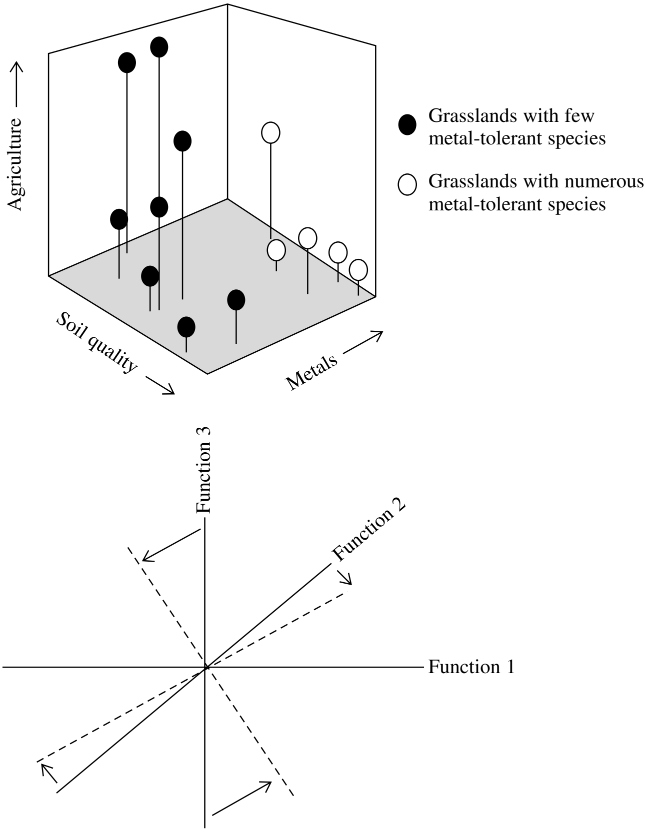

Fig. 5.5. A hypothetical ordination analysis of plant communities relative to heavy metal contamination (top panel). Abundances of species are quantified at five sites near abandoned mines and another eight reference sites. Soil qualities and the history of agricultural use of the sites are also noted as potential confounding factors. After data transformation, ordination analysis results in three orthogonal, linear functions that are assigned interpretations of the influence of soil quality, soil metal concentrations, and agricultural history. The five sites from the mine sites clearly cluster away from the reference sites. There is a gradient of communities relative to soil quality and agricultural history. Ordination axes can be rotated to enhance interpretation using orthogonal and oblique methods (bottom panel)

three functions. The magnitude and signs of the *b* values (loading coefficients) in the linear functions are used to identify an underlying theme for each axis. These loadings represent the extent to which the variables are related to the hypothetical factor. For most factor extraction methods, these loadings may be thought of as correlations between the variables and the function (Comrey 1973). For example, very high loadings in function 2 for species known to be tolerant to toxic metals and low or negative loadings for metal sensitive species would suggest the influence of metal exposure on community composition. For function 3, high loadings for species known to flourish in active agricultural areas might suggest the impact of active agriculture on community structure. The final result at this stage for ordination analyses would be to construct a table with rows of variables and associated loadings for each relevant factor (i.e. a table of unrotated factor loadings).

Several types of ordination methods exist (Boxes 5.1 and 5.2). Principal components analysis (PCA) was the first, and remains the most popular method (Sparks, Scott and Clarke 1999; Sparks 2000). Using PCA, linear combinations of the original variables are extracted that sequentially account for the residual variance in a series of orthogonal (uncorrelated) components. The first component contains the most variance; the second contains the most of the residual variance, etc. Ideally, the first few principal components account for most of the variance and the loadings allow sensible interpretations of these components. If this is not the case, some rotation method might be required.

Another general ordination method, factor analysis, is similar to principal component analysis in that the variables are used to produce linear functions. Instead of being called principal components, these linear functions of the data are called factors. A factor is an unobservable variable that has attributes of a subset of the observed variables. In contrast to PCA in which components are calculated directly as linear functions of the observed variables, the observed variables in factor analysis are envisioned as linear functions of the factors (unobserved variables) plus random error (Sparks, Scott and Clarke 1999).

Numerous other ordination methods are available for applications with specific needs. Ordination can be done with discrete data using correspondence analysis or detrended correspondence analysis (Sparks, Scott and Clarke 1999). Discrete data might consist of presence–absence information or categorized species abundances such as rare, uncommon, common, abundant, or dominant. Nonmetric ordination methods exist (see Sparks 2000 for details) and have been used successfully to describe insect communities exposed to NEEM products (Kreutzweiser, Capell and Scarr 2000), Norwegian oilfield macrofauna (Clarke 1999), and benthic macroinvertebrates of the River Tees (Crane *et al*. 2002).

Methods for extracting functions aim to produce easily interpretable functions. The mathematical functions or axes that are initially generated are uncorrelated or perpendicular. To enhance interpretation of these functions, some methods will rotate the axes at this stage of analysis based on some particular set of rules or criteria. Axes remain uncorrelated with orthogonal rotations but become correlated with oblique rotations. Many rotation methods are available for ordination; however, there is no formal statistical approach for determining which is best, and selection is usually based on user preferences. Among the most widely used rotation methods, the Kaiser Varimax produces orthogonal functions with as few variables with intermediate loadings as possible (Kaiser 1958, 1959; see also Comrey 1973). The concept is that a function with a few variables with very high or very low loadings will be more easily interpretable or parsimonious than one with many variables with intermediate loadings.

Box 5.1 Pollution's signature on the diversity of estuarine benthic communities

To assess the influence of pollution on estuarine benthos, Diaz (1989) plotted species diversity on principal component axes generated from physical and chemical data for several James River (Virginia, USA) locations. Admittedly, one might object to this example because ordination is not being used directly to summarize community data. However, the study is a good illustration of applying two multivariate methods to interpret pollution effects on communities. The direct application of ordination to species abundance data will be described in Box 5.2 after illustrating key aspects of ordination analysis with this example.

The challenge faced by Diaz was to assess the influence of pollution on benthic communities relative to several other confounding variables. Stations were sampled at 5-nautical mile intervals from the fall line to within 10 miles of the river's mouth. Factors potentially influencing the benthic communities were measured including sediment qualities, site-specific point discharges, and general water quality characteristics. Prior to ordination analysis, sites at salinity extremes were omitted to eliminate this obvious factor with a strong influence on community diversity.

Ordination analysis of physical and chemical data from James River sites was done after normalizing data with the formula,

$$Z_{\mathrm{ij}} = \frac{X_{\mathrm{ij}} - M_{\mathrm{j}}}{\mathrm{SD}_{\mathrm{j}}} \tag{5.4}$$

where Z_{ij} = the standardized score of a datum for the j$^{\mathrm{th}}$ variable of the i$^{\mathrm{th}}$ site, X_{ij} = the datum for the j$^{\mathrm{th}}$ variable for the i$^{\mathrm{th}}$ site, and M_{j} and SD_{j} = the mean and standard deviation of the data for the j$^{\mathrm{th}}$ variable, respectively. The normalized data were analyzed by principal components methods with no mention of any rotation of axes. Whether or not a rotation procedure would have produced more parsimonious principal components remains ambiguous.

Table 5.1 summarizes the PCA results. The percentages of total variance explained by each of the first five principal components is provided at the top of the table. Loadings (eigenvectors) for each chemical or physical factor are given for each principal component with large eigenvectors shown in bold typeface. The large eigenvectors for specific variables in the first, fourth and fifth principal components suggested to Diaz (1989) that these

Table 5.1. Loadings (eigenvectors) for five principal components derived by Diaz (1989) for James River physical and chemical data

Principal component	1	2	3	4	5
Percentage of total variance	36%	22%	15%	12%	8%
Discharge biochemical oxygen demand	**0.33**	**0.37**	0.00	0.20	0.05
Discharge chemical oxygen demand	0.24	**0.46**	−0.07	0.20	0.16
Discharge coliform bacteria	**0.31**	−0.09	0.23	0.04	**−0.58**
Discharge total suspended solids	0.23	−0.19	−0.02	0.10	**0.73**
Ammonia concentration in water	0.13	0.02	−0.13	**−0.70**	0.03
Nitrite/nitrate concentration in water	−0.14	**0.49**	−0.26	−0.20	−0.03
Phosphate in water	**0.32**	**−0.30**	0.16	−0.10	−0.07
Suspended solids in water	−0.23	**0.33**	0.25	**−0.37**	0.00
Biochemical oxygen demand in water	**0.39**	0.14	−0.02	**−0.32**	0.00
Number of discharges	**0.32**	**0.31**	−0.01	0.28	−0.17
Percentage silt and clay	−0.19	−0.11	**−0.60**	0.13	−0.10
Cross-sectional area	**−0.36**	0.18	0.15	0.20	−0.02

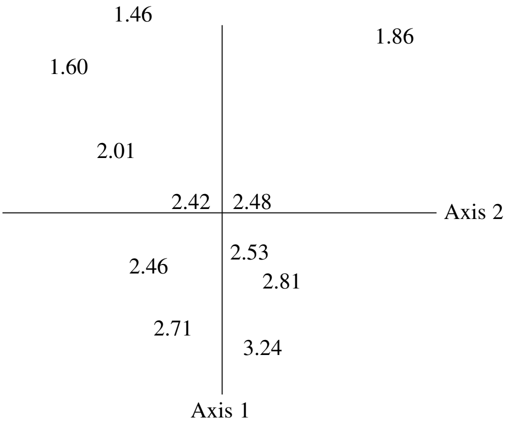

Fig. 5.6. Ordination analysis (PCA) of physical and chemical qualities at sites along the James River (Virginia). Axes 1 and 2 were interpreted as municipal waste discharge and industrial waste discharge, respectively. Numbers at each river site position on the plot are species diversities (H'). (Modified from Figure 7 of Diaz 1989)

principal components reflected municipal waste discharges. Those variables with large eigenvectors in the second principal component suggested industrial discharges. The third principal component seemed to be related to physical characteristics of sediments.

The first two principal components were used as axes for plotting species diversity at the different sampling sites (Fig. 5.6). Assuming the correct interpretation of the first principal component, an increase in municipal waste discharge was clearly associated with a decrease in species diversity (H'). The authors concluded from the plot that, 'the greater the pollution load the lower the species diversity'.

Box 5.2 Pesticide spraying changes mesocosm communities

Kedwards, Maund and Chapman (1999a,b) used ordination to study the impact of the pyrethroid pesticides, cypermethrin and lambda-cyhalothrin, on benthic communities established in 30-m^3 artificial ponds. Treatment involved duplicate mesocosms that were sprayed every 2 weeks for a total

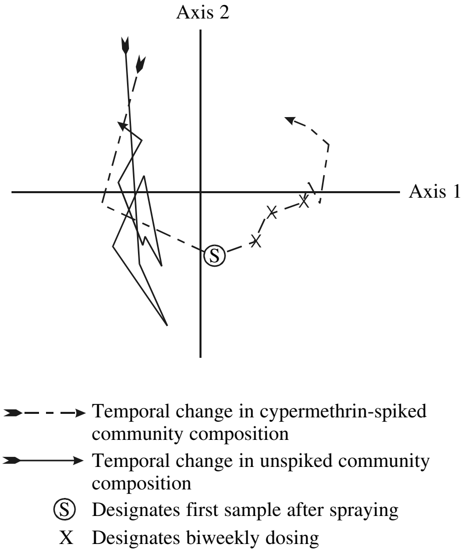

Fig. 5.7. Ordination results for benthic invertebrate community composition for reference and cypermethrin-sprayed mesocosms Community composition shifted abruptly along axis 1 at the sampling after spraying (denoted as S on diagram). Axis 1 and 2 were interpreted as the effect of spraying and the effect of time on community composition, respectively. (Modified from Figure 2 in Kedwards, Maund and Chapman 1999b)

of four sprayings per mesocosm. Pre-application data were collected 5 weeks before the first spraying and sampling continued for 14 weeks after the final spraying occurred.

Redundancy analysis, an ordination technique, was applied to the results from cypermethrin-sprayed mesocosms (Fig. 5.7). The two axes used in this figure accounted for 54 and 14% of the total variance in the data. Immediately after spraying began, the community in the treated mesocosms diverged from that of the controls, and each successive spraying moved the treated community further away. Several months after the last spraying, the communities remained quite divergent.

The authors interpreted the first two axes as being the influence of cypermethrin spraying (Axis 1) and the temporal changes in species abundances (Axis 2). The lines describing temporal changes in the reference mesocosms moved up and down along the second axis, but remained constant in their position relative to the first axis. The communities in the sprayed mesocosms changed with time and with spraying treatment. Spraying shifted community composition further to the right along the first axis, reflecting an increase in abundance of Chironomidae, Planorbidae, Hirudinea and Lymnaeidea, and a decrease in Gammaridae and Asellidae.

5.3.3 DISCRIMINANT AND CLUSTER ANALYSIS

Some multivariate methods, such as cluster and canonical discriminant analysis, explore differences or distances between sampling units. Groups for which differences are being assessed might be defined by the researcher (e.g. communities from polluted versus clean sites), by design (e.g. treatment levels of copper added to a series of microcosms), or by statistical methods (e.g. community groupings identified by cluster analysis). Discriminant analysis aims to develop quantitative rules for separating groups or classes of sampling units. Similar to PCA, some discriminant analysis methods generate functions (canonical variates) that produce maximum discrimination among sampling units. Loading coefficients associated with the different variables suggest which variables contribute the most to the differences among sampling units (Box 5.3).

Box 5.3 Copper exposed communities: what separates treatment groups?

A series of triplicate 17-m^3 freshwater microcosms were spiked at five copper levels in an effort to define techniques for determining differences among toxicant-treated communities (Shaw and Manning 1996). *In situ* bioassays and species abundance data were collected, but only canonical discriminant analysis of macroinvertebrate species abundance data are presented here.

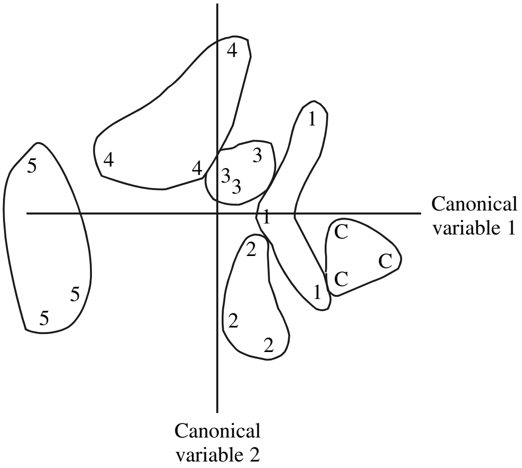

Fig. 5.8. Separation of macroinvertebrate communities of microcosms receiving different copper treatments (spiked amounts being ranked as control $<$ 1 $<$ 2 $<$ 3 $<$ 4 $<$ 5). Results are those obtained for canonical discriminant analysis of species abundance data for the 31 August sampling. The three observations plotted for each treatment are those for the triplicate microcosms. (Modified from Figure 8 of Shaw and Manning 1996)

Canonical variables, linear combinations of species abundance data that are best distinguished among treatments, were produced for a series of times during the trial. Analysis for one sampling date during the spiking period (31 August, 1 month after spiking began and 19 days after the last spiking) is provided in Fig. 5.8. The results show clear separation among treatments based on community composition. Surprisingly, species richness was not affected by copper spiking. However, abundances of annelids, crustaceans, mayflies, and chironomids did change. The mayfly *Caenis* was primarily responsible for separation among spiked treatments along the first canonical axis. (Importantly, *Caenis* bioassays in the spiked microcosms were also among the most useful for measuring effects of copper). Orthocladiinae, Chironominae and Hydrozetes were also important. Only four taxa were needed to separate groups along copper treatments, suggesting that these species are useful indicators of metal pollution.

Cluster analysis also distinguishes among sampling units using multivariate datasets. As discussed in detail by Ludwig and Reynolds (1988) and Matthews, Matthews and Landis (1998), diverse metrics of resemblance or distance are applied to sampling units. Sampling units may be grouped in a hierarchical or non-hierarchical manner using a variety of algorithms. Hierarchical schemes produce tree-like structures (dendrograms) with branching points along groupings suggesting the degree of distinction or similarity among the groups on the various branches. Non-hierarchical methods simply place sampling units into groupings. Sparks, Scott and Clarke (1999) give the example of K-means clustering in which the number of groupings is defined prior to analysis and the sampling units are sorted optimally into these groupings. Using this method, differences are quantified as the square of the Euclidean distance (Matthews, Matthews and Landis 1998) and sampling units are distributed among the groups to produce maximum group separation.

Cluster analysis has many applications in community ecotoxicology. For example, Matthews, Landis and Matthews (1996) used non-metric clustering (Matthews, Matthews and Landis 1995) to study microcosm community structural changes after turbine fuel exposure. The clustering methods revealed that differences among treated microcosms persisted for long periods of times, leading the authors to propose the community conditioning hypothesis described in Chapter 6. In a field setting, Dauer, Rodi and Ranasinghe (1992) used cluster analysis to group benthic communities according to the influence of several physical and water quality characteristics (Box 5.4).

Box 5.4 Cluster analysis identifies benthic communities affected by anoxia

Physical and chemical qualities within estuaries greatly influence the composition of benthic communities. Dauer, Rodi and Ranasinghe (1992) explored Lower Chesapeake Bay (USA) benthic communities in an attempt to quantify the influence of such factors on community structure. Emphasis was placed on identifying communities modified by episodes of anoxia. Benthic species are subjected to anoxia when water produced during seasonal stratification is moved onto nearby shallows by wind-driven seiches. The extent and effect of anoxia are of concern because of potential exacerbation by increased nutrient influx from human activities.

Twenty-one samples were taken along the Lower Chesapeake Bay and in several tributaries. Water quality data, including oxygen concentrations, were available for interpreting benthic species abundance information. Site selection intentionally included those along salinity gradients, those with different sediment types, and those that experienced episodic anoxia. Cluster analysis was carried out using logarithm-transformed species abundance data and the Bray–Curtis similarity coefficient.

Cluster analysis identified groupings that were easily interpreted based on salinity, sediment type, and dissolved oxygen concentration (Fig. 5.9). For explanatory convenience, six clusters are identified in Fig. 5.9. There was a clear clustering of sites relative to salinity: freshwater (cluster 6), transitional (cluster 5), mesohaline (cluster 4), and polyhaline (clusters 2 and 3) sites.

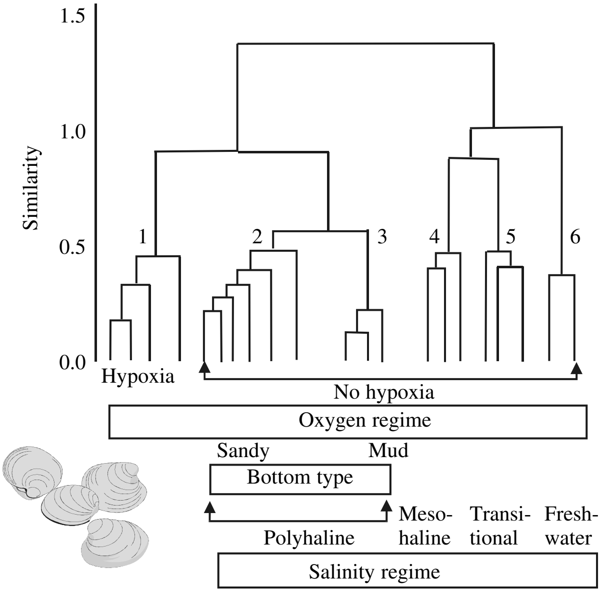

Fig. 5.9. Clustering of 21 benthic macroinvertebrate communities based on Bray–Curtis similarity coefficient. The clustering was interpreted by applying knowledge of salinity, oxygen, and sediment conditions. (Modified from Figure 2 of Dauer, Rodi and Ranasinghe 1992)

Within the polyhaline grouping, the communities split again into those associated with sandy (cluster 2) and muddy (cluster 3) substrates. Sites experiencing anoxia (four sites in cluster 1) were set apart from the other sites (17 sites in clusters 2 through 6) at a relatively high level (e.g. similarity of approximately 0.9). Relative to the other communities sampled, those experiencing periodic anoxia had lower species diversity, lower biomass, and less biomass deeper than 5 cm in the sediments. Results also showed that dominant species tended to be opportunistic, with equilibrium species being less common than in the other communities.

5.3.4 APPLICATION OF MULTIVARIATE METHODS TO LABORATORY DATA

With minor exceptions, most of the multivariate methods described to this point draw from species enumerations in order to describe community-level responses. However, other multivariate methods use results of single species toxicity tests to predict effects on communities. Box 5.5 describes an example that uses laboratory toxicity data for sediment and water to make predictions about community status.

Box 5.5 A risk ranking model based on estuarine fish communities

The Maryland Department of Natural Resources (USA) developed a composite index (risk ranking) for Chesapeake Bay tributaries (Hartwell 1997; also see Hartwell *et al*. 1997) using laboratory toxicity tests of water and sediments from sites of interest. The intent was initially to 'quantify the toxicological risk to populations due to the presence of toxic contamination ...' using ambient toxicity data. (See Newman (1998, 2001) for discussion of the problems in predicting population consequences based on these types of severity judgements.)

Four estuaries were selected to estimate a fish community-based IBI, fish species diversity, and this new ranking model. The ranking model employed water and sediment test results to quantify region status. On several dates, water samples from each site were collected for ambient toxicity tests including: fathead minnow (*Cyprinodon variegatus*) growth and survival, grass shrimp (*Palaemonetes pugio*) growth and survival, and copepod (*Eurytemora affinis*) reproduction and survival. Similarly, sediment toxicity tests were done including those quantifying sheephead minnow embryo–larval survival and teratogenicity, amphipod *(Leptocheirus plumulosus*) reburial, growth, and survival, and polychaete (*Streblospio benedicti*) survival and growth.

This ranking system of risk was influenced by a high hazard score for a particular measure and the uncertainty associated with producing a score for a region. The level of uncertainty influenced the score and the measured level of hazard. The severity of effect (mortality = 3, impaired reproduction = 2, impaired growth = 1), degree of response, variability in testing, site consistency, and the number of endpoints were components of the risk ranking model. The degree of response was the proportional difference from the control. The variability was expressed as the coefficient of variation (CV) for a particular metric for each set of laboratory replicates and each sample site during a particular sampling period. The last part of the ranking model involved consistency, or the level of agreement among assays for a site. Consistency was quantified as the cube root of the difference between half of the number of tests ($N/2$) and the number of statistically non-significant responses at each site (X),

$$\text{consistency} = \sqrt[3]{N/2 - X} \tag{5.5}$$

The consistency is then divided by the number of endpoints measured for a site. The site score is estimated with equation (5.6).

$$\text{Location score} = \frac{[\sum(\text{severity} * \%\ \text{response} * CV)] + \text{consistency}}{\sqrt{N}} \tag{5.6}$$

Scores were calculated for the four sites based on tests of water alone, sediment alone, or water and sediment combined. Pearson correlation coefficients were calculated for these scores versus a fish-based IBI, a benthic species diversity index, and a resident fish diversity index. There were no significant correlations ($\alpha = 0.05$) between the risk scores (water, sediment, or water–sediment combined) and the IBI scores or species diversity based on all resident fish species. Similarly, no significant correlation was noted between water testing-based risk scores and bottom fish species diversity. However, there were significant correlations between bottom fish species diversity and the sediment test-based risk score ($P = 0.0092$) and the combined test risk score ($P = 0.0018$). These results suggest that scores for this risk index are related to bottom fish diversity. Notionally, the relationship involved responses to site-associated toxicant exposures.

The methods described to this point have involved data collected from potentially impacted sites in an attempt to document community changes. However, species sensitivity distribution (SSD) methods use mostly laboratory data to predict potential community changes upon exposure to stressors. The approach extends the common use of one laboratory measure of effect, such as the 96-h LC50, to predict impact to an exposed community. Conventional prediction from one species can be made more credible by making predictions of effect based on information from the most sensitive test species. The SSD method modifies these laboratory-based approaches by using all available laboratory data to make predictions of effect concentrations for the ecological community. Its great advantage is that it uses all of the readily available information to predict community consequences. Its convenience and efficient use of single species data have led to a very rapid increase in its use.

To apply the SSD method, effect concentrations such as acute LC50 or NOEC values are collected for all relevant species. The effect concentration observations are ordered from the smallest to the largest value (e.g. smallest to largest 96-h LC50 values). The ordered values are then given a rank using one of several conventional methods. Currently popular is $i/(n + 1)$, where $i =$ the i^{th} ranked observation and $n =$ the total number of observations. A slightly better but less commonly applied approximation of rank for ordered observations is $(i - 0.5)/n$. At this point, the dataset consists of a series of observations (e.g. 96 h LC50 observations and their corresponding ranks). A lognormal model is often assumed and the probit transformation of each rank is taken. Another model and transformation can be used if there is evidence that the lognormal model is inappropriate. Newman and co-workers (Newman *et al*. 2000, 2001) indicate that the general assumption of a lognormal model is often not appropriate. Regardless, a lognormal model will be assumed here to illustrate the SSD method. A plot of logarithm of effect concentration versus probit of the rank is made, producing a straight line (Fig. 5.10) if the lognormal assumption is appropriate. A regression model is then used to estimate the concentration 'protecting' all but a specified percentage

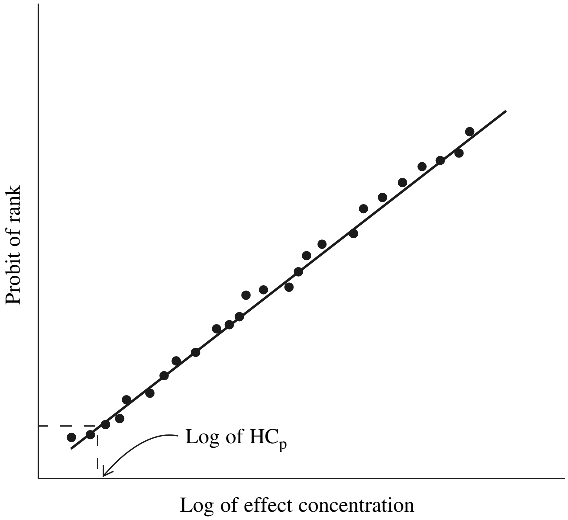

Fig. 5.10. Lognormal model for estimating the HC_p using the SSD method. Transformations are easily done on effect concentrations and effect proportion in order to linearize species sensitivity data. The log of the effect concentration is plotted against the probit of the effect proportion for the lognormal model assumed here

(p%) of the species in the community. This concentration is often called the hazard concentration or HC_p.

Although the SSD approach enjoys increasingly widespread application (Posthuma, Suter and Traas 2001), it does involve several unresolved shortcomings or ambiguities (Newman *et al*. 2000; Newman 2001). First, EC50, LC50, NOEC, LOEC, and MATC effects metrics are used to generate models but they have significant deficiencies as predictors of population persistence in natural communities. Any HC_p derived using these effects metrics will consequently have deficiencies as a predictor of community consequences. Second, the selection of a specified p implies that some loss of species is acceptable for any community because of species redundancy. As will be described in Chapter 6, the extent to which this redundancy hypothesis can be validly applied is still hotly debated. Therefore, any predictions based on the redundancy hypothesis must be viewed as non-conservative predictions at this time. Third, application of the SSD method requires thorough knowledge of the dominant and keystone species, and the importance of species interactions. It has been our experience that this knowledge is often not available in studies applying the SSD method. Fourth, *in situ* exposure is more complex and species-dependent than reflected in the laboratory exposures carried out in toxicity testing. Fifth, there is a bias toward lethality information, although non-lethal effects can result in species disappearance from a community. Finally, the assumption of a specific model, such as the lognormal model, is often made without careful scrutiny (Jagoe and Newman 1997; Newman *et al*. 2000, 2001).

5.4 CONCLUSIONS

In summary, a diverse array of analytical approaches allow description of toxicant effects on communities. Some, such as species diversity indices, reduce abundance data to a single number while others, such as the IBI, apply considerable ecological knowledge to generate *ad hoc* measures of community integrity. Others, like the SSD approach, attempt to use available laboratory data to produce gross predictions of possible community-level effects. Finally, multivariate procedures are devoid of ecological theory and simply identify correlations or associations within a dataset. All of these approaches can be extremely useful for detecting community differences or changes if applied insightfully.

REFERENCES

Bailey RC, Kennedy MG, Dervish MZ and Taylor RM (1998). Biological assessment of freshwater ecosystems using a reference condition approach: comparing predicted and actual benthic invertebrate communities in Yukon streams. *Freshw Biol* **39**: 765–774.

Blair RB (1999). Birds and butterflies along an urban gradient: surrogate taxa for assessing biodiversity? *Ecol Appl* **9**: 164–170.

Boyle TP, Smillie GM Anderson JC and Beeson DR (1990). A sensitivity analysis of nine diversity and seven similarity indices. *Water Pollut Con Fed* **62**: 749–762.

Chambers CL, McComb WC and Tappeiner II JC (1999). Breeding bird responses to three silvicultural treatments in the Oregon Coast Range. *Ecol Appl* **9**: 171–185.

Clarke KR (1999). Nonmetric multivariate analysis in community-level ecotoxicology. *Environ Toxicol Chem* **18**: 118–127.

Clements WH and Kiffney PM (1995). The influence of elevation on benthic community responses to heavy metals in Rocky Mountain streams. *Can J Fisheries Aquat Sci* **52**: 1966–1977.

Clements WH, Cherry DS and Cairns Jr J (1988). The impact of heavy metals on macroinvertebrate communities: a comparison of observational and experimental results. *Can J Fish Aquat Sci* **25**: 2017–2025.

Comrey AL (1973). *A Course in Factor Analysis*. Academic Press, New York, NY.

Crane M, Sorokin N, Wheeler J, Grosso A, Whitehouse P and Morritt D (2002). European approaches to coastal and estuarine risk assessment. In *Coastal and Estuarine Risk Assessment*, ed. by Newman MC, Roberts Jr MH and Hale RC, pp. 15–39. CRC Publishers, Inc, Boca Raton, FL.

Dauer DM, Rodi Jr AJ and Ranasinghe JA (1992). Effects of low dissolved oxygen events on the macrobenthos of the Lower Chesapeake Bay. *Estuaries* **15**: 384–391.

Diaz RJ (1989). Pollution and tidal benthic communities of the James River Estuary, Virginia. *Hydrobiologia* **180**: 195–211.

Fausch KD, Lyons J, Karr JR and Angermeier PL (1990). Fish communities as indicators of environmental degradation. *Am Fish Soc Symp* **8**: 123–144.

Fore LS, Karr JR and Wisseman RW (1996). Assessing invertebrate responses to human activities: Evaluating alternative approaches. *J N Am Benthol Soc* **15**: 212–231.

Gauch Jr HG (1982). *Multivariate Analysis in Community Ecology*. Cambridge University Press, Cambridge, UK.

Gerritsen J (1995). Additive biological indices for resource management. *J N Am Benthol Soc* **14**: 451–457.

Hartwell SI (1997). Demonstration of a toxicological risk ranking method to correlate measures of ambient toxicity and fish community diversity. *Environ Toxicol Chem* **16**: 361–371.

Hartwell SI, Dawson CE, Durell EQ, Alden RW, Adolphson PC, Wright DA, Coehlo GM, Magee JA, Ailstock S and Norman M (1997). Correlation of measures of ambient toxicity and fish community diversity in Chesapeake Bay, USA, tributaries – urbanizing watersheds. *Environ Toxicol Chem* **16**: 2556–2567.

Jagoe RH and Newman MC (1997). Bootstrap estimation of community NOEC values. *Ecotoxicology* **6**: 293–306.

Kaiser HF (1958). The Varimax criterion for analytic rotation in factor analysis. *Psychometrika* **31**: 313–323.

Kaiser HF (1959). Computer program for Varimax rotation in factor analysis. *Ed Psychol Meas* **19**: 413–420.

Karr JR (1981). Assessment of biological integrity using fish communities. *Fisheries* **6**: 21–27.

Karr JR (1993). Defining and assessing ecological integrity: beyond water quality. *Environ Toxicol Chem* **12**: 1521–1531.

Kedwards TJ, Maund SJ and Chapman PF (1999a). Community level analysis of ecotoxicological field studies: I. Biological monitoring. *Environ Toxicol Chem* **18**: 149–157.

Kedwards TJ, Maund SJ and Chapman PF (1999b). Community level analysis of ecotoxicological field studies: II. Replicated-design studies. *Environ Toxicol Chem* **18**: 158–166.

Kerans BL and Karr JR (1994). A benthic index of biotic integrity (B-IBI) for rivers of the Tennessee Valley. *Ecol Appl* **4**: 768–785.

Kremen C (1992). Assessing the indicator properties of species assemblages for natural areas monitoring. *Ecol Appl* **2**: 203–217.

Kremen C, Colwell RK, Erwin TL, Murphy DD, Noss RF and Sanjayan MA (1993). Terrestrial arthropod assemblages: Their use in conservation and planning. *Conserv Biol* **7**: 796–808.

Kreutzweiser DP, Capell SS and Scarr TA (2000). Community-level responses by stream insects to NEEM products containing azadirachtin. *Environ Toxicol Chem* **19**: 855–861.

Lewis CS (1942). *The Screwtape Letters*. Harper Collins Publishers, Inc., New York, NY.

Ludwig JA and Reynolds JF (1988). *Statistical Ecology. A Primer on Methods and Computing*. John Wiley and Sons, New York, NY.

Magurran AE (1988). *Ecological Diversity and its Management*. Princeton University Press. Princeton, NJ.

Matthews RA, Matthews GB and Landis WG (1998). Application of community level toxicity testing to environmental risk assessment. In *Risk Assessment. Logic and Measurement*, ed. by Newman MC and Strojan CL, pp. 225–253. CRC Publishers, Inc, Boca Raton, FL.

Matthews GB, Matthews RA and Landis WG (1995). Nonmetric conceptual clustering in ecology and ecotoxicology. *AI Appl* **9**: 41–48.

Matthews RA, Landis WG and Matthews GB (1996). The community conditioning hypothesis and its application to environmental toxicology. *Environ Toxicol Chem* **15**: 597–603.

Miller DI, Leonard, M, Hughes RM, Karr JR, Moyle PB, Schrader LH, Thompson BA, Daniels RA, Fausch KD, Fitzhugh GA, Gammon JR, Halliwell DB, Angermeier PL and Orth DJ (1988). Regional applications of an index of biotic integrity for use in water resource management. *Fisheries* **13**: 12–20.

Nelson SM and Epstein ME (1998). Butterflies (Lepidoptera: Papilionoidea and Hesperioidea) of Roxborough State Park, Colorado, USA: baseline inventory, community attributes, and monitoring plan. *Environ Manag* **22**: 287–295.

Newman MC (1998). *Fundamentals of Ecotoxicology*. CRC Publishers, Inc, Boca Raton, FL.

Newman MC (2001). *Population Ecotoxicology*. John Wiley and Sons, Chichester, UK.

Newman MC, Ownby DR, Mezin LCA, Powell DC, Christensen TRL, Lerberg SB and Anderson BA (2000). Applying species sensitivity distributions in ecological risk assessment: assumptions of distribution type and sufficient numbers of species. *Environ Toxicol Chem* **19**: 508–515.

Newman MC, Ownby DR, Mezin LCA, Powell DC, Christensen TRL, Lerberg SB, Anderson BA and Padma TV (2001). Species sensitivity distributions in ecological risk assessment: distributional assumptions, alternate bootstrap techniques, and estimation of adequate number of species. In *Species Sensitivity Distributions in Ecotoxicology*, ed. by Posthuma L, Suter II GW and Traas TP, pp. 119–132. CRC Publishers, Inc., Boca Raton, FL.

Philippi TE, Dixon PM and Taylor BE (1998). Detecting trends in species composition. *Ecol Appl* **8**: 300–308.

Plafkin JL, Barbour MT, Porter KD, Gross SK and Hughes RM (1989). *Rapid Bioassessment Protocols for Use in Streams and Rivers: Benthic Macroinvertebrates and Fish. EPA 440/4-89-001*. Washington, DC, US EPA.

Posthuma L, Suter II GW and Traas TP (2001). *Species Sensitivity Distributions in Ecotoxicology*. CRC Publishers, Inc, Boca Raton, FL.

Resh VH, Norris RH and Barbour MT (1995). Design and implementation of rapid assessment approaches for water resource monitoring using benthic macroinvertebrates. *Aust J Ecol* **20**: 108–121.

Reynoldson TB, Norris RH, Resh VH, Day KE and Rosenberg DM (1997). The reference condition: a comparison of multimetric and multivariate approaches to assess water-quality impairment using benthic macroinvertebrates. *J N Am Benthol Soc* **16**: 833–852.

Shaw JL and Manning JP (1996). Evaluating macroinvertebrate population and community level effects in outdoor microcosms: Use of *in situ* bioassays and multivariate analysis. *Environ Toxicol Chem* **15**: 608–617.

Simon TP and Lyons L (1995). Application of the index of biotic integrity to evaluate water resource integrity in freshwater ecosystems. In *Biological Assessment and Criteria: Tools for Water Resource Planning and Decision Making*, ed. by Davis WS and Simon TP, pp. 245–262. Lewis Publ., Boca Raton, FL.

Sparks TH (2000). *Statistics in Ecotoxicology*. John Wiley and Sons, Chichester, UK.

Sparks TH, Scott WA and Clarke RT (1999). Traditional multivariate techniques: potential for use in ecotoxicology. *Environ Toxicol Chem* **18**: 128–137.

Suter II GW (1993). A critique of ecosystem health concepts and indexes. *Environ Toxicol Chem* **12**: 1533–1539.

Walls LD (1999). *Material Faith: Henry David Thoreau on Science*. Houghton Mifflin Co., Boston, MA.

Wolda H (1981). Similarity indices, sample size, and diversity. *Oecologia* **50**: 296–302.

6 Disturbance Ecology and the Responses of Communities to Contaminants

It is one of those refreshing simplifications that natural systems, despite their diversity, respond to stress in very similar ways. (Rapport, Whitford and Hilden 1998)

6.1 THE IMPORTANCE OF DISTURBANCE IN STRUCTURING COMMUNITIES

In this chapter we will compare the ways in which communities respond to natural and anthropogenic disturbances. We suggest that many of the characteristics that determine resistance and resilience of communities to natural disturbance may also influence responses to chemical stressors. For the purposes of this discussion, disturbance is defined as any relatively discrete event that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment (White and Pickett 1985). Key features that determine the impact of disturbance on communities are the magnitude (e.g. how far the disturbance is outside the range of natural variability), frequency, and duration. Some ecologists define disturbance as any event that results in the removal of organisms and creates space. Indeed, some ecology textbooks (e.g. Begon, Harper and Townsend 1990) combine discussion of disturbance and predation in the same chapter because they ultimately have similar effects on communities: the removal of organisms from a community. The impact of a predator on a competitively superior species will have a qualitatively similar influence on community structure as the creation of space by physical disturbance. However, most community ecologists limit the definition of disturbance to include only events that are outside the range of natural variability. In other words, the predictability or novelty of a disturbance event greatly influences community responses and recovery times. Predictability of disturbance is largely influenced by the frequency of occurrence, but also varies among ecosystems and disturbance types (Table 6.1).

Ecologists have long recognized the importance of natural disturbance in structuring communities (Connell 1978), and many consider disturbance a central organizing principle in community ecology (Peterson 1975; Sousa 1979; White and Pickett 1985). In particular, the biotic and abiotic factors that influence

Table 6.1. Frequency and predictability of natural disturbance events in ecosystems. (Modified from Reice 1994)

Ecosystem	Disturbance type	Frequency (years)	Predictability
Forests	Fire	1/40–200	Moderate
	Windstorms	1/10–25	None
	Insect defoliation	Rare	None
Chaparral	Fire	1/15–25	High
Grasslands	Fire	1/5–10	Moderate
Deserts	Frost	1/50–200	None
Rivers	Floods	0–15	None
	Drought	0–2	Moderate to high
Lakes	Freezing	0–1	High
Intertidal zone	Log damage	Annual	Low

recovery from disturbance have received considerable attention. A large body of theoretical and empirical evidence supports the idea that most communities are subjected to natural disturbance and that disturbance regimes influence community structure and life history characteristics of component species. Most of this research has focused on physical perturbations (e.g. hurricanes, floods, volcanoes), whereas relatively few studies have employed basic ecological principles to describe responses to anthropogenic stressors. Just as variability and predictability determine the response of communities to natural disturbance, they also figure prominently in understanding the effects of anthropogenic disturbance (Rapport, Regier and Hutchinson 1985). The goal of this chapter is to describe ways in which ecotoxicologists can use this rich history of research in basic disturbance ecology to understand community responses to contaminants.

6.1.2 DISTURBANCE AND EQUILIBRIUM COMMUNITIES

Much of the historical focus in disturbance ecology is closely aligned with the Clementsian paradigm of community succession and the ‘balance of nature’ (Clements 1936) The equilibrium model of community structure asserts that overall community composition is relatively stable and that communities will return to equilibrium conditions if given sufficient time following a disturbance. The equilibrium model also assumes that species interactions, most notably competition, are the most important factors structuring the community. The idea that communities will return to pre-disturbance conditions following perturbations implicitly assumes the existence of equilibrium conditions. The equilibrium model is in stark contrast to the idea that community structure is determined largely by stochastic processes, such as random colonization and highly variable environmental factors (Table 6.2). Proponents of the non-equilibrium theory assert that community composition is constantly changing over time and that natural systems are

Table 6.2. Characteristics of equilibrium and non-equilibrium communities. (From Wiens 1984)

	Equilibrium communities	Non-equilibrium communities
Biotic interactions	Strong, especially competition	Weak
Number of species	Many	Few
Abiotic factors	Less important	Major importance
Community regulation	Density dependent	Density independent
Overall structure	Deterministic	Stochastic

often recovering from the most recent disturbance (Wiens 1984; Reice 1994). Communities only give the illusion of stability if the frequency of disturbance is relatively low.

The debate over equilibrium and non-equilibrium determinants of community structure has important implications for the study of recovery from anthropogenic disturbance. If communities are determined largely by stochastic processes and therefore constantly changing, then defining recovery as a return to pre-disturbance conditions will be difficult. In contrast, if communities are characterized by equilibrium conditions, then predictable recovery trajectories can be identified. Long-term investigations of pre-disturbance conditions may help define the range of natural variation in non-equilibrium communities. However, if communities show the degree of temporal variation expected based on non-equilibrium models, it will possible to detect only the most severe disturbances.

6.1.3 RESISTANCE AND RESILIENCE STABILITY

Ecologists recognize two different types of community stability when quantifying community responses to disturbance. Resistance stability refers to the ability of a community to maintain equilibrium conditions following a disturbance. Resistance can be quantified by measuring the magnitude of the response of a community compared with pre-disturbance conditions. If two communities are subjected to the same disturbance, the community that shows the least amount of change compared with pre-disturbance conditions has greater resistance. Resilience stability refers to the rate at which a community will return to pre-disturbance conditions. If two communities are exposed to the same disturbance, the community that recovers faster is considered to have greater resilience. Because resistance and resilience are fundamental properties of all ecological systems, some ecologists have proposed that they could be employed as indicators of ecological health (Box 6.1).

Box 6.1 Resistance and resilience as ‘fitness tests’ of ecosystem health

Measures of species richness, diversity, and ecosystem processes are routinely employed in biological monitoring to assess effects of anthropogenic stressors. The ability of a community to withstand and recover from natural disturbance is also recognized as a fundamental characteristic of ecological integrity. If exposure to contaminants or other anthropogenic stressors influences resilience or resistance of a community, responses to natural disturbance may be used as endpoints in ecological assessments. Whitford, Rapport and deSoyze (1999) measured resistance and resilience of a grassland community to a natural disturbance (drought) along a stress gradient induced by livestock grazing. Both resistance and resilience were compromised by grazing, suggesting that natural disturbance will have a greater and longer lasting effect on communities also subjected to anthropogenic disturbance. Whitford, Rapport and deSoyze (1999) proposed using measures of resistance and resilience as an early warning 'fitness test' of ecosystem health. The strength of this approach is that it measures something that really matters (ability to withstand or recover from disturbance) and can be applied across different types of communities. Assuming that effects of natural disturbance in reference and impacted communities can be quantified, this approach provides a unique opportunity for comparisons among communities.

Resistance and resilience to disturbance are not necessarily correlated. Features that determine tolerance of a community to a stressor (resistance) do not always influence how quickly the community will recover (resilience). For example, a climax forest may show high resistance to outbreaks of a herbivorous pest (e.g. gypsy moths); however, resilience will be very low because of the time required for this community to return to pre-disturbance conditions. In contrast, grassland communities subjected to this same stressor may recover very quickly. Stream ecosystems are notoriously resilient and often recover very quickly from disturbance (Yount and Niemi 1990); however, most streams have low resistance and are relatively sensitive to many types of disturbance. Finally, coral reefs are an excellent example of an ecosystem with both low resistance and low resilience.

While these definitions of resilience and resistance stability are useful for classifying the diverse ways that communities may respond to disturbance, they are relatively simplistic concepts and their interpretation is context dependent. Although we can develop some general guidelines for predicting the magnitude of a response or the rate of recovery, it is unlikely that the specific details will be consistent across all types of perturbations.

6.1.4 PULSE AND PRESS DISTURBANCES

In addition to understanding factors that influence susceptibility and recovery trajectories of communities following disturbance, ecologists also distinguish between two different types of perturbations. Pulse disturbances (Bender, Case and Gilpin 1984) are defined as instantaneous alterations in the abundance of species within a community (Fig. 6.1). Factors that influence the recovery of a

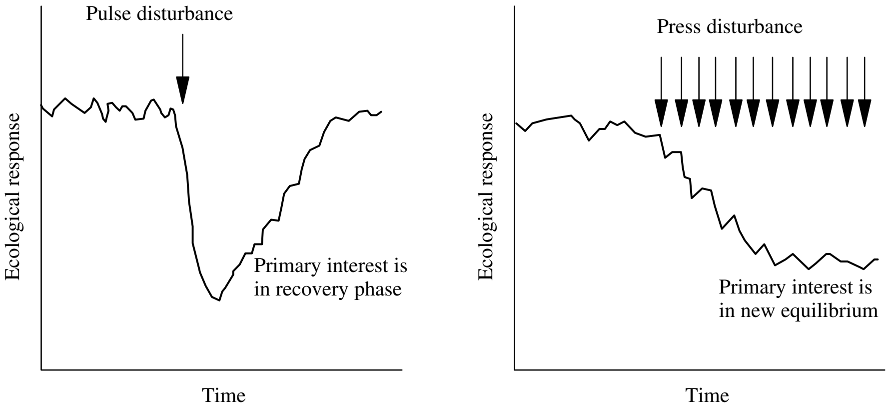

Fig. 6.1. Comparison of pulse and press disturbances showing ecological responses of communities. Pulse disturbances result in instantaneous alterations of community structure and function. The primary research questions following pulse disturbances focus on processes that influence rate of recovery. Press disturbances are sustained alterations in ecological responses that may result in establishment of a new community. Following press disturbances ecologists are particularly interested in understanding characteristics of this new equilibrium

community as it returns to equilibrium are of particular interest in the study of pulse disturbances. The crown fire that occurred in Yellowstone National Park (USA) in 1989 is an example of a large-scale pulse disturbance. Studies of the lodgepole forest communities in Yellowstone have focused primarily on identifying biotic and abiotic factors that influence the time required for this system to return to pre-disturbance conditions.

Press disturbances cause sustained alterations in abundance of species, often resulting in the elimination of some taxa and establishment of a new community. Here, ecologists are particularly interested in understanding community characteristics and factors that control this new equilibrium. Increased temperature associated with global climate change is an example of a press disturbance. Because communities affected by press disturbances are expected to establish new equilibria, investigators often focus on understanding characteristics of this altered community.

While the original theoretical treatment of pulse and press disturbances was developed to improve our quantitative understanding of species interactions (Bender, Case and Gilpin 1984), these concepts are also relevant to our discussion of how communities respond to contaminants. An ecotoxicological example of a pulse disturbance would be a chemical spill that temporarily reduced densities of certain species. Differences in sensitivity to the chemical among species may determine community composition immediately following the spill. However,

Table 6.3. Proposed classification of perturbations by cause (type of disturbance) and community response. (From Glasby and Underwood 1996)

Classification	Type of disturbance	Community response
Discrete pulse	Short term	Short term
Protracted pulse	Short term	Continued
Protracted press	Continuous	Continued
Discrete press	Continuous	Short term

assuming that the chemical was quickly degraded and there were no persistent effects, colonization ability of displaced species would be the primary factor influencing the rate of recovery. Recovery from this pulse disturbance may be rapid if an adequate supply of colonists is available to the system. In contrast to pulse disturbances, a press disturbance is continuous and the community is generally not expected to return to its original condition until the stressor is eliminated. An ecotoxicological example of a press disturbance would be the continuous input of toxic material into a system, such as acid deposition from coal-fired power plants. Here, differences in sensitivity among species will be the primary factor influencing community composition. If recovery is defined as a return to pre-disturbance conditions, it is unlikely that recovery will be observed until levels of the toxic materials are reduced. In the case of highly persistent contaminants (e.g. PCBs associated with lake sediments), recovery may not be observed even after the source has been eliminated.

The definitions used to distinguish between pulse and press disturbances have been criticized because they combine cause (e.g. disturbance) with effect (e.g. the response of the community) and assume a relatively simplistic response to perturbation (Glasby and Underwood 1996). For example, a pulse disturbance such as a chemical spill may have a lasting effect on community structure and function. Similarly, communities subjected to press disturbances could quickly return to equilibrium conditions if populations are able to acclimate or adapt to stressors. Glasby and Underwood (1996) refine these definitions and distinguish between discrete and protracted press and pulse perturbations (Table 6.3). They also suggest sampling procedures and experiments that allow investigators to identify these different categories of disturbance.

6.2 COMMUNITY STABILITY AND SPECIES DIVERSITY

One of the more impassioned debates in the field of community ecology has been over the positive relationship between species diversity and resistance/resilience stability (Elton 1958; May 1973). Darwin (1872) first proposed this intuitively pleasing idea and speculated that species-rich communities should be more stable than communities with few species. Complex food webs are assumed to allow communities better to tolerate disturbance because of greater functional redundancy among pathways of energy flow and nutrient cycling. According to this hypothesis, a species that was eliminated due to disturbance would simply be replaced by a different species that performs a similar ecological function. The hypothesis that greater species diversity results in greater stability also has significant implications for the study of anthropogenic disturbance. If complex systems are more stable, we would expect that the chronic effects of contaminants would be less pervasive in species-rich communities compared with depauperate communities.

In their synthesis of the relationship between diversity and ecological resilience, Peterson, Allen and Holling (1998) describe four models of species richness and stability currently in the literature. The simplest model (the species richness–diversity model) proposes that the addition of species to a community increases the number of ecological functions, thereby increasing stability (Fig. 6.2A). The model assumes that stability continues to increase as new species are added, and makes no allowances for saturation of ecological function. In contrast, the rivet model assumes that there is a limit to the number of functions in a community and that as new species are added functions begin to overlap (Fig. 6.2B). Because of this functional redundancy in diverse communities, a few species can be removed with relatively little influence on stability. However, like removing rivets from the wing of an airplane, as more species are lost from a community a critical threshold is eventually reached and stability will decrease rapidly. The idiosyncratic model (Fig. 6.2C) proposes that the relationship between species richness and stability is highly variable and that the consequences of adding new species is dependent on species interactions. Addition of some species will stabilize ecological function whereas the addition of others will have relatively little influence on community stability. Finally, the drivers and passengers model (Fig. 6.2D) assumes that the influence of species richness on stability depends on which particular species is added to the community. Driver species, including ‘ecological engineers’ and other keystone species, have a greater impact on functional stability of a community than passenger species.

All four models described above assume a positive relationship between stability and diversity. However, despite its intellectual appeal, the relationship between diversity and stability is not straightforward and relatively few experimental studies have provided strong support for this hypothesis. In fact, theoretical treatment of the diversity–stability relationship has suggested that complex communities are actually *less* stable than simple communities (May 1973). Microcosm experiments conducted with protists support these models and show that addition of more trophic levels resulted in reduced stability (Lawler and Morin 1993). One potential explanation for these conflicting results is that different researchers have used different measures to define stability. Peterson (1975) reported different relationships between diversity and stability depending on whether one

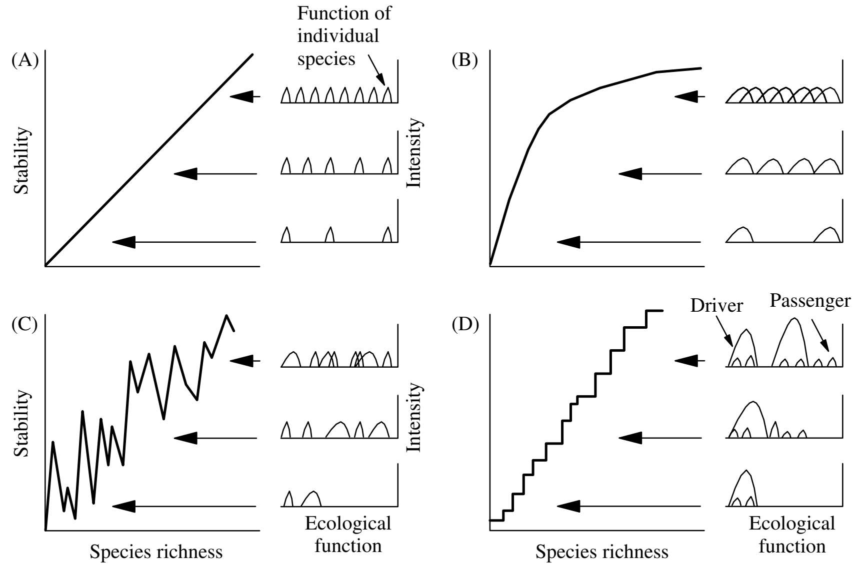

Fig. 6.2. Four models showing the relationship between species richness and functional stability in communities. (A) The species diversity model assumes that stability decreases linearly as species are removed from the community. (B) The rivet model assumes that functional redundancy protects communities from loss of species, but that stability decreases rapidly once species are reduced to a critical threshold level. (C) The idiosyncratic model proposes that the effect of removing species is dependent on species interactions. (D) The drivers and passengers model assumes that the influence of species richness on stability depends on which species are removed from the community. Loss of driver species or keystone species have a greater impact on functional stability of a community than loss of passenger species. (Modified from Figures 1–4 in Peterson, Allen and Holling 1998)

measured stability at the species level (variance of individual populations) or at the community level (variation in community composition). In contrast to the theoretical studies of diversity–stability relationships, the most influential empirical studies have used temporal variation in productivity or biomass as a measure of stability (Doak *et al.* 1998). In a long-term experimental study of grassland plots Tilman (1996) reported that increased biodiversity stabilized community and ecosystem processes but not population-level processes (Fig. 6.3). Variability of community biomass decreased (i.e. stability increased) as more species were added to the community, whereas variability of individual populations increased (although this relationship was relatively weak). These results may help resolve the long-standing debate over the diversity–stability relationship. It appears that increased diversity does stabilize community biomass and productivity as predicted by Elton (1958), but decreases population stability, consistent

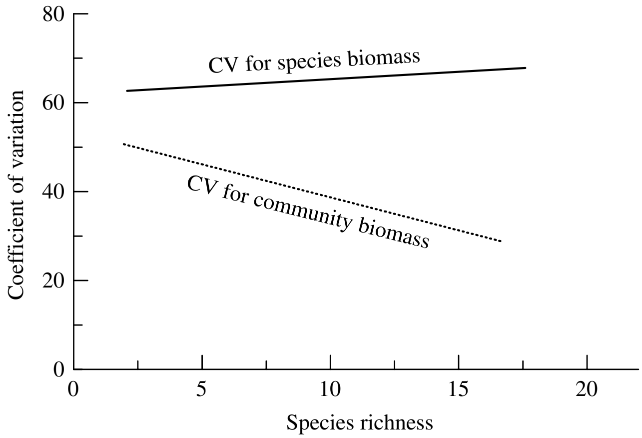

Fig. 6.3. Proposed resolution of the diversity–stability debate. The figure shows a relationship between species richness and two measures of stability in plant communities. Population and community stability was characterized by measuring the coefficient of variation (CV = 100 × standard deviation/mean) for species and community biomass. As more species are added to the community, population stability decreases (the CV for species biomass increases), whereas community stability increases (the CV for community biomass decreases). (Modified from Figures 7 and 9 in Tilman 1996)

with May's (1973) mathematical models. The underlying mechanism responsible for these differences appears to be interspecific competition (Tilman 1996).

Some researchers have argued that the relationships between diversity and stability reported in the literature are an inevitable outcome of averaging the fluctuations of individual species' abundances (Doak *et al.* 1998). The premise for this argument is that community-level properties such as total biomass will be less variable as a greater number of species are included simply because of this averaging effect. This same statistical phenomenon is observed for other measures of community composition. For example, total abundance is generally less variable than abundance of individual species, especially for rare species. A practical aspect of this statistical averaging effect is that aggregate measures of community composition are often less variable and therefore more useful for assessing impacts of stressors than abundance of individual species (Clements *et al.* 2000). From an ecological perspective the relative importance of this statistical relationship must be quantified in order to understand the role of species interactions in structuring communities. Previously, the diversity–stability relationship was assumed to be exclusively a result of species interactions. However, this statistical averaging effect associated with aggregate measures occurs regardless of the importance of competition or predation in a community (Doak *et al.* 1998).

Much of the experimental research investigating the relationship between diversity and stability has involved establishing a diversity gradient in which individual species are excluded from some treatments. While many of these experiments have shown a positive relationship between diversity and stability, it is uncertain if similar patterns occur in systems where diversity varies along natural gradients. Sankaran and McNaughton (1999) report results of a study of savannah grasslands in which plant communities along a natural disturbance gradient were exposed to experimental perturbations, including fires and grazing. These researchers observed that the relationship between diversity and resistance stability was dependent on the specific measure of stability being considered. Resistance to species turnover, measured as the proportion of species in both pre- and post-disturbance plots, increased with species diversity. This result is consistent with the hypothesis that stability is positively associated with diversity. In contrast, resistance to compositional change, measured as change in the relative contribution of different species before and after disturbance, decreased with species diversity. Because community composition is a reflection of numerous extrinsic factors, including disturbance regime and site history, it may be a more important determinant of stability than the actual number of species in a community. Sankaran and McNaughton's (1999) results demonstrate that the relationship between diversity and stability is largely influenced by these extrinsic factors and that species-rich communities may not necessarily be better at 'coping' with disturbance.

The diversity–stability debate has serious implications for understanding how communities respond to anthropogenic stressors. Measures of stability based on aggregate properties, such as total abundance or biomass, appear to be related to the number of species in a community. The degree to which other measures of stability, such as community resistance and resilience, are influenced by this statistical relationship is uncertain. For example, is the greater resilience of species-rich communities to anthropogenic disturbances a result of community redundancy or simply a statistical artifact? Alternatively, communities subjected to anthropogenic perturbations may be resistant to additional disturbance because they are dominated by stress-tolerant species. Understanding the causes of the diversity–stability relationship and quantifying the relative importance of these statistical averaging effects requires that theoretical and empirical ecologists agree on common definitions of stability.

6.3 SPECIES DIVERSITY AND ECOSYSTEM FUNCTION

Another controversial topic in contemporary ecology concerns the hypothesized relationship between species diversity and ecosystem function (Hooper and Vitousek 1997; Grime 1997; Huston 1997). The relationship between the number of species and ecosystem processes (e.g. primary production, respiration, energy flow) is a logical offshoot of the diversity–stability controversy with direct relevance to community ecotoxicology. Much of the debate centers on the notion that ecosystem health is dependent on the number of species and that the loss of species will affect ecosystem processes. Species richness is predicted to influence ecosystem function in several fundamental ways. First, communities with a large number of species have a greater probability of containing taxa with important functional roles. Second, communities with more species will likely use available resources more efficiently, resulting in greater productivity. Finally, a large number of species provides functional redundancy in a community and acts as a buffer against loss of species due to anthropogenic disturbance.

The positive influence of species richness on ecosystem function has recently acquired new significance as conservation biologists have used this relationship as another reason to protect species. The accelerating loss of biodiversity has intensified efforts to clarify the diversity–productivity relationship and to identify mechanistic explanations. In a review of experimental evidence supporting the relationship, Chapin *et al.* (1998) concluded that high species diversity maximizes resource acquisition across trophic levels, reduces the risk associated with large, stochastic changes in environmental conditions, and protects communities from exposure to pathogens or exotic species. If we assume that different species in a community have different functional roles and that the functions performed by an individual species are limited, it follows that alterations in community composition resulting from anthropogenic disturbance will affect ecosystem processes. However, identifying specific mechanistic explanations for the diversity–productivity relationship and characterizing its form (e.g. linear versus curvilinear) has been difficult. Some ecologists suggest that this relationship is inconsistent across communities because the relative contributions of individual species to ecosystem function varies with environmental context (Cardinale, Nelson and Palmer 2000). Others argue that the observed pattern is a sampling artifact resulting from inappropriate experimental designs and hidden treatment effects (Grime 1997; Huston 1997). Below, we will present empirical evidence that supports the diversity–productivity relationship, describe the limitations of this model, and discuss the implications for community ecotoxicology.

Large-scale field experiments conducted in grasslands by Tilman and colleagues have contributed to our understanding of the relationship between diversity and plant productivity (Tilman *et al.* 1997). By adding a known number of species (0–32) or functional groups (0–5) to 289 plots (169 m^2 each), these researchers found that both species diversity and functional diversity influenced plant productivity (Fig. 6.4). When results were analyzed based on functional composition the relationships were stronger, suggesting that composition of the community was actually more important than the number of species present. Similarly, Hooper and Vitousek (1997) reported that the composition of plant functional groups was more closely related to ecosystem processes than functional group richness. These results demonstrate that the different functional roles of species may be a more important predictor of ecosystem health than

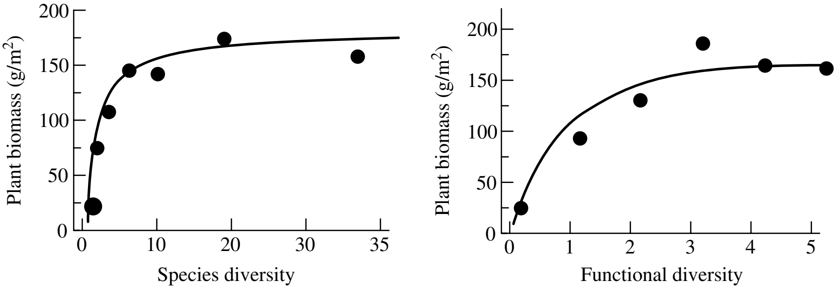

Fig. 6.4. The influence of species diversity and functional diversity on productivity (measured as aboveground biomass) in grassland plots. Species diversity and functional diversity were manipulated by adding a known number of species or functional groups to experimental plots. (Modified from Figure 1 in Tilman *et al.* 1997)

the actual identity of those species. Consistent with predictions of the driver and passenger model described previously (Fig. 6.2D), the loss of some functionally important species will have greater impacts on ecological integrity than the loss of other species. One of the key goals of basic ecology will be to identify those functionally important species.

A large-scale experimental test of the relationship between grassland plant diversity and productivity was conducted at eight European field sites (Hector *et al*. 1999). Five levels of species richness were established at each site across a broad geographic region (Germany, Portugal, Switzerland, Greece, Ireland, Sweden, and two sites in the United Kingdom). Although productivity (measured as aboveground biomass) varied among locations, the overall pattern was a reduction in productivity with lower species richness at all sites. The mechanisms proposed to account for this pattern involve niche complementarity, whereby variation among species results in more complete utilization of resources, and positive mutualistic interactions among species. Although distinguishing among these alternative explanations will not be easy, the results demonstrate that the loss of species and the alteration in community composition will significantly alter ecosystem processes. Thus, in addition to measuring the direct effects of anthropogenic disturbances on ecosystems, it is important that community ecotoxicologists recognize the indirect effects on ecosystem processes due to loss of species.

Because most experimental investigations of the diversity–productivity relationship have focused on primary producers, the widespread generality of patterns observed by Tilman and others is uncertain. At the very least, our understanding of this relationship is biased by the emphasis on terrestrial plants. The complex functional interactions among trophic groups may require that ecologists adopt a multitrophic approach to predict ecosystem responses to changes in diversity. Naeem, Hahn and Schuurman (2000) reported that neither increased producer nor decomposer diversity alone could account for greater algal production observed in freshwater microcosms. Duffy *et al*. (2001) investigated the relationship between grazer diversity and plant productivity in marine seagrass beds. Grazer species composition strongly influenced seagrass productivity and was more important than species richness. These results indicate that studies focusing on a single trophic level may underestimate ecosystem effects of anthropogenic disturbance on biodiversity.

6.4 RELATIONSHIP BETWEEN NATURAL AND ANTHROPOGENIC DISTURBANCE

A unifying feature that has emerged from research on disturbance is the remarkable resilience of some communities to a wide range of natural disturbances. The characteristics that account for rapid recovery of communities following disturbance are diverse, but most often relate to the availability of colonists. One fundamental question from an ecotoxicological perspective is how can research on responses to natural disturbance be employed to predict recovery from anthropogenic disturbance. In particular, can we expect to see patterns of resistance and resilience to chemical stressors similar to those of physical disturbances? Comparisons of natural and anthropogenic disturbance will allow researchers to answer these questions and improve their ability to predict responses to future disturbances.

Unfortunately, relatively few studies have compared responses of communities to both natural and anthropogenic disturbances. Foster *et al*. (1997) conducted several large-scale experiments designed to investigate the impacts of physical restructuring (a blowdown induced by a hurricane), nitrogen additions, and soil warming in a second-growth forest. Results of this study showed that despite obvious effects of the blowdown on forest structure, there was little change in ecosystem processes (Table 6.4). Because species in this forest were adapted to frequent disturbance associated with hurricanes, recovery was observed soon after the blowdown. In contrast, N addition and soil warming had a much greater impact on ecosystem processes, but little influence on community composition. These researchers contend that because species in this community were not adapted to these novel stressors, little evidence of recovery was observed.

Table 6.4. Effects of natural (blowdown) and anthropogenic (N addition; soil warming) disturbances in a second growth forest. The table shows percentage changes of ecosystem processes. (From Foster *et al*. 1997)

Process	Blowdown	N addition	Soil warming
Mineralization	+15.9	+138	+50
Methane uptake	−2.4	−36	+20
Soil respiration	+6.2	0	+76

A long-term program of field monitoring and experiments conducted in Antarctica, 'one of the most extreme physical environments in the world' compared the impacts of natural and anthropogenic disturbance on marine benthic communities (Lenihan and Oliver 1995). Anthropogenic disturbance included chemical contamination in sediments around McMurdo Station (primarily hydrocarbons, heavy metals, and PCBs), whereas natural disturbance included anchor ice formation and scour. Results showed remarkable similarity between anthropogenic and natural disturbances. Communities in contaminated sites and physically disturbed sites were dominated by the same assemblages of polychaete worms, species with highly opportunistic life history strategies. Despite the similarity in responses, these researchers suggested that recovery from chemical contamination would require considerably more time because of the slow degradation of these persistent contaminants in sediments.

6.4.1 THE ECOSYSTEM DISTRESS SYNDROME

Although there is some empirical support for the hypothesis that effects of contaminants vary among communities (Poff and Ward 1990; Howarth 1991; Kiffney and Clements 1996; Medley and Clements 1998), there have been few attempts to identify specific factors responsible for this variation. Fragility may be an inherent property of some communities, regardless of the history of disturbance (Nilsson and Grelsson 1995). Resistance and resilience to anthropogenic disturbances may vary among different communities or among similar communities in different locations. This variation greatly complicates our ability to predict community responses and recovery times. If some communities are inherently more fragile than others, identifying characteristics that increase sensitivity and the mechanisms responsible for ecosystem recovery are important areas of research.

Rapport, Regier and Hutchinson (1985) suggested that communities in unstable environments may be 'preadapted' to moderate levels of anthropogenic stress. Howarth (1991) speculated that ecosystems with fewer opportunistic species, lower diversity, and closed element cycles would be sensitive to contaminants. In an experimental investigation of resistance and resilience, Steinman *et al.* (1992) reported that initial community structure was relatively unimportant in determining community responses to chlorine. In this study community biomass, which was regulated by grazing herbivores, determined resistance to chlorine exposure. These results are consistent with experiments showing that trophic status of a community influences resistance and resilience (Lozano and Pratt 1994).

Rapport, Regier and Hutchinson (1985) evaluated the responses of several communities to different types of disturbance and developed an 'ecosystem distress syndrome'. They argue that community responses to disturbance are analogous to the generalized adaptation syndrome that occurs when individual organisms are subjected to environmental stress (Seyle 1973). Because the perturbations considered in their analysis included a range of natural and anthropogenic stressors (physical restructuring, overharvesting, pollution, exotic species, extreme natural

Table 6.5. Characteristic responses of the ecosystem distress syndrome. The table shows the expected response of each indicator as increasing (+), decreasing (−), or unknown (*). (From Rapport, Regier and Hutchinson 1985)

Disturbance type	Nutrient pool	Primary productivity	Species diversity	Size distribution	System retrogression
Harvesting renewable resources					
Aquatic	*	*	−	−	+
Terrestrial	−	−	−	−	+
Pollutant discharges					
Aquatic	+	+	−	−	+
Terrestrial	−	−	−		+
Physical restructuring					
Aquatic	*	*	−	−	+
Terrestrial	−	−	−	−	+
Introduced species					
Aquatic	*	*	*	−	+
Terrestrial	*	*	*	*	+
Extreme natural events					
Aquatic	*	*	−	−	+
Terrestrial	−	−	−	−	+

events), the results may be used to compare responses across disturbance types and among communities (Table 6.5). Because it is not feasible to measure every potential indicator in all ecosystems, identifying general responses to disturbance across a diverse array of ecosystems and disturbance types is essential. Furthermore, identifying similarities between natural and anthropogenic disturbances will allow ecotoxicologists to benefit from the long history of research on natural disturbance better to understand how communities respond to chemical stressors.

6.4.2 THE INTERMEDIATE DISTURBANCE HYPOTHESIS

Communities subjected to moderate levels of disturbance may have greater species richness or diversity compared with communities existing under benign conditions. The intermediate disturbance hypothesis (IDH) was first proposed by Connell (1978) to explain higher levels of species diversity observed in rocky intertidal habitats subjected to moderate levels of physical disturbance. The mechanism suggested to account for this somewhat counterintuitive observation was that moderate levels of disturbance reduced competition for limited resources and allowed more species to coexist. Diversity is low under benign conditions because a small number of species dominate resources and are capable of excluding subordinate species. Diversity is also low under extreme levels of disturbance because relatively few species are able to persist. Thus, according to predictions of the IDH we would expect the greatest species diversity under moderate levels of perturbation (Fig. 6.5).

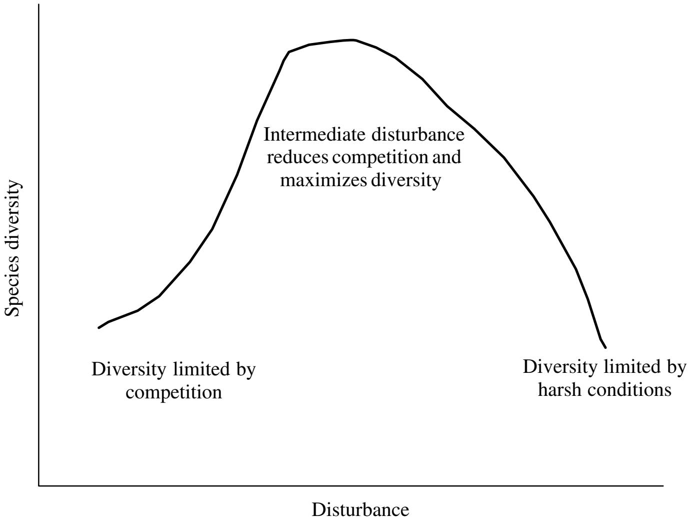

Fig. 6.5. According to the intermediate disturbance hypothesis (Connell 1978) species diversity is maximized under conditions of intermediate levels of disturbance. Species diversity is low in stable, highly predictable communities because a small number of species dominate resources and are capable of excluding subordinate species. Species diversity increases with moderate levels of disturbance because the ability of dominant groups to exclude subordinates decreases. Species diversity is also low under extreme levels of disturbance because relatively few species are able to persist under these harsh environmental conditions

There is general support for the IDH in the literature, and natural communities in a variety of habitats seem to fit predictions of the IDH fairly well. According to this hypothesis, the rich biological diversity observed in tropical rainforests and coral reefs is maintained by a combination of high productivity, habitat complexity, and disturbance from hurricanes. Sousa (1979) conducted a series of experiments to test the IDH in marine intertidal communities associated with boulders. Because small boulders are more likely to be disturbed by waves, Sousa used boulder size as an index of the probability of disturbance. He initially demonstrated that the greatest number of species was found on intermediate-sized boulders, a finding consistent with predictions of the IDH. He then anchored the small boulders to prevent disturbance and observed an increase in the number of species. These results demonstrated that substrate stability was more important than size in determining species richness.

The IDH is now widely embraced by many ecologists, and examples of the positive effects of moderate disturbance on species diversity have been reported in many different systems. However, there are examples where the IDH was not supported, most notably in freshwater streams where rapid recolonization swamps the effects of disturbance. For example, Death and Winterbourn (1995) reported that species richness in New Zealand streams increased with habitat stability, but showed no relationship with disturbance. Similar results were reported by Reice (1985) following experimental manipulation of cobble substrate designed to simulate flood disturbance. Although the importance of natural disturbance in structuring many communities was recognized, Reice concluded that the IDH did not apply to streams. Failure to account for the effects of disturbance on multiple trophic levels may also limit the predictive ability of the IDH. Natural communities consist of several potentially interacting trophic levels, and disturbance to multitrophic communities may show very different results than disturbance to a single trophic level (Fig. 6.6). Wootton (1998) developed a mathematical model to determine if predictions of the IDH were applicable to multiple trophic levels. Results of these analyses helped explain why the IDH successfully predicted patterns in some communities but not in others. Clearly, any application of the IDH to anthropogenic disturbances must consider systems with more than one trophic level.

Similar to research on disturbance in general, most tests of the IDH have focused on natural, physical perturbations in systems where space is the primary

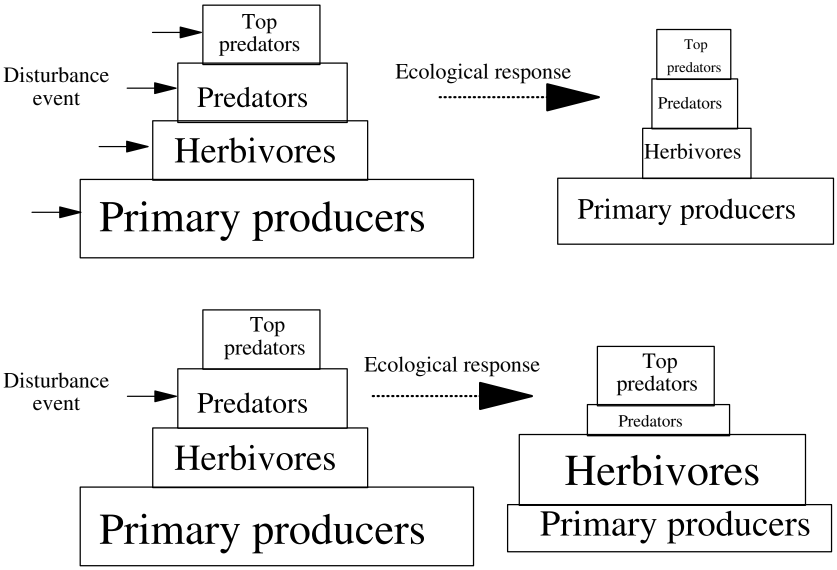

Fig. 6.6. Conceptual model showing the effects of disturbance in multiple trophic level systems. In the upper panel, disturbance to each of the trophic levels (represented by the solid arrows) results in a proportional reduction in biomass of each group. In the lower panel predators are disproportionately impacted by the disturbance, resulting in a cascading effect on lower trophic levels. (Modified from Figure 1 in Wootton 1998)

limiting resource. It is uncertain if predictions of this model can be applied to toxicological stressors. Are there examples where exposure to intermediate levels of toxic stressors prevent competitively superior species from dominating resources and reducing species richness? Because species richness and diversity are common indicators of perturbation used in biological assessments, the IDH is relevant to community ecotoxicology. If species richness is enhanced under low levels of contaminant exposure as predicted by the IDH, then it may be difficult to detect subtle impacts on communities.

6.4.3 SUBSIDY–STRESS GRADIENTS

The theoretical treatment of subsidy–stress gradients by Odum, Finn and Franz (1979) offers some insight into the responses of communities to different types of chemical stressors. According to this model, certain types of disturbances, such as the input of nutrients or organic material, may enhance or subsidize a community. However, when levels of these materials exceed a critical threshold, the system becomes stressed resulting in a unimodal response. In contrast to patterns observed for inputs of usable resources, the input of toxicants into a system generally does not subsidize a community (Fig. 6.7). In fact, very small amounts of toxic chemicals may have a similar effect on communities as large amounts of usable (e.g. subsidizing) materials. The shape of the perturbation–response curve for toxicant input or the location of the peak in the subsidy–stress gradient is dependent on numerous factors and varies greatly among communities. In addition, because of the hierarchical arrangement of natural systems, inputs

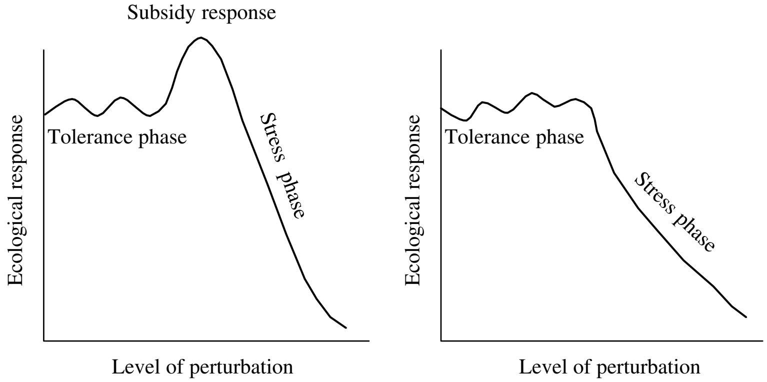

Fig. 6.7. Odum's model of subsidy–stress gradients. The model predicts that certain types of stressors, such as the input of nutrients or organic material, may subsidize a community. When levels of these materials exceed some threshold of tolerance, the system becomes stressed resulting in a unimodal response to the stressor. In contrast, the addition of toxic materials generally does not subsidize ecological function and therefore results in a tolerance phase followed by a stress phase. (Modified from Figure 1 in Odum, Finn and Franz 1979)

of nutrients and organic matter may subsidize one level of organization (e.g. increase species diversity and productivity) but have a negative impact on some individual species. A good example to illustrate this point is the eutrophication observed in aquatic ecosystems resulting from the input of nutrients. In general, low input of nutrients into an oligotrophic system will stimulate primary and secondary productivity and may increase species diversity. However, these changes are likely to be accompanied by alterations in community structure, as nutrient-sensitive species are replaced by nutrient-tolerant species. The use of subsidy–stress models (Odum, Finn and Franz 1979) for predicting responses to anthropogenic disturbances requires a thorough understanding of natural temporal changes in community composition. The initial increase in productivity and species diversity following the input of nutrients into an oligotrophic lake is often followed by a slow decline as the system adjusts to these novel conditions.

In summary, the input of either toxic chemicals or subsidizing materials can alter community composition because of differential sensitivity among species. The subsidy–stress model predicts that small inputs of usable materials in a system will increase primary productivity and may increase species diversity (Odum, Finn and Franz 1979). In contrast, the input of toxic materials in a system will generally not increase productivity. It is unlikely that low concentrations of toxic materials will increase species diversity unless these chemicals remove competitively superior species or alter the outcome of species interactions, as predicted by the intermediate disturbance hypothesis (Section 6.4.2).

6.5 CONTEMPORARY HYPOTHESES TO EXPLAIN COMMUNITY RESPONSES TO ANTHROPOGENIC DISTURBANCE

Populations chronically exposed to contaminants often exhibit increased tolerance relative to naive populations (Newman 2001). Two general explanations are proposed to account for this observation: physiological acclimation and genetic adaptation. Physiological responses may include reduced contaminant uptake or increased production of detoxifying enzymes. In contrast, genetic adaptation results from higher survival rate of tolerant individuals and subsequent changes in gene frequencies. The distinction between acclimation and adaptation is somewhat arbitrary, as physiological processes may also have a genetic basis. For example, increased levels of metallothionein in response to metal exposure may indicate either acclimation or genetic adaptation, as adapted populations have developed the capacity for greater protein production.

Although increased tolerance has often been demonstrated in populations previously exposed to contaminants, few studies have examined tolerance at higher levels of biological organization. As noted above, the most common explanations for increased tolerance at the population level include acclimation and selection for resistant genotypes. We argue that these same intraspecific mechanisms also account for resistance of communities to contaminants. In other words, community-level tolerance is at least partially a result of physiological and genetic changes of populations. However, because communities consist of large numbers of interacting species, it is likely that other mechanisms, unique to these systems, will contribute to tolerance. For example, increased tolerance at the community level may result from replacement of sensitive species by tolerant species. This shift, termed 'interspecific selection' (Blanck and Wangberg 1988), is a common response in contaminated systems and a consistent indicator of anthropogenic disturbance. Interspecific selection is also a likely explanation for pollution-induced community tolerance, a new ecotoxicological approach for demonstrating causation in community assessments.

6.5.1 POLLUTION-INDUCED COMMUNITY TOLERANCE

Increased resistance of a population to a contaminant may indicate selection pressure and provide strong evidence that the population has been affected (Luoma 1977). Similarly, increased tolerance at the community level may also indicate ecologically important effects. Pollution-induced community tolerance (PICT) has been proposed as an ecotoxicological tool to assess the effects of contaminants on communities (Blanck and Wangberg 1988). PICT is tested by collecting intact communities from polluted and reference sites and exposing them to contaminants under controlled conditions. Increased community tolerance resulting from the elimination of sensitive species is considered strong evidence that community restructuring was caused by the pollutant. Proponents of the PICT argue that while differences between communities from reference and polluted sites can be attributed to many factors, increased tolerance observed in communities is less sensitive to natural variation and most likely a result of contaminant exposure (Blanck and Dahl 1996). Furthermore, because acquisition of community tolerance is generally not influenced by environmental conditions, locating identical reference and polluted sites for comparison is less critical (Millward and Grant 2000).

The use of PICT to assess impacts of contaminants at the level of communities is based on three assumptions: (1) sensitivity to contaminants varies among species; (2) contaminants will restructure communities, with sensitive species being replaced by tolerant species; and (3) differences in tolerance among communities can be detected using short-term experiments (Gustavson and Wangberg 1995). The first two assumptions are relatively straightforward and easy to verify with field sampling. The third assumption is more problematic and significantly constrains application of PICT as an assessment tool. While tolerance at the population level can be assessed using a variety of species, logistical considerations will limit the types of communities where tolerance can be investigated experimentally. For obvious reasons, most of the original research on PICT has been conducted using small organisms with relatively fast life cycles (Table 6.6).

Table 6.6. Experimental tests of the pollution-induced community tolerance hypothesis showing the types of stressors, endpoints, and diversity of communities examined

Community	Stressors	Endpoints	Reference
Marine periphyton	Arsenate	Photosynthesis, biomass, species composition	Blanck and Wangberg (1988)
	TBT	Photosynthesis	Blanck and Dahl (1996)
Lentic phytoplankton	Arsenate, Cu	Photosynthesis, biomass, community composition	Wangberg (1995)
Lentic periphyton	Cu, atrazine	Photosynthesis	Gustavson and Wangberg (1995)
Marine phytoplankton	TBT	Primary production	Petersen and Gustavson (1998)
Freshwater protozoans	Zn	Primary production, biomass, species richness	Niederlehner and Cairns (1992)
Lotic microalgae	Cd, Zn	Biomass, carbohydrates, community composition	Ivorra *et al*. (2000)
Estuarine nematodes	Sediment Cu	Survival time	Millward and Grant (2000)
Benthic macro-invertebrates	Cd, Cu, Zn	Community composition, richness, susceptibility to predation	Clements (1999)

The PICT hypothesis was originally developed for marine periphyton, but has now been tested in several different communities. Protozoan communities developed under low levels of zinc stress were more tolerant of zinc than naive (e.g. unexposed) communities (Niederlehner and Cairns 1992). Relative resistance to zinc in acclimated communities increased by >3× compared with unacclimated communities. Schwab *et al*. (1992) reported that periphyton communities in experimental streams rapidly increased their tolerance to surfactants. Metal tolerance of nematodes collected from sediments along a contamination gradient increased with concentrations of copper in the environment (Millward and Grant 1995). Finally, benthic macroinvertebrate communities collected from a site with moderate levels of heavy metals were significantly more tolerant to subsequent cadmium, copper, and zinc exposure than those collected from pristine sites (Clements 1999; Courtney and Clements 2000).

Studies testing the PICT hypothesis have also examined a variety of endpoints. As noted above, increased tolerance in communities may result from either population-level responses (acclimation or adaptation) or interspecific selection. For example, tolerance of nematode communities from a Cu-polluted estuary resulted from increased abundance of tolerant species, evolution of Cu-tolerance, and exclusion of sensitive species (Millward and Grant 1995). Endpoints examined in PICT studies should be selected to allow investigators to distinguish between population and community-level mechanisms. Greater tolerance of populations can be evaluated by comparing responses of individual species collected from reference and polluted sites. Greater tolerance at the community level can be evaluated by measuring effects on structural and functional endpoints. An important consideration when selecting endpoints in PICT studies is the potential for functional redundancy in the restructured communities. Dahl and Blanck (1996) reported that some functional endpoints were inadequate for validating the PICT hypothesis because sensitive species were replaced by tolerant species with a similar functional role.

Although there has been widespread support for the PICT hypothesis in the literature, several issues must be resolved before the approach becomes a useful ecotoxicological tool. PICT is most likely to be observed in communities that show a large amount of variation in sensitivity among species. Nystrom *et al.* (2000) reported difficulty demonstrating PICT in algal communities exposed to atrazine because of the narrow distribution of tolerances among species. Development of tolerance in phytoplankton communities was reported to be size specific (Petersen and Gustavson 1998). Although microplankton showed tolerance to tri-butyl-tin (TBT), other size fractions of the community showed relatively little response. Finally, Ivorra *et al.* (2000) reported that the influence of exposure history on tolerance of periphyton is complicated by maturity of the community. Immature communities from a reference site were more sensitive to metals than those from a polluted site, supporting the PICT hypothesis; however, there was no difference in the responses of mature periphyton communities between the two sites.

One potential advantage of using PICT as an assessment tool is the opportunity to isolate effects of individual stressors in systems impacted by multiple stressors (Wangberg 1995). If we assume no interactions among stressors and that tolerance to one chemical does not influence tolerance to another, PICT could be used to quantify effects of a specific chemical. However, previous research has shown that co-tolerance may occur in some communities, especially when modes of action and detoxification mechanisms are similar (Blanck and Wangberg 1991). For example, Gustavson and Wangberg (1995) reported that communities exposed to copper also showed increased tolerance to zinc. In contrast, Wangberg (1995) observed that exposure to copper reduced tolerance for arsenate. These results indicate that some caution is necessary when using PICT to identify effects of specific chemicals in environments where multiple contaminants are present.

6.6 BIOTIC AND ABIOTIC FACTORS THAT INFLUENCE COMMUNITY RECOVERY

In addition to studying how communities respond to disturbance, ecologists are frequently interested in understanding how communities recover from disturbance. The definition of recovery, the characteristics of communities that influence rate of recovery, and the influence of disturbance type on recovery have been topics of considerable discussion in community ecology. From an applied perspective, predicting the rate of recovery from disturbance is at least as important as understanding the initial responses. If we assume that recovery is a non-stochastic process, then information on biotic and abiotic factors that influence rate of recovery may allow us to predict how long it will require communities to reach pre-disturbance conditions. More importantly, the study of recovery from natural disturbance may allow researchers to understand and predict how communities recovery from anthropogenic disturbance (Box 6.2). For example, a study of lizard and spider populations in the Bahamas showed that the risk of extinction from hurricanes was related to population size only when disturbance was moderate (Spiller, Losos and Schoener 1998). Following a catastrophic disturbance large population size did not protect populations from extinction. Recovery of these assemblages was more related to fecundity and dispersal ability. Other research has demonstrated that species initially colonizing disturbed habitats are characterized by small body size and short life cycles. If these generalizations also apply to anthropogenic disturbances, we predict that disturbed communities would initially be dominated by relatively small species with short life cycles and high reproductive output and that recovery would be greatly influenced by the dispersal ability of the species.

Box 6.2 Recovery of communities from large-scale disturbances

Three large-scale disturbances that have occurred over the past several decades have provided ecologists with unprecedented opportunities to examine recovery and test various hypotheses concerning biotic and abiotic factors that influence resistance and resilience. Two of these disturbances were natural (the eruption of Mt. St. Helens and the crown fires at Yellowstone National Park), whereas a third (the *Exxon Valdex* oil spill) was anthropogenic, providing an opportunity to examine recovery from different types of disturbances.

The eruption of Mt. St. Helens in May 1980 and the associated blowdown, mud flows, avalanches, and ash deposits affected over 700 km^2 in southwestern Washington (USA). The fires in Yellowstone National Park (YNP) during the summer of 1988 were larger than any in the previous 200–300 years. A total of 2500 km^2 of the park burned, creating a complex mosaic of disturbed and undisturbed habitats. Finally, the break-up of the *Exxon Valdez* in March 1989 spilled approximately 41×10^6 l of crude oil in northeastern Prince William Sound (Alaska, USA) and oiled an estimated 800 km of shoreline. By any account, each of these disturbance events was large-scale, novel, and had a major impact on the surrounding communities. Ecologists rushed to these sites to validate predictions of theoretical and empirical models derived from nearly a century of studying community succession. While some of the original predictions were well supported by field studies, others were not. For example, recovery of plant and animal communities on Mt. St. Helens occurred through a bewildering array of mechanisms, many of which involved the persistence of ‘biological legacies’ (e.g. living and dead habitat structure that remained following the blast). In the Yellowstone fires geographic location and the proximity of new colonists were more important for predicting recovery than burn severity and patch size (Turner *et al*. 1997). Finally, despite the dramatic impact of the *Exxon Valdez* oil spill on bird populations which caused mortality of hundreds of thousands of birds, seabird communities in Prince William Sound showed unexpected resilience (Wiens *et al*. 1996). The lessons learned from intensive study of these large-scale disturbances have forced ecologists to re-evaluate many of their models of community perturbation and recovery (Franklin and MacMahon 2000).

Recovery from natural or anthropogenic disturbance is determined by a complex suite of factors related to the characteristics of the community, severity of the disturbance, and physical features of the disturbed habitat. Because disturbance is an integral part of the evolutionary history of many organisms, recovery from natural disturbance may be quite rapid. Communities dominated by opportunistic species capable of rapid colonization will generally recover quickly. Species that initially colonize disturbed habitats are often trophic generalists, capable of exploiting a wide range of resources. Magnitude (spatial extent) and novelty of disturbance will also influence recovery times. Thus, communities will require considerably more time to recover from severe, novel disturbances that have a large spatial extent (e.g. a large oil spill) than from small-scale, predictable perturbations.

The timing of a disturbance with respect to critical life stages for organisms will also influence the rate of recovery. For example, juvenile and immature life stages are generally more sensitive to disturbance than adults. Consequently, a disturbance that occurs when these immature life stages are present will have a disproportionately greater impact on a community. Other phenological considerations, such as the seasonal availability of seeds or other life stages that are critical for dispersal, also influence rates of recovery. Experiments conducted with salt marsh plants showed that differences in recovery rates among species were primarily determined by the season when the disturbance occurred (Allison 1995).

Specific features of the disturbed habitat, such as environmental heterogeneity and proximity to sources of colonists, must be considered when assessing potential for recovery. Communities in patchy environments that contain refugia and are located near undisturbed habitats will generally recover faster than communities in isolated, homogeneous environments. Finally, rates of recovery will also be influenced by the potential interplay between these different features. For example, the effects of size of the disturbed area on recovery will depend on the colonization ability of nearby species. Recovery from a small-scale disturbance may require a significant amount of time if the dispersal ability of local species is limited.

Understanding the spatial and temporal dynamics of community recovery following anthropogenic disturbance is critical to the field of restoration ecology. Fundamental issues regarding the definition of recovery and the specific indicators of recovery must be considered before generalizations are possible. For example, is the return to an equilibrium number of species sufficient to demonstrate recovery or should the actual composition of the community matter? If the composition of a community returns to pre-disturbance conditions but certain ecosystem processes (e.g. decomposition, nutrient cycling) remain altered, has recovery occurred? Although our ability to predict contaminant effects on communities has increased greatly, there has been considerably less effort devoted to measuring recovery from anthropogenic disturbance. The vast majority of field investigations of disturbance focus on short-term effects and often fail to monitor recovery. A report prepared by an intergovernmental task force in the USA on biological monitoring concluded that despite the large amount of effort devoted to improving environmental quality, our understanding of the effectiveness of remediation programs is hampered by the failure to assess recovery (Hart 1994). In other words, restoration and remediation programs are often assumed to be successful; however, rigorous verification of this assumption is lacking because of the paucity of funding available to monitor communities during the recovery phase. As a consequence, much of the available data on recovery of ecosystems from contaminants is anecdotal, and relatively few studies have documented recovery using adequate experimental designs (Yount and Niemi 1990).

Failure to consider recovery may provide misleading information on the magnitude of a particular disturbance. For example, consider two different communities exposed to the same disturbance (Fig. 6.8). Effects on one community are initially greater (e.g. a greater shift from pre-disturbance conditions), but the community eventually returns to pre-disturbance conditions. In contrast, the second community shows less impact but recovery is not observed. Samples collected soon after the disturbance (t_1) would show that the effects on community A were greater than those on community B. However, samples collected later in the recovery trajectory (t_2) would show just the opposite results. Thus, sampling programs designed to measure recovery must be conducted at the appropriate temporal scale to quantify the relative impacts of disturbance.

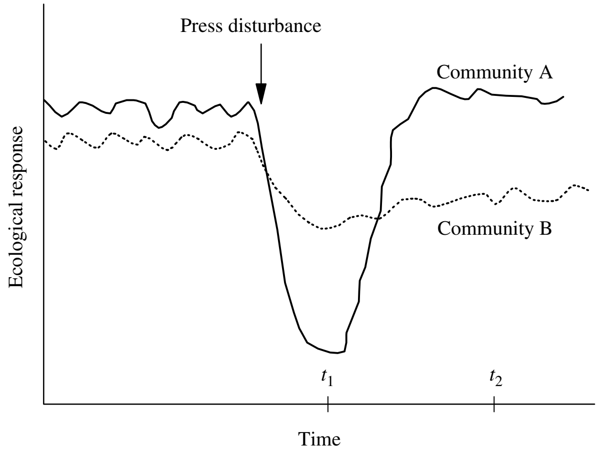

Fig. 6.8. The importance of considering recovery trajectories when assessing responses to press disturbances is illustrated by comparing two communities subjected to the same stressor. Samples collected soon after the disturbance (t_1) would show that effects on community A were greater. However, because of the more rapid recovery observed in community A, samples collected later in time (t_2) would show greater effects on community B. (Modified from Figure 1 in Niemi *et al.* 1990)

6.6.1 CROSS COMMUNITY COMPARISONS OF RECOVERY

Comparative studies of stream communities have shown that these systems often recover quite rapidly from both natural and anthropogenic disturbances. Because natural variation of streams is generally high, many species have flexible life history characteristics and are adapted to fluctuating conditions. These same characteristics may help explain the rapid recovery from anthropogenic disturbances. Niemi *et al.* (1990) reviewed over 150 case studies of stream communities in which some aspect of recovery was monitored. Because the study examined many types of disturbance (floods, drought, application of biocides, timber harvesting, mining, and toxic spills), the review provides an excellent opportunity to compare responses to natural and anthropogenic stressors. The most striking generalization from these studies was the rapid recovery observed in many lotic ecosystems. For macroinvertebrates, over 90% of the studies reported recovery of density, biomass, and richness within 1–2 years after disturbance. Although recovery for fish communities generally required more time, the majority of studies showed recovery within 2 years. In general, longer recovery times were reported for physical disturbance than for chemical disturbance. The most important exception to this pattern was for persistent organic chemicals, which remained in systems for longer periods of time. The rapid recovery of lotic systems was determined by (1) life history characteristics of species that allowed for rapid recolonization; (2) the proximity of upstream and downstream undisturbed sites to provide a source of colonists; (3) the high flushing rate of lotic systems; and (4) the general adaptations of many stream organisms to natural disturbance.

These cross community comparisons of recovery are especially useful for developing a broad understanding of responses to anthropogenic disturbances. However, these approaches provide relatively little insight into the mechanisms responsible for observed changes (Fisher and Grimm 1991). To test the hypothesis that communities resistant to one disturbance will also be resistant to a different disturbance requires that all variables except the disturbance be controlled by the investigator. Similarly, to test the hypothesis that one community is more resistant to a specific disturbance than another community requires that both systems be subjected to the same disturbance under the same conditions. Fisher and Grimm (1991) argue that while cross community comparisons are useful for generating hypotheses, responses to disturbance should initially be investigated in similar systems.

6.6.2 IMPORTANCE OF LONG-TERM STUDIES FOR DOCUMENTING RECOVERY

Continuing research conducted at Mt. St. Helens and Yellowstone National Park has demonstrated the value of long-term studies for characterizing the range of natural variability in communities. Long-term data are especially important for developing a general model of recovery for communities dominated by long-lived species. In addition, conclusions based on short-term studies of recovery can often be misleading. For example, benthic macroinvertebrate communities in burned watersheds in Yellowstone National Park were progressing rapidly to pre-disturbance conditions within 1–2 years following the fires. However, these same communities showed an abrupt downturn in subsequent years (Minshall, Robinson and Lawrence 1997). Community inertia, defined as the tendency for species to remain dominant under unfavorable conditions, can mask recovery from anthropogenic disturbances for many years (Milchunas and Lauenroth 1995). Finally, because most communities are subjected to multiple stressors, long-term studies of recovery are essential for separating cumulative impacts from the responses to a specific perturbation. Long-term biomonitoring of systems following remediation can provide strong evidence that a specific stressor was responsible for observed changes in a community (Box 6.3).

Box 6.3 Long-term recovery of a metal-polluted stream in Colorado

The upper Arkansas River basin is located in the Southern Rocky Mountain ecoregion in central Colorado (USA). Mining operations have had a major impact on this stream since the late 1800s when gold was discovered in California Gulch. Concentrations of heavy metals (cadmium, copper, zinc) are greatly elevated in the Arkansas River, and often exceed acutely toxic levels.

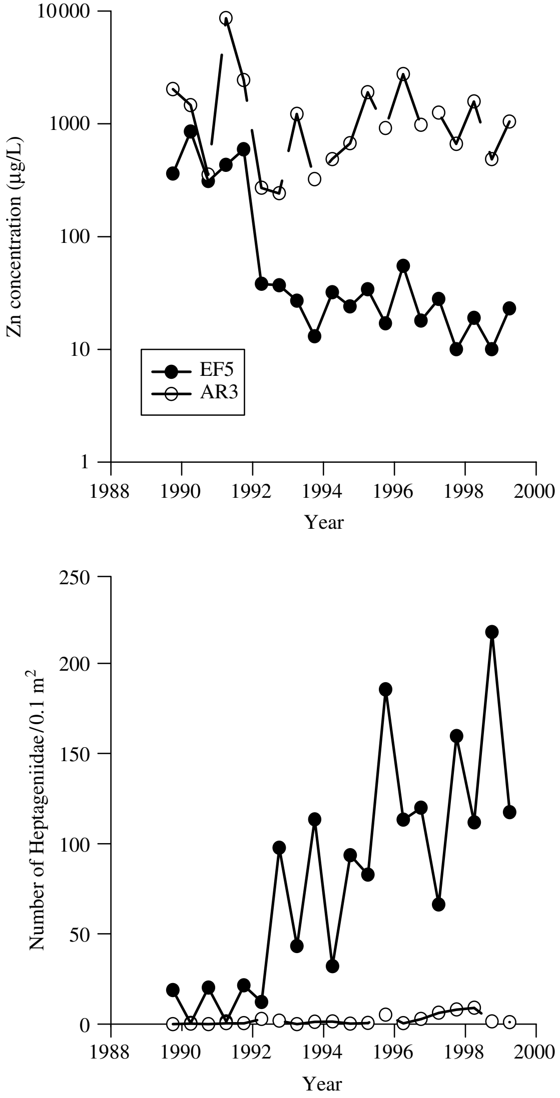

Fig. 6.9. Results of a long-term 'natural' experiment showing changes in Zn concentration and responses of heptageniid mayflies (Ephemeroptera: Heptageniidae) at two stations in the Arkansas River, Colorado (USA). Reduction in Zn concentration at station EF5 was associated with an immediate increase in abundance of these metal-sensitive organisms. In contrast, there was little evidence of recovery at station AR3 where Zn levels remained elevated. These results provide evidence that the lower abundance of Heptageniidae at station EF5 prior to 1992 was a direct result of elevated Zn concentration

Between 1989 and 1999 heavy metal concentrations and benthic macroinvertebrate community structure were examined seasonally (spring and fall) from stations located upstream and downstream from Leadville Mine Drainage Tunnel (LMDT) and California Gulch (CG), the primary sources of heavy metals in the system. In 1992, a large-scale restoration project was initiated to reduce metal concentrations in the river. Because data were collected before and after remediation, these long-term data provide an opportunity to examine community responses to improvements in water quality.

Heavy metal levels in the Arkansas River varied temporally (seasonally and annually) and spatially (Fig. 6.9). The highest concentrations were observed during periods of spring runoff and downstream from CG (station AR3). Zinc concentrations upstream from CG (station Ef5) prior to remediation were generally between 200 and 600 μg/l. After 1992 these levels decreased to less than 100 μg/l. In contrast, remediation of CG has resulted in relatively little change in metal concentrations downstream.

Heptageniid mayflies, organisms known to be highly sensitive to heavy metals (Clements 1994, 1999; Kiffney and Clements 1994), quickly responded to improvements in water quality. The density of heptageniids increased significantly following remediation of LMDT. In contrast, abundance of these metal-sensitive organisms has shown relatively little change downstream from CG where metal levels remained elevated. Results of this long-term ‘natural experiment’ demonstrate the resilience of the Arkansas River and provide strong support for the hypothesis that elevated metal levels were responsible for observed changes in benthic communities.

6.6.3 COMMUNITY-LEVEL INDICATORS OF RECOVERY

Currently, there is little agreement among ecologists as to the precise definition or the appropriate measures of recovery. This lack of objective indicators will hamper our ability to determine if a system has recovered from disturbance. For example, if 90% of the species that were affected by an oil spill return to pre-disturbance conditions, does this mean that the system has recovered? Does recovery require that community composition and relative abundance be exactly the same as prior to the disturbance? If functional characteristics have returned to pre-disturbance conditions but community composition is different, has the system recovered? Our definition of recovery could also vary with community type. Characteristics of recovery for communities primarily regulated by stochastic factors will be quite different than for equilibrium communities. Objectively defining recovery is also complicated by the fact that different components of communities may recover at different rates. In the classic series of experiments conducted by Wallace and colleagues in Coweeta Hydrological Forest, recovery of trophic structure following additions of insecticides to a small stream occurred within 2 years. In contrast, taxonomic recovery required much longer (Wallace

1990). Disturbed communities generally show greater temporal variability than undisturbed communities, a finding that is consistent with theoretical predictions and some empirical investigations (Odum, Finn and Franz 1979). Because disturbance-induced variability may be a reflection of reduced community stability (Lamberti *et al.* 1991), there is the intriguing possibility that temporal variability could be used as an indicator of recovery.

Although return to equilibrium conditions is an intuitively appealing definition of recovery, we know from long-term biogeographic studies that considerable turnover in species composition occurs in communities, even in the absence of disturbance. Simberloff and Wilson's (1969, 1970) study of recolonization of mangrove islands following insecticide fumigation demonstrated that the number of species rapidly returned to pre-disturbance values; however, the composition of these communities was often quite different, reflecting a high degree of species turnover. Similarly, research on metal pollution in the Arkansas River described in Box 6.3 has shown that the total number of species is similar between impacted and unimpacted sites. However, community composition is quite different because metal-tolerant species have replaced sensitive species (Fig. 6.10). Similar results were reported for an eastern US stream disturbed by flooding (Palmer *et al.* 1995). Despite rapid recovery in total abundance after a flood, composition of the recovering community remained distinct throughout the study period. These results demonstrate that before ecologists can determine if recovery has occurred in a community it will be necessary to identify appropriate endpoints.

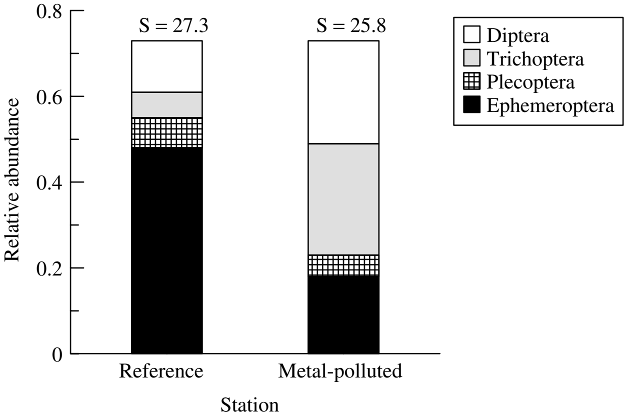

Fig. 6.10. Comparison of species richness (S) and community composition of benthic macroinvertebrates at reference and metal-polluted sites in the Arkansas River, CO. Despite similar species richness at these two sites, the relative abundance of major macroinvertebrate groups was quite different. The reference site was dominated by mayflies (Ephemeroptera) whereas the metal-polluted site was dominated by caddisflies (Trichoptera) and dipterans

Because of weaknesses associated with using any specific indicator of recovery, it is probably best to use a suite of biological measures to demonstrate a return to pre-disturbance conditions. Furthermore, if sensitivity of these indicators changes over time (e.g. Matthews, Landis and Matthews 1996; Landis *et al.* 2000), it is possible that no single variable will be useful throughout a study. Investigations that focus on only a single indicator of recovery, such as abundance of economically important, rare, or charismatic species, often provide an incomplete picture of recovery. For example, studies of birds following the *Exxon Valdez* oil spill were generally limited to a few high profile species which suffered significant mortality. The emphasis on individual species may miss important aspects of recovery that can only be assessed at the community level (Wiens *et al.* 1996). The same criteria used to select indicators of ecological effects in monitoring studies (Chapter 3) can also used to select indicators of recovery. Because many disturbed systems are inherently variable, the most important characteristic of any indicator of recovery is a relatively large signal-to-noise ratio (defined as the ratio of indicator response to the sampling variability). Assuming that recovery is operationally defined as 'not significantly different from pre-disturbance conditions', indicators that are highly variable or relatively insensitive can provide misleading information or lead to premature conclusions. Finally, because we are generally interested in knowing that both patterns and processes have returned to pre-disturbance conditions, indicators of recovery should include structural and functional measures.

Multivariate analysis of communities that considers spatial and temporal changes in composition is a powerful tool for assessing recovery from disturbance. Multivariate analyses provide a graphical representation of separation and overlap of communities based on linear combinations of a large number of variables (e.g. abundances of species). By conducting analyses at different time periods following disturbance, this approach could be used to test the hypothesis that a disturbed community has become more similar to either a reference community or to pre-disturbance conditions (Fig. 6.11). A key strength of this approach is that it evaluates recovery based on the entire community, not just a few members. In addition, the relative importance of individual species in distinguishing the disturbed community from the pre-disturbed community can be evaluated. The use of multivariate approaches for assessing responses and recovery of communities after disturbance was described in Chapter 5.

The lack of pre-disturbance data imposes the greatest limitation on our ability to define recovery. Most commonly, disturbed sites are compared with reference sites that are presumed to represent pre-disturbance conditions. Although the selection of appropriate reference sites is a reasonable alternative to the lack of pre-disturbance data, this approach is also problematic. The same weaknesses associated with demonstrating causal relationships between stressors and responses in descriptive studies also apply to the study of recovery. For example, observed changes in community composition following improvements in water

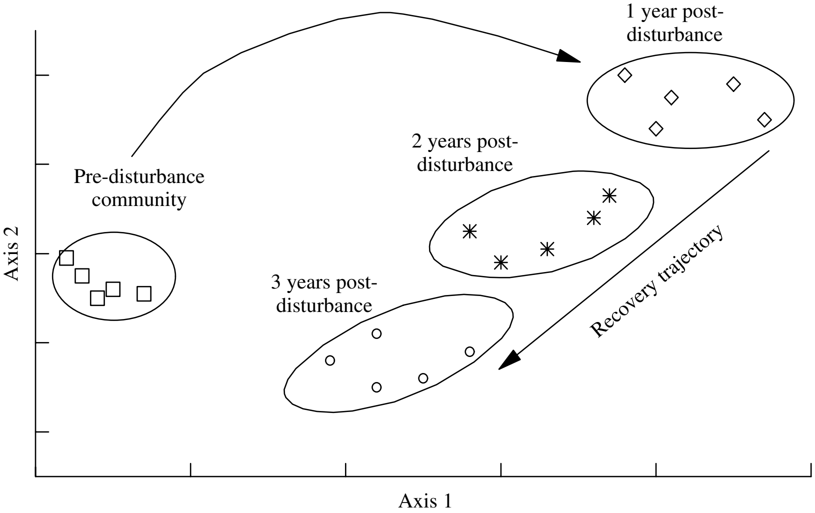

Fig. 6.11. Multivariate analysis showing temporal changes in community composition 1, 2, and 3 years following disturbance. This hypothetical analysis is based on abundance of the dominant taxa sampled in each time period. The figure shows that the communities become more similar to pre-disturbance conditions over time

quality at a contaminated site could be a result of remediation. However, because other factors could be responsible for these changes, pre-disturbance data are necessary to support a causal relationship between restoration and community responses.

Most studies of recovery have focused on temporal changes in species richness, abundance, and community composition after a disturbance. However, some disturbances produce gradients where recovery can be observed over a large spatial scale. The best example of spatial gradients of recovery are streams receiving point source discharges or other anthropogenic stressors that decrease in severity downstream. The most common experimental design in many stream biomonitoring studies compares upstream reference sites with downstream impacted sites along a gradient of contamination. Ignoring for a moment the concerns about pseudoreplication or the confounding influence of natural longitudinal variation (Chapter 3), the opportunity to substitute space for time to assess recovery is an attractive alternative. For example, communities along a gradient of reduced disturbance may provide some insight into the temporal patterns of recovery. This approach was used to evaluate fish communities along a disturbance gradient downstream from a hydroelectric dam (Kingsolving and Bain 1993). The design limitations associated with upstream versus downstream comparisons were addressed in this study by using a reference stream and by selecting a specific indicator (species richness of fluvial specialists) that was expected to respond to

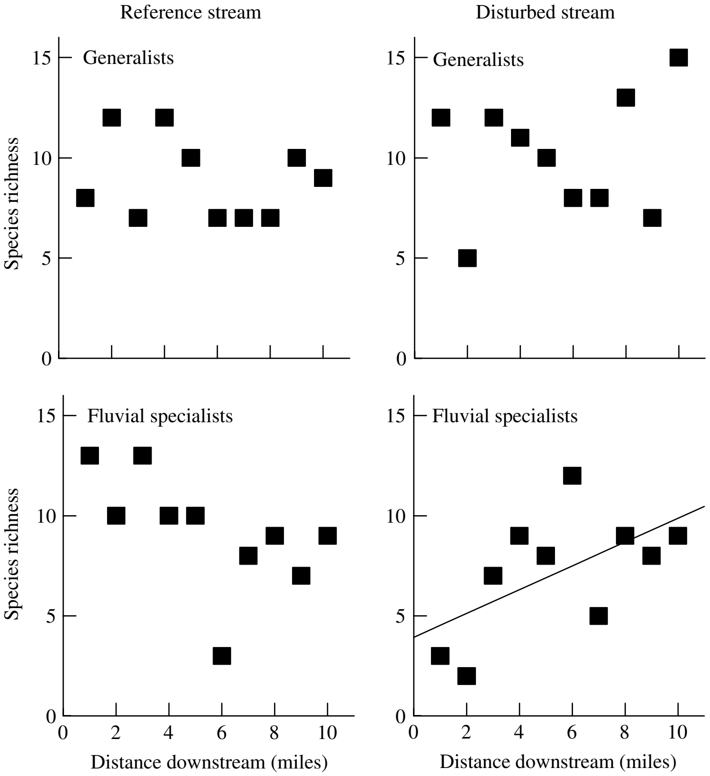

Fig. 6.12. An alternative approach to evaluate recovery of fish communities along a disturbance gradient. Fluvial specialists are expected to be negatively affected by flow alterations and therefore should increase with distance downstream from impoundments. In contrast, fluvial generalists are not expected to be affected by flow alterations. By comparing responses of sensitive and insensitive indicators to this gradient in both reference and disturbed streams, the authors make a strong case that observed spatial patterns are a result of recovery. (Modified from Figure 6 in Kingsolving and Bain 1993)

the disturbance gradient (Fig. 6.12). By comparing this indicator to one considered insensitive to the disturbance gradient (species richness of fluvial generalists), the authors make a strong case that observed spatial patterns were a result of recovery.

6.6.4 COMMUNITY CHARACTERISTICS THAT INFLUENCE RATE OF RECOVERY

Understanding factors that determine resilience may enable researchers to estimate the amount of time necessary for communities to return to pre-disturbance conditions. In this section we describe some of the community-level characteristics that influence recovery from natural and anthropogenic disturbance. Steinman and McIntire (1990) reviewed biological factors that influence recovery rates of stream periphyton communities. Characteristics such as community maturity, life history features of dominant species, and frequency of disturbance were especially important predictors of recovery. Kaufman (1982) reported that communities obtained from high stress environments were more tolerant than those from stable environments. Recovery times were also influenced by community complexity as younger, simpler communities showed greater resilience than older communities. In contrast to these findings, Ivorra *et al.* (2000) reported that immature biofilm communities were more sensitive to heavy metals than mature communities. They attributed this difference to reduced metal penetration in thicker, mature biofilm communities. Finally, the striking resilience of seabird communities following the *Exxon Valdez* oil spill (Box 6.2) was attributed to recolonization over a large spatial scale, indicating the importance of regional factors when evaluating recovery from anthropogenic disturbances (Wiens *et al.* 1996).

Some researchers have questioned the suitability of traditional models used to explain recovery from natural and anthropogenic disturbance. These models often assume that communities will return to a predictable equilibrium condition following exposure to a stressor. Landis *et al.* (2000) state that 'the search for the recovery of an ecological structure is meaningless in terms of the ecological system'. The basis for their argument is that natural communities retain a long-term record of events that occurred in the past. This intriguing concept, called the community conditioning hypothesis, has been proposed to account for the persistence of toxicant effects long after a contaminant has degraded (Landis, Matthews and Matthews 1996; Matthews, Landis and Matthews 1996; Landis *et al.* 2000). Just as genetic structure reflects the unique history of a population over evolutionary time, communities are a reflection of their unique history and etiology. Events that occurred in the past are difficult to erase and can potentially influence structural characteristics for long periods of time. Note that the community conditioning hypothesis also provides a unified explanation for the pollution-induced community tolerance hypothesis described earlier. Previous exposure to a stressor is simply a special case of the community conditioning hypothesis, and increased tolerance is a result of this unique historical event.

Support for the community conditioning hypothesis is based on results of a series of standardized microcosm experiments and therefore the relevance of these findings to natural communities is open to debate (Box 6.4). However, field studies conducted by Jenkins and Buikema (1998) support the basic idea that communities established under very similar environmental conditions often differ in terms of structure. Our failure to recognize the stochastic nature of communities may be a result of our poor understanding of dispersal or, as suggested by Landis and colleagues, our failure to measure relevant community variables. Non-metric clustering and other multivariate techniques advocated by these researchers for assessing contaminant effects in microcosms may also be applicable to the study of persistent ecological effects in the field.

Box 6.4 The community conditioning hypothesis

The community conditioning hypothesis was proposed by Matthews and Landis (Landis, Matthews and Matthews 1996; Matthews, Landis and Matthews 1996) to describe the historical aspects of community structure. The hypothesis was initially proposed to explain results of a series of microcosm experiments that were inconsistent with predictions of traditional disturbance-recovery models. In these experiments, standardized communities were exposed to a non-persistent chemical stressor (water-soluble fraction of jet fuels). Because these chemicals degrade within about 10 days, differences observed several weeks after initial exposure are probably a result of persistent direct or indirect effects (Landis, Matthews and Matthews 1996). Some of the population-level characteristics (e.g. abundance of the cladoceran *Daphnia*) showed gradual recovery over time as predicted by equilibrium models of disturbance. However, differences in some community-level variables persisted long after the chemicals had degraded and were attributed to the unique history of each microcosm.

The assumptions of the community conditioning hypothesis are that:

(1) No two communities will ever be alike because each community is a function of its unique history and etiology.

(2) All events that influence the structure and function of a community remain a part of that community.

(3) Because historical information may be stored in a variety of compartments and layers, no single indicator will reflect the response of the entire community.

(4) Although information about previous events in a community may be difficult to extract, these events may continue to influence communities and alter future responses.

(5) Almost every environmental event has lasting effects on the community.

The community conditioning hypothesis has important implications for how ecotoxicologists study disturbance and recovery (Matthews, Landis and Matthews 1996). According to this model, the effects of a disturbance event are long lasting and communities are unlikely to return to pre-disturbance conditions. More importantly, if individual communities are unique, our definition of reference conditions in both field and experimental studies will require revision. Note that the individualistic nature of communities is in stark contrast to Rapport's ecosystem distress syndrome (Rapport, Regier and Hutchinson 1985), which argues that responses to disturbance are predictable and consistent among communities and stressors. The general validity of the community conditioning hypothesis remains to be tested in other systems and will ultimately require field verification. However, if persistent historical events play a role in community organization, this will greatly complicate our attempts to define recovery using traditional equilibrium methods.

6.7 INFLUENCE OF ENVIRONMENTAL VARIABILITY ON RESISTANCE AND RESILIENCE

Although the precise mechanism by which environmental variability influences community composition is a topic of considerable debate in ecology, the positive relationship between physical heterogeneity and species richness is well supported in the literature. Natural disturbance is likely to play an important role in maintaining environmental heterogeneity and increasing species richness. Natural and anthropogenic disturbance may also operate as a filter (sensu Southwood 1977) that constrains the types of species present in an area and ultimately determines life history characteristics, community composition, and trophic structure (Poff 1997) (see Fig. 2.1). Local and regional habitat conditions create selective forces that determine life history characteristics and other traits of resident species. Taxa within a regional species pool must possess traits that allow them to pass through this hierarchical set of filters to be present within the local habitat. Using this model, the presence of anthropogenic stressors, which may occur at several different levels, is simply another filter that determines local species composition. The absence of a species is a result of its failure to pass through one of these filters, which is determined by functionally important species traits. Thus, the most important first step for predicting community composition is to identify functionally significant species traits at each level in this hierarchy. Recognizing the importance of these filters within the context of environmental heterogeneity offers an unprecedented opportunity to improve our ability to predict effects of anthropogenic disturbance on communities.

Natural disturbance is a highly selective filter that also operates at any level of this hierarchy. The influence of natural disturbance on life history characteristics, patterns of species diversity, and ecosystem processes has been examined by ecologists for many years (Southwood 1977; Poff and Ward 1990; Matthaei *et al*. 1996). Variable systems characterized by high levels of natural disturbance are often dominated by trophic generalists and other opportunistic species capable of rapid dispersal and high rates of reproduction. Thus, we expect that communities from these variable systems would show greater resistance and resilience to subsequent disturbances. Studies conducted in streams support the hypothesis that life history characteristics of species occupying highly variable habitats allow these organisms to tolerate natural disturbance. Matthaei *et al.* (1996) demonstrated that invertebrates from a more variable reach of a subalpine stream recovered from experimental disturbance faster than organisms from a site with less variability.

Despite an appreciation for the importance of environmental variability and natural disturbance on community composition, there is little information concerning how natural variability influences responses to contaminants. We propose that the same genetic, physiological, and life history characteristics that allow species to tolerate highly variable and physically stressful environments will also confer resistance and resilience to anthropogenic disturbances. In other words, frequency and intensity of natural disturbance in a community may influence its ability to withstand additional perturbations. For example, effects of an oil spill

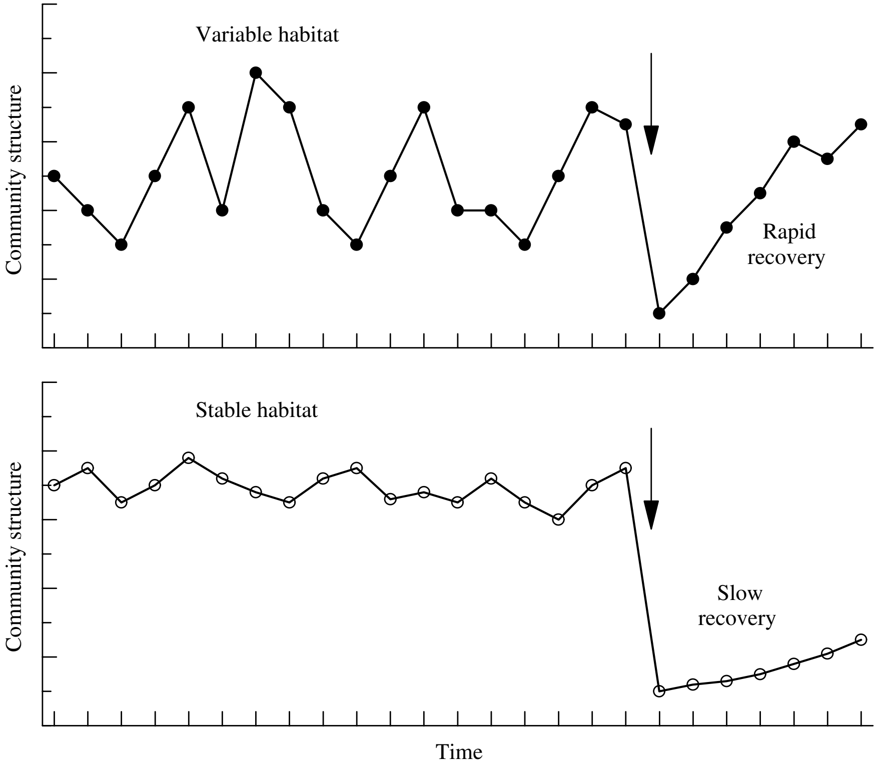

Fig. 6.13. Conceptual model showing recovery in stable and naturally variable communities. The model assumes that because of genetic, physiological, and life history characteristics, populations in naturally variable habitats are pre-adapted to disturbance. Therefore, these populations are expected to recover from natural or anthropogenic disturbance faster than populations from stable habitats

in a marine ecosystem will be much greater on a stable coral reef community than in a highly variable estuarine community. Similarly, communities in stable environments would probably require more time to recover from anthropogenic disturbance than those in variable environments (Fig. 6.13). These predictions have important implications for the study of resistance and resilience among ecosystem types and across latitudinal gradients.

A review of studies conducted in aquatic systems suggests that natural variability may influence responses to contaminants. In general, communities from variable environments that were subjected to high levels of natural disturbance were more tolerant of anthropogenic stressors and recovered faster than communities from stable habitats (Poff and Ward 1990). Experiments conducted in microcosms also demonstrate that responses to chemical stressors vary among locations and that natural heterogeneity may influence these responses. Kiffney and Clements (1996) reported that effects of metals were significantly greater on communities from more stable, high elevation streams compared with those from more variable low elevation streams. These results were supported by field studies which also showed that impacts of metals were often greater on smaller headwater streams compared with large rivers.

6.8 QUANTIFYING THE EFFECTS OF MULTIPLE PERTURBATIONS

Like the historical emphasis on single stressors in aquatic toxicology, ecologists have generally limited their investigations of disturbance to single events. Because of the focus on individual stressors, we lack the ability to predict how communities will respond to multiple perturbations and have implicitly assumed that responses to multiple stressors are additive. Because anthropogenic stressors are often superimposed on natural disturbance regimes, multiple perturbations are probably common in nature. Paine, Tegner and Johnson (1998) examined responses of communities subjected to a variety of single and multiple perturbations, including El Niño events, storms, exotic species, wildfires, deforestation, and hypoxia. Their theoretical model of ecological responses to multiple perturbations has important implications for the study of contaminants and other anthropogenic stressors. Although most communities can recover from natural disturbance (Fig. 6.14A), a sequential perturbation, especially one that occurs during the recovery phase, may reset the community to an alternative stable state (Fig. 6.14B). Finally, the addition of natural or anthropogenic disturbance to a community already subjected to a chronic stressor may alter patterns of recovery. Paine, Tegner and Johnson (1998) suggest that disturbance in chronically stressed systems may impede recovery and force the system to a new stable state (Fig. 6.14C). One very likely scenario for multiple perturbations involves systems currently subjected to widespread global perturbations such as climate change, UVB radiation, and acidification (Chapter 7).

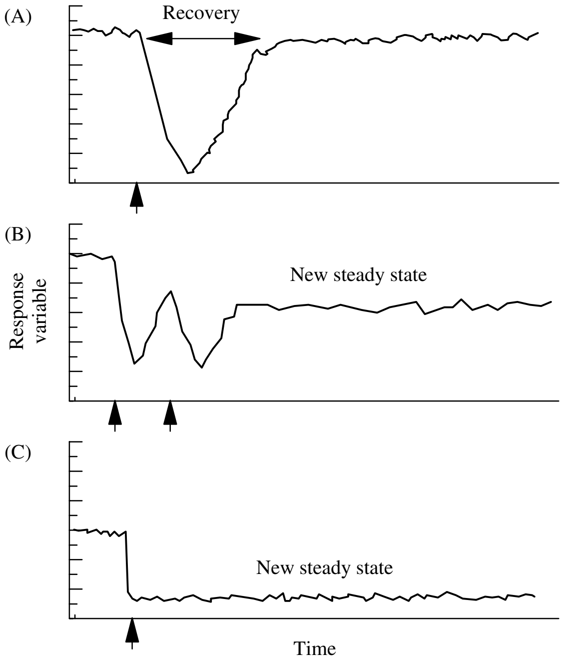

Fig. 6.14. Compound perturbations in ecological systems. (A) A single disturbance is followed by gradual recovery to pre-disturbance conditions. (B) A single disturbance is followed by a second disturbance before recovery has occurred. The system is reset to a new steady state. (C) A single disturbance is superimposed on a system already altered by perturbations. The system is reset to a new steady state. (Modified from Figure 1 in Paine, Tegner and Johnson 1998)

6.8.1 SENSITIVITY OF COMMUNITIES TO NOVEL STRESSORS

Although there is evidence to support the hypothesis that previously-exposed populations will be tolerant to contaminants, there is a need to understand mechanisms responsible for increased tolerance. We argue that both physiological acclimation and adaptation to contaminants may have specific costs. For example, while induction of metal-binding proteins such as metallothionein increases tolerance to subsequent exposure, it also utilizes energy normally available for other metabolic processes (e.g. growth, reproduction). High metabolic costs associated with sequestering metals and/or producing metal-binding proteins decreases productivity in metal-tolerant plants (Wilson 1988). Springtails (Collembola) exposed to copper and lead exhibited reduced growth rates due to increased molting necessary to eliminate metals (Hollaway, Sibly and Povey 1990). Similarly, genetic changes associated with exposure to contaminants may also have costs to populations. Reduced genetic heterozygosity has been reported in populations exposed to contaminants (Mulvey and Diamond 1991; Heagler *et al.* 1993) and may cause population bottlenecks. Furthermore, as metal-sensitive genotypes are eliminated from a population, the reduced genetic diversity may increase the susceptibility of this population to other stressors.

Acclimating or adapting to one set of environmental stressors may also increase an organism's sensitivity to novel stressors (Antonovics, Bradshaw and Turner 1971; Wilson 1988). Although most of the research on cost of tolerance has focused on populations, communities from chemically-stressed environments may also be at greater risk from novel stressors. Support for this hypothesis is provided by results of experimental studies in which communities from metal-polluted and unpolluted sites were exposed to acidification and UV radiation (Box 6.5). In all instances, communities from the metal-polluted sites were more sensitive to novel stressors (Kiffney, Clements and Cady 1997; Clements, 1999; Courtney and Clements 2000). An understanding of the potential effects of novel stressors on chronically disturbed systems is essential for predicting ecological responses. This understanding can only be achieved by integrating long-term monitoring with laboratory and field experiments.

Box 6.5 The effects of novel stressors on chronically-impacted communities

Microcosm experiments have shown that organisms collected from the Arkansas River, a metal polluted stream in central Colorado, were more tolerant of metals than organisms collected from an unpolluted stream (Fig. 6.15). The mechanisms for increased tolerance most likely included physiological and genetic changes in these populations (Clements 1999; Courtney and Clements 2000). To test the hypothesis that these metal-tolerant organisms are more susceptible to novel stressors, a series of experiments was conducted in which benthic macroinvertebrate communities from the Arkansas River and a reference stream were exposed to acidification, UV-B radiation, and predation. Despite greater tolerance to metals, organisms from the Arkansas River were generally more susceptible to each of the novel stressors. Exposure to acidic pH decreased mayfly survival at all three sites (Fig. 6.15); however, organisms from the most polluted station were especially sensitive. Similar results were observed for benthic communities exposed to UV-B radiation (Fig. 6.15). Mayflies from a reference stream were relatively tolerant of UV-B radiation, whereas organisms from the Arkansas River were more sensitive. Finally, results of microcosm and field experiments showed that mayflies from the Arkansas River were more susceptible to stonefly predation than organisms from a reference stream (Fig. 6.15).

Results of these experiments demonstrate that these three communities responded with varying degrees of sensitivity to physical, chemical, and biological stressors, and that differences were related to differences in exposure history and community structure. Chronic metal pollution in the Arkansas

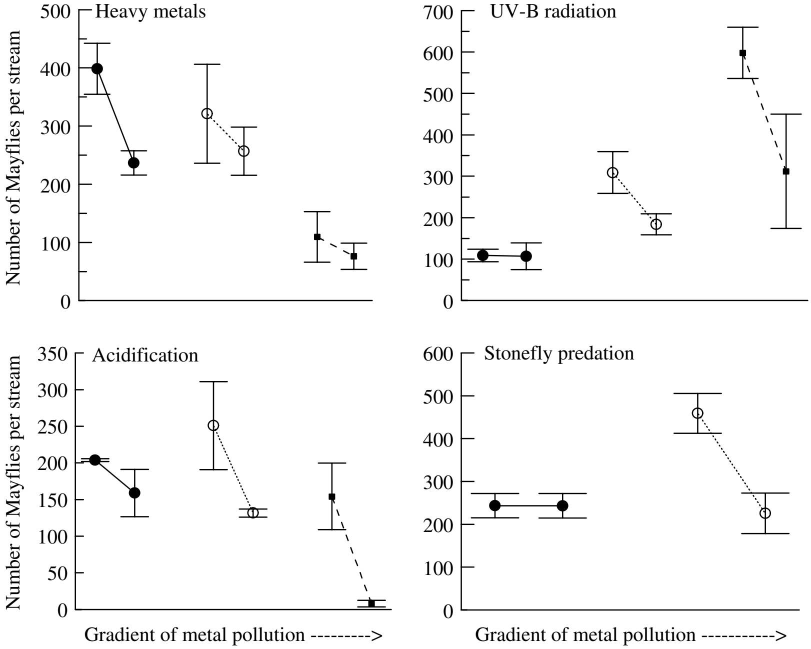

Fig. 6.15. Results of microcosm experiments showing differences in sensitivity of mayflies collected from reference and metal-impacted sites to heavy metals, UV-B radiation, acidification, and stonefly predation. Macroinvertebrate communities for these experiments were collected from field sites along a gradient of metal pollution. Each pair of points connected by a line shows abundance of mayflies in control microcosms and treated microcosms. (Data from Clements 1999; Courtney and Clements 2000; and Peter M. Kiffney, Northwest Fisheries Science Center, Seattle, WA 98112, unpublished data)

River has influenced community structure and resulted in a community that is tolerant to metals but more sensitive to novel stressors. These results support the hypothesis that the physiological and genetic mechanisms responsible for increased tolerance to heavy metals may have a cost.

6.9 SUMMARY AND CONCLUSIONS

In summary, although there has been significant improvement in our ability to quantify the effects of single chemical stressors on communities over the past 20 years, we generally have a poor understanding of the interactions among stressors and how these stressors interact with other physical and biological disturbances. Laboratory research has focused on quantifying interactions among chemicals using single species toxicity tests; however, the effects of stressor interactions on field populations have rarely been investigated. Because of the opportunity to isolate and control the effects of individual variables, experimental approaches are the most direct way to estimate the relative importance of individual stressors in systems impacted by multiple perturbations. Factorial experimental designs, where the effects of chemicals are investigated individually and in combination, can be used to identify potential synergistic or antagonistic interactions among stressors. An improved understanding of the effects of multiple perturbations is necessary to predict responses to anthropogenic disturbances and better to prepare for the inevitable 'ecological surprises' that may occur (Paine, Tegner and Johnson 1998).

REFERENCES

Allison SK (1995). Recovery from small-scale anthropogenic disturbances by northern California salt marsh plant assemblages. *Ecol Appl* **5**: 693–702.

Antonivics J, Bradshaw AD and RG Turner (1971). Heavy metal tolerance in plants. *Adv Ecol Res* **7**: 1–85.

Begon M, Harper JL and Townsend CR (1990). *Ecology: Individuals, Populations and Communities*. Blackwell Scientific Publications, Cambridge, MA.

Bender EA, Case TJ and Gilpin ME (1984). Perturbation experiments in community ecology: theory and practice. *Ecology* **65**: 1–13.

Blanck H and Dahl B (1996). Pollution-induced community tolerance (PICT) in marine periphyton in a gradient of tri-n-butyltin (TBT) contamination. *Aquat Toxicol* **35**: 59–77.

Blanck H and Wangberg S (1988). Induced community tolerance in marine periphyton established under arsenate stress. *Can J Fish Aquat Sci* **45**: 1816–1819.

Blanck H and Wangberg SA (1991). Pattern of co-tolerance in marine periphyton communities established under arsenate stress. *Aquat Toxicol* **21**: 1–14.

Cardinale BJ, Nelson K and Palmer MA (2000). Linking species diversity to the functioning of ecosystems on the importance of environmental context. *Oikos* **91**: 175–183.

Chapin FS, Sala OE, Burke IC, Grime JP, Hooper DU, Lauenroth WK, Lombard A, Mooney HA, Mosier AR, Naeem S, Pacala SW, Roy J, Steffen WL and Tilman D (1998). Ecosystem consequences of changing biodiversity – experimental evidence and a research agenda for the future. *BioScience* **48**: 45–52.

Clements FE (1936). Nature and structure of the climax. *J Ecol* **24**: 252–284.

Clements WH (1994). Benthic invertebrate community responses to heavy metals in the Upper Arkansas River Basin, Colorado. *J N Am Benthol Soc* **13**: 30–44.

Clements WH (1999). Metal tolerance and predator–prey interactions in benthic macroinvertebrate stream communities. *Ecol Appl* **9**: 1073–1084.

Clements WH, Carlisle DM, Lazorchak JM and Johnson PC (2000). Heavy metals structure benthic communities in Colorado mountain streams. *Ecol Appl* **10**: 626–638.

Connell JH (1978). Diversity in tropical rain forests and coral reefs. *Science* **199**: 1302–1310.

Courtney LA and Clements WH (2000). Sensitivity to acidic pH in benthic invertebrate assemblages with different histories of exposure to metals. *J N Am Benthol Soc* **19**: 112–127.

Dahl B and Blanck H (1996). Pollution-induced community tolerance (PICT) in periphyton communities established under tri-n-butyltin (TBT) stress in marine microcosms. *Aquat Toxicol* **34**: 305–325.

Darwin C (1872). *The Origin of Species* (6th London edn). Thompson and Thomas, Chicago, IL.

Death RG and Winterbourn MJ (1995). Diversity patterns in stream benthic invertebrate communities: the influence of habitat stability. *Ecology* **76**: 1446–1460.

Doak DF, Bigger D, Harding EK, Marvier MA, O'Malley RE and Thomson D (1998). The statistical inevitability of stability–diversity relationships in community ecology. *Am Nat* **151**: 264–276.

Duffy JE, Macdonald KS, Rhode JM and Parker JD (2001). Grazer diversity, functional redundancy, and productivity in seagrass beds: an experimental test. *Ecology* **82**: 2417–2434.

Elton CS (1958). *The Ecology of Invasions by Animals and Plants*. Methuen, London, UK.

Fisher SG and Grimm NB (1991). Streams and disturbance: are cross-ecosystem comparisons useful? In *Comparative Analyses of Ecosystems: Patterns, Mechanisms, and Theories*, ed. by Cole J, Lovett G and Findlay S, pp. 196–221. Springer-Verlag, New York, NY.

Foster DR, Aber JD, Melillo JM, Bowden RD and Bazzaz FA (1997). Forest response to disturbance and anthropogenic stress. *BioScience* **47**: 437–445.

Franklin JF and MacMahon JA (2000). Messages from a mountain. *Science* **288**: 1183–1185.

Glasby TM and Underwood AJ (1996). Sampling to differentiate between pulse and press perturbations. *Environ Monitor Assess* **42**: 241–252.

Grime JP (1997). Biodiversity and ecosystem function: the debate deepens. *Science* **277**: 1260–1261.

Gustavson K and Wangberg SA (1995). Tolerance induction and succession in microalgae communities exposed to copper and atrazine. *Aquat Toxicol* **32**: 283–302.

Hart DD (1994). Building a stronger partnership between ecological research and biological monitoring. *J N Am Benthol Soc* **13**: 110–116.

Heagler MG, Newman MC, Mulvey M and Dixon PM (1993). Allozyme genotype in mosquitofish, *Gambusia holbrook*i, during mercury exposure: temporal stability, concentration effects and field verification. *Environ Toxicol Chem* **12**: 385–395.

Hector A, Schmid B, Beierkuhnlein C and 31 others. (1999). Plant diversity and productivity experiments in European grasslands. *Science* **286**: 1123–1127.

Holloway GJ, Sibly RM and Povey SR (1990). Evolution in toxin-stressed environments. *Funct Ecol* **4**: 289–294.

Hooper DU and Vitousek PM (1997). The effects of plant composition and diversity on ecosystem processes. *Science* **277**: 1302–1305.

Howarth RW (1991). Comparative responses of aquatic ecosystems to toxic chemical stress. In *Comparative Analyses of Ecosystems: Patterns, Mechanisms, and Theories*, ed. by Cole J, Lovett G and Findlay S, pp. 169–195. Springer-Verlag, New York, NY.

Huston M (1997). Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* **110**: 449–460.

Ivorra N, Bremer S, Guasch H, Kraak MHS and Admiraal W (2000). Differences in the sensitivity of benthic microalgae to Zn and Cd regarding biofilm development and exposure history. *Environ Toxicol Chem* **19**: 1332–1339.

Jenkins DG and Buikema Jr AL (1998). Do similar communities develop in similar sites? A test with zooplankton structure and function. *Ecol Monogr* **68**: 421–443.

Kaufman LH (1982). Stream aufwuchs accumulation: disturbance frequency and stress resistance and resilience. *Oecologia* **52**: 57–63.

Kiffney PM and Clements WH (1994). Effects of heavy metals on a Rocky Mountain stream macroinvertebrate assemblage in experimental streams. *J N Am Benthol Soc* **13**: 511–523.

Kiffney PM and Clements WH (1996). Effects of metals on stream macroinvertebrate assemblages from different altitudes. *Ecol Appl* **6**: 472–481.

Kiffney PM, Clements WH and Cady TA (1997). Influence of ultraviolet radiation on the colonization dynamics of a Rocky Mountain stream benthic community. *J N Am Benthol Soc* **16**: 520–530.

Kingsolving AD and Bain MB (1993). Fish assemblage recovery along a riverine disturbance gradient. *Ecol Appl* **3**: 531–544.

Lamberti GA, Gregory SV, Ashkenas LR, Wildman RC and Moore KMS (1991). Stream ecosystem recovery following a catastrophic debris flow. *Can J Fish Aquat Sci* **48**: 196–208.

Landis WG, Markiewicz AJ, Matthews RA and Matthews GB (2000). A test of the community conditioning hypothesis: persistence of effects in model ecological structures dosed with the jet fuel JP-8. *Environ Toxicol Chem* **19**: 327–336.

Landis WG, Matthews RA and Matthews GB (1996). The layered and historical nature of ecological systems and the risk assessment of pesticides. *Environ Toxicol Chem* **15**: 432–440.

Lawler SP and Morin PJ (1993). Food web architecture and population dynamics in laboratory microcosms of protists. *Am Nat* **141**: 675–686.

Lenihan HS and Oliver JS (1995). Anthropogenic and natural disturbance to marine benthic communities in Antarctica. *Ecol Appl* **5**: 311–326.

Lozano R and Pratt JR (1994). Interaction of toxicants and communities: the role of nutrients. *Environ Toxicol Chem* **13**: 361–368.

Luoma SN (1977). Detection of trace contaminant effects in aquatic ecosystems. *J Fish Res Bd Can* **34**: 436–439.

Matthaei CD, Uehlinger U, Meyer EI and Frutiger A (1996). Recolonization by benthic invertebrates after experimental disturbance in a Swiss prealpine river. *Freshw Biol* **35**: 233–248.

Matthews RA, Landis WG and Matthews GB (1996). The community conditioning hypothesis and its application to environmental toxicology. *Environ Toxicol Chem* **15**: 597–603.

May RM (1973). *Stability and Complexity in Model Ecosystems*. Princeton University Press, Princeton, NJ.

Medley CN and Clements WH (1998). Responses of diatom communities to heavy metals in streams: The influence of longitudinal variation. *Ecol Appl* **8**: 631–644.

Milchunas DG and Lauenroth WK (1995). Inertia in plant community structure: state changes after cessation of nutrient enrichment stress. *Ecol Appl* **5**: 452–458.

Millward RN and Grant A (1995). Assessing the impact of copper on nematode communities from a chronically metal-enriched estuary using pollution-induced community tolerance. *Mar Pollut Bull* **30**: 701–706.

Millward RN and Grant A (2000). Pollution-induced tolerance to copper of nematode communities in the severely contaminated Restronguet Creek and adjacent estuaries, Cornwall, United Kingdom. *Environ Toxicol Chem* **19**: 454–461.

Minshall GW, Robinson CT and Lawrence DE (1997). Postfixed responses of lotic ecosystems in Yellowstone National Park, USA. *Can J Fish Aquat Sci* **54**: 2509–2525.

Mulvey M and Diamond SA (1991). Genetic factors and tolerance acquisition in populations exposed to metals and metalloids. In *Ecotoxicology of Metals: Current Concepts and Applications*. ed. by Newman MC and McIntosh AW, pp. 301–321. Lewis Publishers, Chelsea, MI.

Naeem S, Hahn DR and Schuurman G (2000). Producer–decomposer co-dependency influences biodiversity effects. *Nature* **403**: 762–764.

Newman MC (2001). *Population Ecotoxicology*. Wiley and Sons, Ltd, Chichester, UK.

Niederlehner BR and Cairns Jr J (1992). Community response to cumulative toxic impact: effects of acclimation on zinc tolerance of aufwuchs. *Can J Fish Aquat Sci* **49**: 2155–2163.

Niemi GJ, Devore P, Detenbeck N, Taylor D, Lima A, Yount JD and Naiman RJ (1990). Overview of case-studies on recovery of aquatic systems from disturbance. *Environ Manag* **14**: 571–587.

Nilsson C and Grelsson G (1995). The fragility of ecosystems: a review. *J Appl Ecol* **32**: 677–692.

Nystrom B, Paulsson M, Almgren K and Blanck H (2000). Evaluation of the capacity for development of atrazine tolerance in periphyton from a Swedish freshwater site as determined by inhibition of photosynthesis and sulfolipid synthesis. *Environ Toxicol Chem* **19**: 1324–1331.

Odum EP, Finn JT and Franz EH (1979). Perturbation theory and the subsidy–stress gradient. *BioScience* **29**: 349–352.

Paine RT, Tegner MJ and Johnson EA (1998). Compounded perturbations yield ecological surprises. *Ecosystems* **1**: 535–545.

Palmer MA, Arensburger P, Botts PS, Hakenkamp CC and Reid JW (1995). Disturbance and the community structure of stream invertebrates: Patch-specific effects and the role of refugia. *Freshw Biol* **34**: 343–356.

Petersen S and Gustavson K (1998). Toxic effects of tri-butyl-tin (TBT) on autotrophic pico-, nano-, and microplankton by a size fractionated pollution-induced community tolerance (SF-PICT) concept. *Aquat Toxicol* **40**: 253–264.

Peterson CH (1975). Stability of species and of community for the benthos of two lagoons. *Ecology* **56**: 958–965.

Peterson G, Allen CR and Holling CS (1998). Ecological resilience, biodiversity, and scale. *Ecosystems* **1**: 6–18.

Poff NL (1997). Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *J N Am Benthol Soc* **16**: 391–409.

Poff NL and Ward JV (1990). Physical habitat template of lotic systems: recovery in the context of historical pattern of spatiotemporal heterogeneity. *Environ Manag* **14**: 629–645.

Rapport DJ, Regier HA and Hutchinson TC (1985). Ecosystem behavior under stress. *Am Nat* **125**: 617–640.

Rapport DJ, Whitford WG and Hilden M (1998). Common patterns of ecosystem breakdown under stress. *Environ Monitor Assess* **51**: 171–178.

Reice SR (1985). Experimental disturbance and the maintenance of species diversity in a stream community. *Oecologia* **67**: 90–97.

Reice SR (1994). Nonequilibrium determinants of biological community structure. *Am Sci* **82**: 424–435.

Sankaran M and McNaughton SJ (1999). Determinants of biodiversity regulate compositional stability of communities. *Nature* **401**: 691–693.

Schwab BS, Maruscik DA, Ventullo RM and Palmisano AC (1992). Adaptation of periphytic communities to a quaternary ammonia surfactant. *Environ Tox Chem* **11**: 1169–1177.

Seyle H (1973). The evolution of the stress concept. *Amer Sci* **61**: 692–699.

Simberloff DS and Wilson EO (1969). Experimental zoogeography of islands: The colonization of empty islands. *Ecology* **50**: 278–296.

Simberloff DS and Wilson EO (1970). Experimental zoogeography of islands: a two-year record of colonization. *Ecology* **51**: 934–937.

Sousa WP (1979). Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology* **60**: 1225–1239.

Southwood TRE (1977). Habitat, the templet for ecological strategies? *J Anim Ecol* **46**: 337–367.

Spiller DA, Losos JB and Schoener TW (1998). Impact of a catastrophic hurricane on island populations. *Science* **281**: 695–697.

Steinman AD and McIntire CD (1990). Recovery of lotic periphyton communities after disturbance. *Environ Manag* **14**: 589–604.

Steinman AD, Mulholland PJ, Palumbo A, DeAngelis D and Flum, T (1992). Lotic ecosystem response to a chlorine disturbance. *Ecol Appl* **2**: 341–355.

Tilman D (1996). Biodiversity: population versus ecosystem stability. *Ecology* **77**: 350–363.

Tilman D, Knops J, Wedin D, Reich P, Ritchie M and Siemann E (1997). The influence of functional diversity and composition on ecosystem processes. *Science* **277**: 1300–1302.

Turner MG, Romme WH, Gardner RH and Hargrove WW (1997). Effects of fire size and pattern on early succession in Yellowstone National Park. *Ecol Monogr* **67**: 411–433.

Wallace JB (1990). Recovery of lotic macroinvertebrate communities from disturbance. *Environ Manag* **14**: 605–620.

Wangberg SA (1995). Effects of arsenate and copper on the algal communities in polluted lakes in the northern parts of Sweden assayed by PICT (Pollution-Induced Community Tolerance). *Hydrobiologia* **306**: 109–124.

White PS and Pickett STA (1985). *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, New York, NY.

Whitford WG, Rapport DJ and deSoyze AG (1999). Using resistance and resilience measurements for ‘fitness’ tests in ecosystem health. *J Environ Manag* **57**: 21–29.

Wiens JA (1984). On understanding a non-equilibrium world: myth and reality in community patterns and processes. In *Ecological Communities: Conceptual Issues and the Evidence*, ed. by Strong DR, Simberloff D, Abele LG and Thistle AB, pp. 439–457. Princeton University Press, Princeton, NJ.

Wiens JA, Crist TO, Day RH, Murphy SM and Hayward GD (1996). Effects of the Exxon Valdez oil spill on marine bird communities in Prince William Sound. *Ecol Appl* **6**: 828–841.

Wilson JB (1988). The cost of heavy-metal tolerance: an example. *Evolution* **42**: 408–413.

Wootton JT (1998). Effects of disturbance on species diversity: a multitrophic perspective. *Am Nat* **152**: 803–825.

Yount JD and Niemi GJ (1990). Recovery of lotic ecosystems from disturbance – a narrative review of case studies. *Environ Manag* **14**: 547–569.

7 Community Responses to Global and Atmospheric Stressors

7.1 INTRODUCTION

Several decades ago our concerns about atmospheric pollutants were primarily limited to those associated with the combustion of fossil fuels (e.g. SO_2, NO_x, H^+). While fossil fuel combustion is still regarded as a major source for many atmospheric pollutants, our contemporary definition of atmospheric pollutants has broadened considerably. We now recognize that many stressors have a global distribution (Table 7.1) and that the temporal scale of effects ranges from days to centuries. Today we have serious concerns not only about the direct effects of atmospheric pollutants such as CH_4 and CO_2, but also their indirect effects on global climate. In addition, persistent organic pollutants (POPs), once regarded as a local problem primarily associated with industrial and agricultural discharges, are now globally distributed and occur in very remote environments such as the Canadian arctic. We now understand that not only is ozone (O_3) a serious atmospheric stressor for many plants, but that *loss* of stratospheric ozone due to release of chlorofluorocarbons (CFCs) has significantly increased levels of ultraviolet radiation (UVR) striking the earth's surface over the past 20 years.

Effects of atmospheric stressors on communities are likely to be complex, interactive, and difficult to predict. The regional and global distribution of atmospheric pollutants presents unique challenges for study design and interpretation. Long-range transport of some atmospheric pollutants (e.g. SO_2, NO_x) and geographic variation in exposure to other stressors (e.g. UV-B radiation) complicate assessment of effects. Researchers are often forced to extrapolate results of relatively small-scale and short duration studies to much larger spatiotemporal scales. Some communities, particularly those characterized by long-lived species (e.g. forests), will respond very slowly to atmospheric stressors. Because long-term data from these systems are often unavailable, simply demonstrating that forest health has declined is challenging. Attempting to associate forest decline to a particular atmospheric stressor such as acidification is a daunting task. Finally, differences in sensitivity to global atmospheric stressors among communities further complicate our ability to make predictions about ecological effects. For example, Rusek (1993) observed that alpine communities were more sensitive to acidic deposition than either subalpine or forest communities. If the greater sensitivity

Table 7.1. Spatial and temporal scale, sources, and primary concerns of major atmospheric pollutants. (Modified from Taylor, Johnson and Anderson 1994)

Category	Pollutant	Temporal scale	Spatial scale	Primary anthropogenic source	Primary concerns
Carbon	CH_4	Years	Globe	Agriculture, fossil fuels	Global warming
	CO_2	Decades	Globe	Fossil fuels, deforestation	Global warming, direct effects on plants
	CO	Days	Hemisphere	Fossil fuels	Toxic effects on plants
Nitrogen	NO_2	Days	Region	Fossil fuels	Nutrient enrichment
	HNO_3	Hours/days	Region	Fossil fuels	Acidification, nutrient enrichment
	NH_3	Hours/days	Region	Agriculture	Nutrient enrichment
Sulfur	SO_2	Days	Region	Fossil fuels	Acidification
Chlorinated compounds	CFCs	Century	Globe	Refrigerants, aerosols	Ozone depletion
	Persistent organic pollutants (POPs)	Decades	Globe	Agriculture, industry	Bioaccumulation
Miscellaneous	O_3	Days	Region	Photochemical reactions with fossil fuels	Toxic effects on plants
	Hg	Years	Globe	Industrial	Bioaccumulation

of alpine communities to disturbance is a general phenomenon, changes in community structure and function observed in these habitats may provide an early warning of stress.

As with each class of anthropogenic disturbance we have considered in this book, community responses to global atmospheric stressors are a result of both direct and indirect effects. Significant changes in community composition will likely occur as a result of species-specific differences in exposure and sensitivity to atmospheric stressors. However, some researchers speculate that indirect effects of global warming, acidification, and UVR on species interactions will be greater than direct effects (Field *et al.* 1992). For example, increased susceptibility to disease or parasites may be a more likely cause of forest decline than direct effects of acidification.

Our discussion of atmospheric and global pollutants in this chapter will be limited to three classes of stressors: CO_2 and associated global warming, acidic deposition, and UV-B radiation due to stratospheric ozone depletion. Although we recognize the importance of other globally-distributed pollutants, particularly POPs, very few studies have examined community-level responses to these contaminants. In contrast, effects of elevated CO_2, UV-B radiation, and acidification have received considerable attention in the literature and are known to have significant effects on terrestrial and aquatic communities. Furthermore, there is recent evidence that exposure of communities to any one of these global atmospheric stressors is likely to influence responses to other contaminants.

7.2 CO_2 AND CLIMATE CHANGE

The causes and consequences of global climate change and the specific role of CO_2 are among the most contentious environmental issues today. However, the connection between the atmosphere and biological processes and the occurrence of a natural greenhouse effect are indisputable facts. The chemical composition of the atmosphere is largely determined by biological processes, and life on earth would probably not exist without the natural greenhouse phenomenon. The key controversies about global climate change relate to: (1) separating these natural changes from those related to anthropogenic stressors; and (2) predicting the ecological consequences of these changes. Although our understanding of the ecological effects of climate change is relatively poor, preliminary data suggest that effects on aquatic and terrestrial communities will be significant. At the very least we expect that sustained alterations in global climate will have far reaching consequences for the distribution of plants and animals. Understanding the details of these alterations and how they may influence susceptibility to other stressors are among the greatest challenges in community ecology and ecotoxicology today.

Evidence from a variety of sources indicates that global temperatures have increased by approximately 0.5 to 1.0 °C over the past century. This increase is closely associated with an unprecedented increase in anthropogenic emissions of atmospheric CO_2 and other greenhouse gases. Although correlation between increased temperature and greenhouse gases strongly implicates CO_2 as a culprit, global temperatures are highly variable and have fluctuated greatly over the past several thousand years. Thus, one of the most significant challenges to understanding the effects of humans on global climate is to separate natural variation from that due to anthropogenic emissions of CO_2. Understanding the effects of global warming is further complicated by the large spatial and temporal scales over which predicted changes will occur. Because global climate varies relatively little during a human lifetime (and even less during the tenure of most political leaders), society's willingness to act on this issue is limited. The difficulty obtaining empirical data and the necessary reliance on relatively coarse Global Circulation Models (GCMs) to predict climate change is unsettling to many scientists. However, it is important to note that much of the debate within the scientific community is over the details of climate change (e.g. how much of the observed increase is due to greenhouse gases; what is the role of carbon sinks in ameliorating increased CO_2 from anthropogenic sources; what are the most likely ecological effects). Despite uncertainty over these details, the majority of scientists today believe that global warming is real and a direct consequence of human activity. If even the most conservative estimates of increased temperatures are correct, global warming will undoubtedly be the most significant environmental issue faced by humanity during this century.

7.2.1 FACTS AND EVIDENCE

The hypothesized relationship between global climate change and greenhouse gases is not a new idea. In the late 1800s the Swedish chemist Arrhenius proposed that increased levels of CO_2 in the atmosphere could influence global temperatures. Short- and long-term records indicate that levels of CO_2 have increased dramatically and are currently the highest in human history. Ice core data reflecting CO_2 concentrations for 400 000 years prior to the industrial revolution showed that levels in the atmosphere remained relatively constant, fluctuating between 180–280 μl/l. More recent data from the Vostok ice core in Antarctica show that levels of CO_2 remained below 300 μl/l until approximately 100 years before the present (Fig. 7.1A), followed by a steady increase. Finally, direct measurements obtained from the Mauna Loa Observatory indicate that CO_2 concentrations are now approximately 100 μl/l higher than historic levels and have steadily increased over the past 50 years (Fig. 7.1B). This rate of increase is approximately 10–100 times faster than at any period prior to the industrial revolution. The Mauna Loa data also show a strong seasonal signal in CO_2, reflecting variation in photosynthesis and respiration in the northern hemisphere.

There is little doubt that the increased levels of atmospheric CO_2 over the past 50 years are a direct result of anthropogenic emissions. There is also convincing evidence that global temperatures have increased by approximately 0.6 °C over

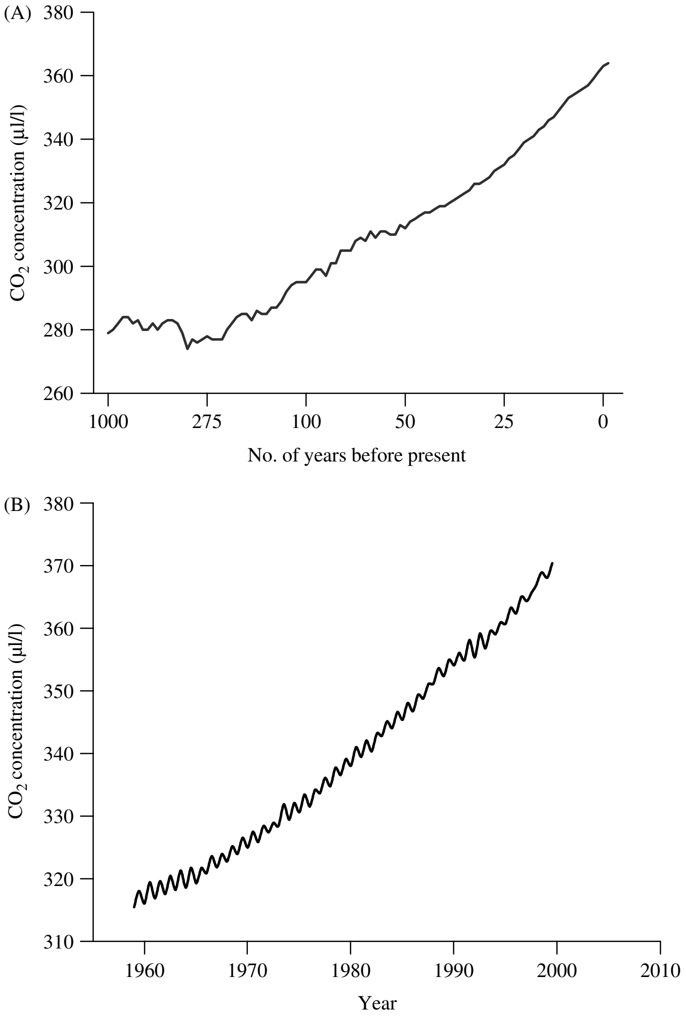

Fig. 7.1. (A) Long-term changes in CO_2 concentrations based on Vostok ice core data (Boden *et al*. 1994). (B) Increased levels of atmospheric CO_2 collected from the Mauna Loa Observatory over the past 50 years (Keeling and Whorf, 1998). Seasonal variation in CO_2 concentrations reflect seasonal changes in respiration and primary productivity in the northern hemisphere

the past century. The more challenging task and indeed the issue that generates the greatest controversy is attributing increased temperature to global emissions of CO_2. The strongest evidence of a relationship between CO_2 and climate change is derived from paleoclimatic and geochemical data. Crowley and Berner (2001) report variation in CO_2 (estimated using several geochemical proxies) with global temperature and continental glaciation over the past 600 million years. They report good agreement between CO_2 and glaciation, indicating that CO_2 has played a major role in shaping the earth's climate. Data from marine systems also show a significant increase in global temperatures. Despite the fact that oceans cover greater than 70% of the earth's surface, most models of climate change are based on atmospheric or near surface temperatures. Barnett, Pierce and Schnur (2001) report that large-scale increases in heat content have also been observed in the world's oceans. The strong agreement between their model predictions and observed changes in ocean heat content supports the hypothesis that temperature increases are a direct result of anthropogenic emissions of greenhouse gases.

Not surprisingly, there is considerable uncertainty in estimates of future global warming derived from these models. An Intergovernmental Panel on Climate Change (IPCC) recently modified its projections of global warming over the next century. The predicted upper limit of warming has been increased from the 1995 estimate of 3.5 °C to 5.8 °C. However, the IPCC also notes greater uncertainty in these estimates. Much of this uncertainty involves the complex role of global carbon sinks (see Section 7.2.2). The influence of natural factors such as volcanic release of aerosols and variation in solar activity must also be considered relative to anthropogenic emissions of CO_2. For example, using data obtained from marine and lake sediments, tree rings, and glaciers, Overpeck *et al*. (1997) report that changes in arctic temperatures resulted from a combination of natural and anthropogenic factors. Initiation of warming in the mid-19th century most likely resulted from increased solar irradiance and decreased volcanic activity. However, most of the warming during the 20th century was due to greenhouse gases. When both natural and anthropogenic factors were considered, Stott *et al.* (2000) found good agreement between model simulations and observed temperature patterns from 1860 to the present. More importantly, their results show that warming trends are expected to continue at a rate similar to that of recent decades.

7.2.2 CARBON CYCLES AND SINKS

> *...although natural sinks can potentially slow the rate of increase in atmospheric CO_2, there is no natural savior waiting to assimilate all the anthropogenic CO_2 in the coming century* (Falkowski *et al*. 2000)

In order to estimate future changes in global temperature we need to understand the sensitivity of climate to changes in CO_2. Levels of CO_2 in the atmosphere are determined by human activity and interactions with global carbon sinks (Table 7.2). Predicting the effects of increased CO_2 on global climate will require a better understanding of the size and spatial distribution of these sinks. The relatively constant glacial–interglacial concentrations of atmospheric CO_2 over the past 400 000 years suggests a strong feedback between the atmosphere and marine

Table 7.2. Carbon pools in the major reservoirs on earth. (From Falkowski *et al.* 2000)

Carbon pool	Quantity (Pg)
Atmosphere	720
Oceans	38 400
Terrestrial biosphere (living and dead biomass)	2000
Aquatic biosphere	1–2
Fossil fuels	4130

and terrestrial carbon sinks (Falkowski *et al.* 2000). Over the past 20 years only about half of the CO_2 released from fossil fuel combustion has remained in the atmosphere. The remaining CO_2 has been sequestered by oceans and terrestrial ecosystems, which on average have removed between 4 to 5 Pg C/year during the 1990s (1 Pg $= 10^{15}$ g). Although a large amount of inorganic carbon is stored in sediments, the major regulators of atmospheric CO_2 are oceans and forests. Biological processes in marine ecosystems (e.g. photosynthesis) remove significant amounts of CO_2 from the atmosphere and export carbon to deep ocean reservoirs. However, oceanic carbonate systems are primarily responsible for determining atmospheric CO_2 levels and maintaining an equilibrium between the atmosphere and surface water (Falkowski *et al.* 2000). Finally, carbon storage in terrestrial ecosystems, especially forests, contributes significantly to the global flux of carbon. Although the total amount of carbon stored in terrestrial systems is relatively large, turnover is much slower than in marine ecosystems.

Most studies of global carbon cycles have considered marine and terrestrial systems separately, thus limiting the opportunity to develop a comprehensive model of carbon flux. Using conceptually similar models for terrestrial and marine primary producers, Field *et al.* (1998) estimated a global net primary production (NPP) of 105 Pg/year. The contribution of marine and terrestrial components to global NPP was roughly equal (ocean = 48.5 Pg; terrestrial = 56.4 Pg), with a distinct latitudinal pattern. Spatial and temporal variation in NPP result from the limiting influences of light, nutrients, temperature, and water. Although marine ecosystems are a large sink for global carbon, the vast majority of the open ocean is relatively unproductive. An analysis of CO_2 balance in freshwater and marine ecosystems indicates that unproductive systems such as the open ocean tend to be heterotrophic, with a disproportionately higher rate of respiration than photosynthesis (Duarte and Agusti 1998). Unproductive aquatic ecosystems are generally sources of CO_2, whereas productive systems act as CO_2 sinks. The findings of Duarte and Agusti (1998) also illustrate that despite low productivity of the open ocean, there is a balance between production and consumption on a global scale. While 80% of the open ocean is heterotrophic and a net carbon source, this excess carbon can be balanced by relatively high production of the remaining 20%.

Large-scale spatial patterns greatly complicate analysis of global carbon sinks. A latitudinal gradient of 3 to 4 p.p.m. of CO_2 from the northern to the southern hemisphere has been attributed to greater CO_2 emissions from population centers in the north. Recently, scientists have also identified a temporal component to global carbon flux. Accumulation rates of CO_2 in the atmosphere have varied considerably over the past two decades, despite relatively little change in emissions from fossil fuels. This variation is most likely a result of changes in the flux of CO_2 from the atmosphere to marine and terrestrial sinks (Bousquet *et al.* 2000). Recognizing that atmospheric CO_2 levels are controlled by marine and terrestrial processes, some researchers have speculated that ecosystems can be managed to maximize CO_2 sequestration. In particular, adding nutrients to the oceans to stimulate primary productivity, reducing the rate of deforestation, and changing forestry management practices to increase NPP are being seriously considered as a ways to mitigate anthropogenic CO_2 emissions (Dixon *et al.* 1994; Falkowski *et al.* 2000). Much of the discussion concerning ways to increase sequestration of carbon has focused on forests, especially low latitude tropical systems. The world's forests account for a large fraction of aboveground and belowground terrestrial carbon (Table 7.3). Changes in forest area and other carbon sinks, and flux of carbon from forests to the atmosphere varies greatly with latitude. Although tropical forests occupy approximately 13% of the total land surface they account for about 40% of the world's plant carbon. On an annual basis, these systems naturally remove approximately 3% of the carbon from the atmosphere. Because of the importance of tropical ecosystems in sequestering carbon, the rapid rate of tropical deforestation has a significant impact on global carbon cycles, resulting in a relatively large (1.1 to 2.0 Pg C/year) net flux of carbon to the atmosphere.

Despite the obvious attraction of managing biological and biogeochemical systems to increase carbon storage and ameliorate effects of anthropogenic emissions, we must acknowledge that marine and terrestrial ecosystems have a finite capacity to sequester carbon. In addition, it is likely that increased levels of

Table 7.3. Carbon pools and flux in forest ecosystems of the world. (From Dixon *et al.* 1994)

Latitudinal belt	Change in forest area (10^6 Ha/year)	Carbon pools in terrestrial vegetation and soils (Pg)	Carbon flux to (−) and from (+) the atmosphere (Pg/year)
High (Russia, Canada, Alaska)	−0.7	559	+0.48
Mid (Continental USA, Europe, China, Australia)	+0.7	159	+0.26
Low (Asia, Africa, Americas)	−15.4	428	−1.65

atmospheric CO_2 and global temperature will directly influence the global carbon cycle. In a warmer, CO_2-enriched world, transport of carbon from the surface to deep oceans will be reduced, terrestrial plants will become less of a carbon sink, and increased microbial respiration may counteract effects of greater NPP (Falkowski *et al.* 2000). Most ecologists would agree that slowing the rate of tropical deforestation will have positive benefits aside from increased carbon storage. However, remediation strategies designed to increase sequestration of atmospheric carbon, especially at the large spatial and temporal scale necessary to influence global cycles, will likely have unpredictable effects on other biological and biogeochemical processes. Because of this uncertainty, we should not consider manipulation of global carbon cycles as an alternative to the more politically and socioeconomically challenging task of reducing global emissions of CO_2.

7.2.3 THE MISMATCH BETWEEN CLIMATE MODELS AND ECOLOGICAL STUDIES

> *...most ecological studies are carried out in areas roughly the size of a tennis court, while the resolution of most climate models is approximately the size of the state of Colorado* (Root and Schneider 1993)

Much of the difficulty in predicting the ecological consequences of global climate change on communities results from our inability to link large-scale climate models to smaller scale ecological studies. Currently we lack regional projections of climate change that can be applied to local ecosystems. General circulation models (GCMs) have allowed scientists to predict potential increases in global temperatures associated with elevated CO_2 and to quantify interactions among atmospheric, oceanic, and terrestrial compartments. However, the coarse spatial scale of GCMs (generally >500 km^2) is much larger than most ecological investigations. One proposed solution to this mismatch is to integrate regional models of climate change within GCMs (Hauer *et al.* 1997), thus allowing researchers to resolve the complexities of regional variation in climate, topography, vegetation, and hydrology. In addition, if we are to make any progress in understanding the ecological consequences of global climate change, interdisciplinary studies that integrate physiology, population biology, community ecology, and climatology are necessary. Clark *et al.* (2001) predicted climate change effects on trout populations in the southern Appalachians (USA) by integrating individual-based models with a geographic information system (GIS). Although the focus of this investigation was on life history characteristics (growth, spawning, feeding, mortality), the study demonstrates a unique approach for predicting regional population changes based on individual responses to climate. Root and Schneider (1993) show how large-scale climatic factors can be used to predict distribution of wintering North American birds. They describe a mechanism based on physiological constraints to explain the strong association between winter temperatures and geographical distributions. These types of studies represent an important step in resolving the mismatch between global climate models and ecological investigations.

Another way to link spatially-extensive analyses of climate with ecological studies is to develop regional models to forecast changes in vegetation under various scenarios of climate change. Regional models have been used to predict the responses of grassland, forest, and tundra ecosystems to changes in climate (Pacala and Hurtt 1993). Most model projections for the northern hemisphere show a generally northward expansion of plant communities as a result of increased temperature. Under a scenario of doubled CO_2 levels, Lassiter *et al*. (2000) predicted northerly retraction and expansion of different mixed forests in the mid-Atlantic region of North America. These results demonstrate the potential for significant range shifts of dominant plant communities in response to moderate warming. More dramatic effects are expected in extreme northern and southern latitudes where climate change is predicted to be greatest. Because the boundary between boreal and tundra ecosystems is abrupt and closely associated with climate, the response of boreal ecosystems to global climate change has received considerable attention. Using a model to predict effects of transient changes in climate, Starfield and Chapin (1996) report that a 3 °C increase in temperature would result in the transition of tundra to boreal forest within 150 years.

7.2.4 PALEOECOLOGICAL STUDIES OF CO_2 AND CLIMATE CHANGE

A significant challenge in the study of global climate change is to distinguish natural variation in climate from the variation associated with anthropogenic emissions of greenhouse gases. Because of the difficulty conducting manipulations at spatial scales compatible with GCMs, integrating models of environmental change with paleoecological records can improve our understanding of how climate influences communities. Today, interdisciplinary teams of atmospheric scientists, geologists, and paleoecologists integrate evidence from diverse sources to support the link between CO_2 concentrations and increased global temperatures (Table 7.4). Tree ring analyses provide high resolution of annual variation in climate over relatively short time periods (10^2–10^3 years), whereas pollen grains, ice cores and marine sediments yield much longer records (10^5–10^7 years). Recent studies have given atmospheric scientists a much better understanding of the correlation between atmospheric CO_2 levels and global temperature. Paleoecologists have contributed to this understanding by reconstructing relationships between global climate and prehistoric communities.

Modern plant species have persisted over the past 2.5 million years in the face of extensive changes in climate. Climate warming at the start of the Holocene era was relatively rapid and provides a reasonable model for predicting changes associated with anthropogenic impacts. Climatic changes since the last glacial period have had profound effects on plant and animal communities in North America. Adaptation to climate change and extensive range expansion (e.g. migrations)

Table 7.4. Paleoecological and other techniques employed to reconstruct global changes in greenhouse gases and climate. (From Stokstad, 2001)

Method	Information obtained	Resolution	Typical time range
Tree rings	Temperature, rainfall, wildfires	Annual	500–700 years
Pollen grains	Changes in community composition related to temperature and precipitation	50 years	Present to several million years
Geomorphology	Extent of glaciers and ice sheets, sea level changes	Variable	Glaciation to 2.9 billion years
Ice cores	CO_2 concentration, volume of continental ice, snow accumulation rates	Seasonal to decades	Present to 440 000 years
Corals	Sea surface temperatures, precipitation cycles	Months	400 years
Marine sediments	Temperature, salinity, ice volume, atmospheric CO_2	Thousands of years to centuries	180 million years

have characterized plant responses over this period. For example, records based on pollen grain analyses showed that many forest tree species migrated northward at rates of 100–1000 m/year during the period of post-Pleistocene warming. Because of interspecific differences in tolerance to climate change and migration rates, this northward movement generally occurred on a species-by-species basis and not at the level of assemblage. These results suggest that predicting future community structure may require an autecological focus (Harrison 1993).

Although the ability of some organisms to adapt to changing climate and disperse over relatively long distances during post-glacial periods is encouraging, the unprecedented rate of climate change expected over the next century makes extrapolation from paleoecological records tenuous. Future climates may lie outside the range of historical records and therefore caution is required when using paleoecological data to predict ecological effects. Because rapid climate change will most likely preclude the ability of plants to adapt, it is generally believed that range extension and retraction will be a common response. However, migration may not provide an alternative in the face of rapid climate change. Based on current climate projections for the next century, plants would be required to migrate 300 to 500 km/century, a rate significantly greater than previously reported for many tree species (Davis and Shaw 2001). For example, spruce trees, known to have a rapid rate of dispersal, have expanded their range to about 200 km/century over the past 9000 years. Some model projections of forest succession in a changing climate are inconsistent with known rates of range expansion and illustrate our poor understanding of this process. Forest succession models predict that temperature increases associated with a two-fold increase in CO_2 would force the boreal zone in central Sweden 1000 km northward within 150–200 years (Prentice, Sykes and Cramer 1991). Based on paleoecological records it is unlikely that species are capable of this unprecedented rate of range expansion. In addition, land use changes and habitat fragmentation represent significant impediments to range extension and gene flow, thus increasing the likelihood that many species will go extinct (Davis and Shaw 2001).

7.2.5 EFFECTS OF CLIMATE CHANGE ON TERRESTRIAL VEGETATION

Unlike many of the anthropogenic stressors considered in our examination of community ecotoxicology, significant research on effects of CO_2 has focused on terrestrial ecosystems. For example, most of the chapters in the book *Biotic Interactions and Global Change* by Karieva, Kingsolver and Huey (1993) examine effects on terrestrial communities. Community-level responses to elevated levels of atmospheric CO_2 include direct effects associated with alterations in primary productivity and indirect effects attributed to changes in global climate, especially temperature and precipitation. If CO_2 limits primary productivity (Bazzaz 1990), we would expect to see alterations in community composition as a direct result of species-specific responses to elevated CO_2. Faster growing species or those that employ C_3 photosynthetic pathways will likely be favored by increased levels of CO_2. In addition, differential responses of C_3 and C_4 plants to CO_2 enrichment may modify competitive relationships. Finally, these changes in plant community composition will likely have significant impacts on grazers and other herbivores. For example, plants that respond to elevated CO_2 generally have lower nutrient content, thus requiring herbivores to consume more food (Vitousek 1994).

Small-scale experiments have been conducted to measure responses of plant communities to both elevated concentrations of CO_2 and increased temperature. To manipulate temperature, researchers have employed a variety of approaches, including plastic enclosures, snow fences, heating cables, and overhead heaters. Robinson *et al*. (1998) used polythene tents to investigate the response of an arctic plant community to warming. Results showed that a 3.5 °C increase in air temperature increased total plant cover over a season. However, this response was not consistent between years, suggesting that short-term responses to warming may be poor predictors of longer term impacts.

As with communities located at higher latitudes, we expect greater effects of global warming on communities at higher elevations because of relatively short growing seasons. Harte and Shaw (1995) used overhead heaters suspended above 30-m^2 plots to simulate effects of warming on composition of a montane plant community. Results of these experiments showed that aboveground biomass of forbs decreased and biomass of shrubs (primarily sagebrush) increased in response to warmer soil temperatures and lower soil moisture (Fig. 7.2). The

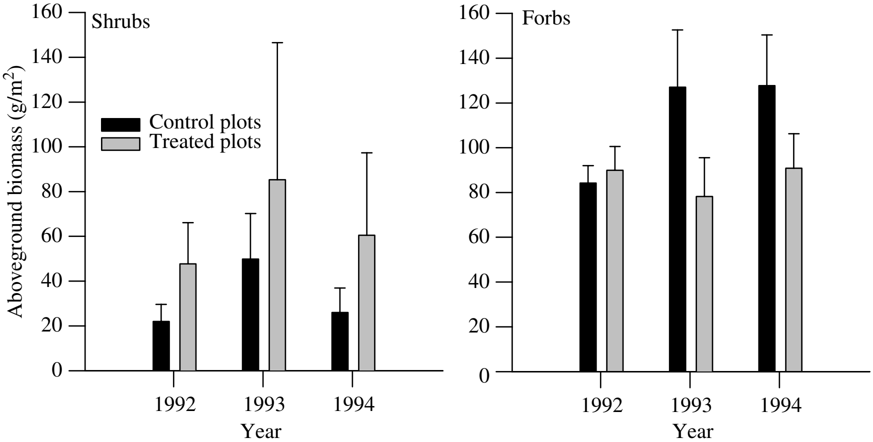

Fig. 7.2. Results of a climate warming experiment showing shifts in dominance of montane plant communities in the Rocky Mountains. The figure shows changes in aboveground biomass of shrubs and forbs following experimental manipulation of soil temperature using overhead radiators. Increased temperature in these treatments corresponded to a concentration of CO_2 approximately 2 × greater than pre-industrial levels. (Data from Table 2 in Harte and Shaw 1995)

response of forbs to warming was species-specific, and differences were attributed to effects on soil resource availability (Valpine and Harte 2001). Although the warming-induced shift from forbs to drought-tolerant sagebrush reported by Harte and Shaw (1995) is consistent with our expectations, reanalysis of these data using a different statistical model casts some doubt on the findings. Price and Waser (2000) suggest that differences in sagebrush biomass between control and heated plots reported by Harte and Shaw (1995) were attributable to pre-treatment differences. These researchers observed no effects of warming in their study, and argued that soil desiccation and reduced microbial activity in treated plots offset the influence of earlier snowmelt. The contradictory findings of these two investigations highlight the difficulty of conducting field experiments and the need for long-term studies to assess community responses to climate change.

Several characteristics influence responses of plant communities to global warming, including previous exposure to climatic extremes, species richness, functional composition, and successional stage (Grime *et al.* 2000). Consequently, we expect that different plant communities will respond to climate change in very different ways. This hypothesis was tested by comparing responses of a mature, stable grassland community to those of an immature, early successional community (Grime *et al.* 2000). Soil temperatures in treated plots were increased by 3 °C using heating cables placed at the soil surface. Results showed that early successional communities composed of fast-growing or short-lived species were more sensitive to warming than mature communities. Because landscape alterations that maintain early successional communities are becoming increasingly common, these authors speculate that climate change may have disproportionate effects on these previously disturbed communities.

7.2.6 ECOLOGICAL RESPONSES TO CO_2 ENRICHMENT

Although the effects of increased CO_2 on global climate change have received considerable attention, relatively few studies have investigated the direct response of plant communities to CO_2 enrichment. Elevated levels of CO_2 are likely to have profound effects on plant community composition as well as a significant influence on belowground processes. Owensby *et al.* (1993) investigated effects of CO_2 enrichment (2 × ambient levels) on species composition, biomass production, and leaf area in a tall grass prairie ecosystem. These authors note that because rangelands account for 47% of the earth's land area, responses of these ecosystems to elevated CO_2 have important implications for global carbon budgets. In contrast to expectations, elevated levels of CO_2 increased production of C_4 grass species but not C_3 species. The enhanced productivity of C_4 species was related to greater water-use efficiency. There was little indication of a shift in competitive relationships between C_3 and C_4 species.

Tree species that employ the C_3 photosynthetic pathway are carbon-limited and are expected to increase productivity in response to enhanced CO_2. Increased NPP in forests dominated by C_3 trees may therefore reduce the amount of CO_2 from anthropogenic sources. While some studies have shown that productivity of seedlings is increased under an enriched CO_2 regime, analysis of tree rings shows relatively little relationship between growth rate and atmospheric CO_2 (DeLucia *et al.* 1999). To reconcile the differences between results of growth chamber experiments and these paleoecological investigations, research conducted at larger spatial scales is necessary. DeLucia *et al.* (1999) investigated responses of loblolly pines to CO_2 enrichment (+200 μl) in 30-m diameter experimental plots (Fig. 7.3A). Results showed that growth rate was approximately 26% greater after 2 years of exposure to elevated CO_2 (Fig. 7.3B). In contrast to model simulations that predict only a 9% increase in NPP in response to doubling CO_2, DeLucia *et al.* observed that ecosystem NPP increased by 25% in enriched plots relative to controls. If applied globally, this increase in NPP could sequester about 50% of the total anthropogenic carbon expected to be released by 2050; however, these researchers speculate that this may represent the upper limit of forest carbon uptake.

Because the amount of carbon stored in soil organic matter is two to three times greater than in terrestrial vegetation, changes in soil processes can significantly influence global carbon cycles and sequestration. Elevated CO_2 is expected to control belowground processes in terrestrial ecosystems by influencing NPP, soil respiration, decomposition, and nitrogen mineralization. The relationship between CO_2 enrichment and belowground processes was investigated using experimental

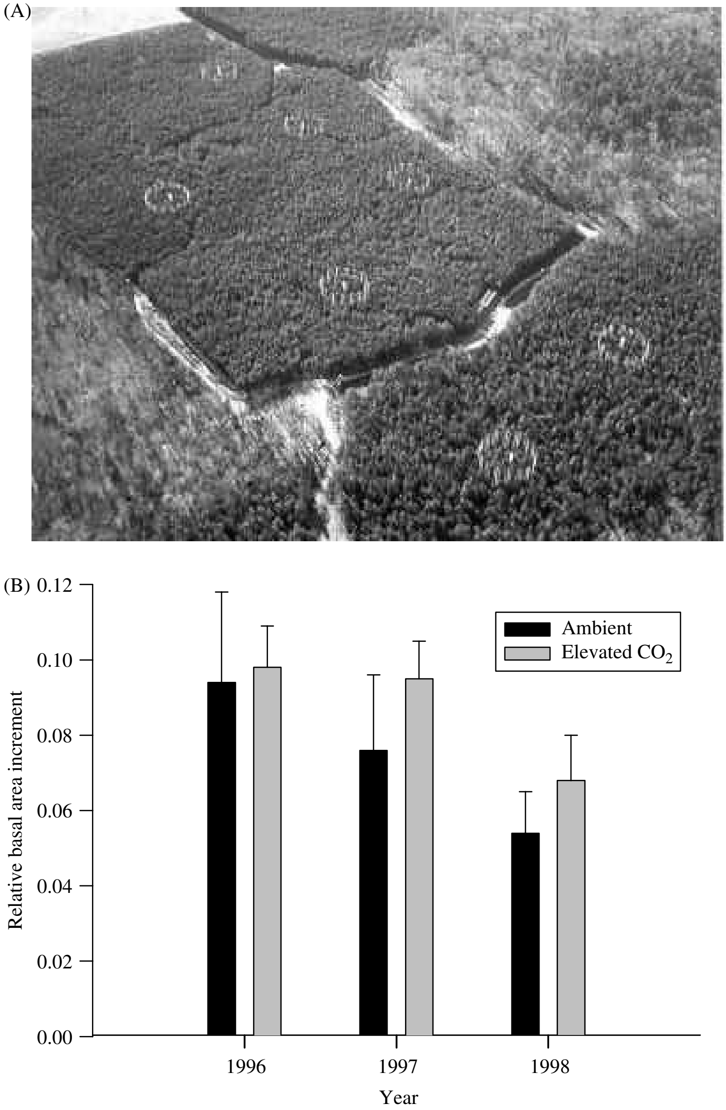

Fig. 7.3. (A) Experimental plots used for the free-air CO_2 enrichment (FACE) studies of the effects of elevated CO_2 on growth of loblolly pines in North Carolina, USA. Each ring in the photograph is 30 m in diameter and contains about 100 trees. (From Figure 3 in Allen *et al*. 2000; Reproduced by permission of the Ecological Society of America.) (B) Relative basal area increment for loblolly pines growing in ambient and elevated CO_2 conditions. (Data from Table 1 in DeLucia *et al*. 1999)

plots in the loblolly pine forest described above (Allen *et al.* 2000). Although litterfall mass and fine root biomass increased in treated plots, there was no influence of enriched CO_2 on litterfall C:N ratios, nutrient cycling, microbial biomass, or nitrogen mineralization. These results are consistent with other studies of belowground processes and indicate that elevated CO_2 may accelerate the input of organic matter to carbon pools in soils. Changes in soil organic matter and carbon pools are likely to influence belowground communities and food chains. Experiments conducted in terrestrial microcosms showed increased abundance and changes in community composition of fungal-feeding arthropods (Collembola) in response to CO_2 enrichment (Jones *et al.* 1998). The authors concluded that these structural changes were a result of alterations in the fungal community, which responded to increased dissolved organic carbon in soil.

7.2.7 EFFECTS OF CLIMATE CHANGE ON TERRESTRIAL ANIMAL COMMUNITIES

In addition to the direct effects of increased temperature on animals, changes in the distribution and abundance of plants will likely have significant impacts on animal communities. Alterations in climate may modify terrestrial food webs in systems regulated by top-down or bottom-up control (Box 7.1) Assuming other environmental factors are favorable, the most consistent responses of species limited by temperature will be a northward (or southward in the southern hemisphere) range expansion. The geographic distributions of many animal species are strongly correlated with vegetation, and some species are obligate associates of a particular vegetation type. Thus, while many animals are expected to migrate in response to changes in climate, their dependence on slower dispersing plants could limit these range shifts and result in extinctions (Root 1993).

Box 7.1 The influence of global climate change on interactions between wolves and moose

As noted above, it is generally assumed that most effects of climate change on animals are a secondary result of changes in distribution and abundance of plants. However, in systems where top predators exert control over community structure and function (see Chapter 8), animals may actually regulate responses of plants to climate. Long-term (40 years) records of predator–prey interactions between wolves and moose on Isle Royale, USA have demonstrated top-down control in this system. Wolves regulate moose density and moose control abundance of balsam fir, their primary winter forage. Recent analyses have shown that variation in global climate also plays an important role in these interactions. Annual variation in snow depth associated with the North Atlantic Oscillation influences the foraging behavior and efficiency of wolves. During years with heavy snowfall, wolves tend to hunt in larger packs and their predation rate on moose is increased. Thus, densities of moose are lower during years of heavy snowfall and growth of balsam fir is greater due to reduced herbivory. In contrast, predation is reduced during years of low snowfall, moose populations are larger, and growth of balsam fir is limited by grazing. Results of this study demonstrate the unique influence of climate on top-down regulation of plant production. Assuming that winter snowpack in this region will be reduced due to climate warming, results of these long-term studies suggest that moose populations will increase and growth of balsam fir will be reduced.

Much of the research on effects of climate change on birds and mammals has been conducted at the population level (Larson 1994). For example, Sillett, Holmes and Sherry (2000) report that regional variation in climate affects survival and reproductive success of migratory songbirds. The timing of reproduction in many passerines corresponds with peak abundance in local food supply. Thomas *et al*. (2001) show that the earlier leaf flush and the associated pulse of food expected under climate warming will result in a mismatch between peak food abundance and nestling demand. In a comprehensive analysis of 148 land bird species, Root (1988) identified six major environmental factors (minimum January temperature, length of frost-free period, humidity, precipitation, elevation, and vegetation) which limited the distribution of North American land birds (Fig. 7.4). With the exception of elevation, all of these variables are expected to change in response to global warming.

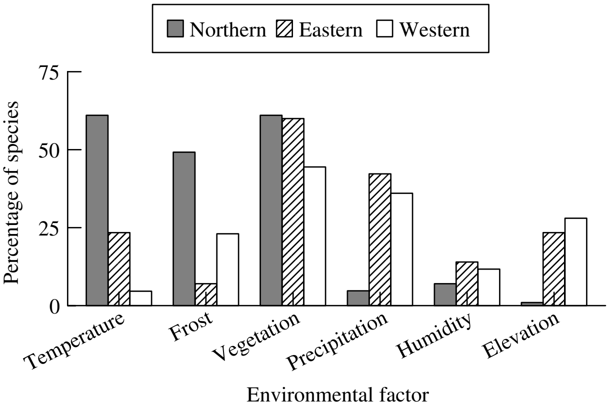

Fig. 7.4. The influence of environmental factors on the distribution of birds. The figure shows the percentage of bird species' northern, eastern, and western boundaries that are associated with six environmental variables. Note that five of these factors (temperature, frost, vegetation, precipitation, and humidity) will likely be affected by climate change. (Modified from Figure 4 in Root 1993)

McDonald and Brown (1992) provide one of the more insightful approaches for investigating effects of climate change on small mammal communities. By integrating the theory of island biogeography with data on distribution and abundance of mammals inhabiting isolated mountain ranges, these researchers developed a quantitative model to predict the number and identity of species expected to go extinct as a result of global warming. Assuming a relatively conservative (based on recent estimates) 3 °C increase in temperature, McDonald and Brown first estimated the amount of boreal habitat that will be lost on 19 isolated mountain ranges in the Great Basin (USA). Next, they estimated the response of 14 boreal mammal species based on the proportion of lost habitat. Their results were striking. Under a 3 °C increase in temperature, more than 50% of the boreal mammal species on individual mountain ranges would go extinct locally and an additional three species would go extinct throughout the region. Although this analysis makes several simplifying assumptions, McDonald and Brown have provided a useful framework for predicting the probability of extinction based on model projections of vegetation change and present geographic distributions. Boggs and Murphy (1997) used a similar approach to predict effects of climate change on butterfly communities in this same region. Their analysis showed that the butterfly community would experience a 23% reduction in number of species, with the greatest effects on less mobile species. These analyses support the hypothesis that montane communities are at high risk of extinction from global warming and associated habitat loss.

7.2.8 EFFECTS OF CLIMATE CHANGE ON FRESHWATER COMMUNITIES

> *The effects of climate change on freshwaters have been largely disregarded in major global change programs.* (Schindler *et al*. 1990)

Although much of the basic research in aquatic ecology is relevant to global climate change, relatively few studies have considered how freshwater communities will respond to climate change (Carpenter *et al*. 1992). Complex changes in lakes and streams in response to global climate are expected as a result of alterations in thermal regime and hydrologic characteristics. Many aquatic organisms are adapted to a relatively narrow range of temperature. In particular, coldwater, stenothermal species (e.g. salmonids in high elevation lakes and streams) are likely to be impacted by increased water temperatures. The longitudinal distribution of net-spinning caddisflies (Trichoptera) in Rocky Mountain (USA) streams provides a good example of the close association between elevation (and presumably water temperature) and community composition (Fig. 7.5). Predictable changes in abundance of dominant species are observed from headwater streams to larger, warmer rivers. With increased water temperatures associated with climate change, the distribution of temperature-sensitive species will likely shift

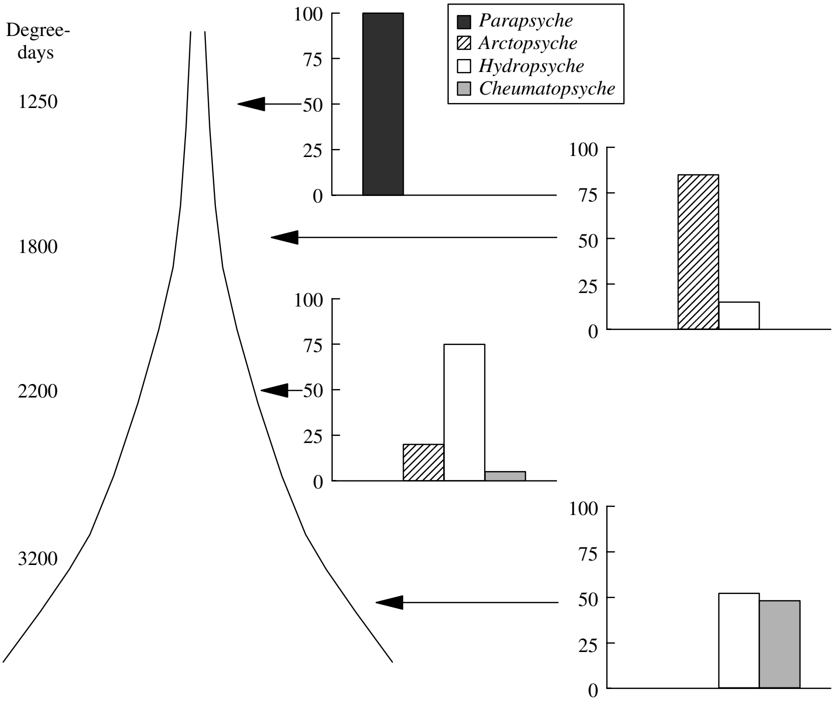

Fig. 7.5. The longitudinal distribution of net-spinning caddisflies (Trichoptera: Hydropsychidae) along an elevation and temperature gradient in Rocky Mountain streams of southern British Columbia. The figure shows the relative abundance of four dominant genera at four locations from headwaters to downstream reaches. It is expected that increased water temperature will shift the distribution of some species to higher elevations and may result in the extirpation of stenothermal taxa such as *Parapsyche elsis*. (Modified from Figure 3 in Hauer *et al*. 1997)

to higher elevations. These shifts are likely to result in the extirpation of many coldwater species currently restricted to alpine habitats.

Increased temperature may also modify species interactions in aquatic ecosystems, thus indirectly altering community composition. Laboratory experiments have shown that brook trout (an introduced species in many western streams) have a competitive advantage over native cutthroat trout at higher temperatures (DeStato and Rahel 1994). Thus, we would expect a greater rate of extirpation of some native species under conditions of increased water temperatures.

A long-term study of boreal lakes and streams in northwestern Ontario (Canada) provides some insight into potential physicochemical and ecological modifications associated with climate change (Schindler *et al*. 1996). Between 1970 and 1990 researchers at the Experimental Lakes Area (ELA) observed a gradual increase in air temperature (approximately 1.6 °C) and a decrease in precipitation (approximately 200 mm). While it is uncertain if these changes are a direct result of global climate change, they provide an excellent opportunity to document the influence of climate on hydrologic, biogeochemical, and ecological characteristics of freshwater systems. Some permanent first-order streams became ephemeral and stream discharge and export of base cations were significantly reduced as a result of lower precipitation. Physicochemical changes in lakes included increased surface water temperature, increased water clarity and light penetration, and a deeper thermocline. Complex changes in biomass and diversity of phytoplankton were also associated with these physicochemical alterations. However, the most striking ecological response was the complete loss of habitat for lake trout and other stenothermal species as a result of lower dissolved oxygen levels and a deeper thermocline. Because the magnitude and duration of climatic change observed at ELA were less than predicted by relatively conservative GCMs, these results show that modest alterations in temperature and precipitation can have significant consequences for freshwater ecosystems (Schindler *et al*. 1996). Finally, an increase in water clarity and reduced levels of dissolved organic matter (DOM) may cause significant interactions between climate change, UV-B exposure, and acidification in aquatic ecosystems (Section 7.5).

Alterations in functional characteristics of aquatic ecosystems may result from direct physiological effects of increased temperature as well as changes in trophic structure. Using microcosm experiments containing bacteria, algae, and diatoms, Petchey *et al*. (1999) showed significant extinction of species (30–40%) and altered ecosystem function in response to warming. Frequency of extinction varied among trophic levels, with greatest impacts on herbivores and top predators. Temperature-dependent physiological responses and changes in community structure were related to alterations in function, as warmer communities showed increased rates of primary production and decomposition. These experiments also provided support for the hypothesis that impacts of climate change (and other anthropogenic disturbances) are less in species-rich communities because of the greater likelihood of retaining tolerant taxa (Petchey *et al*. 1999).

As in terrestrial systems, logistical challenges limit the use of large-scale experimental approaches for investigating effects of climate change on freshwater communities. Consequently, most studies in aquatic systems are based either on long-term monitoring at sites where known changes in climate have been recorded (Schindler *et al*. 1990), or relatively small-scale microcosm experiments such as the one described above. The study by Hogg and Williams (1996) is unique because it measured responses of a stream benthic community to increased temperature in a relatively large-scale experimental system. These researchers divided a first order stream longitudinally and increased water temperature on one side by 2–3.5 °C. Using a before–after control-impact (BACI) design (Chapter 4), Hogg and Williamson characterized pre-treatment community composition and then measured responses to warming over a 2-year period. The focus of the study

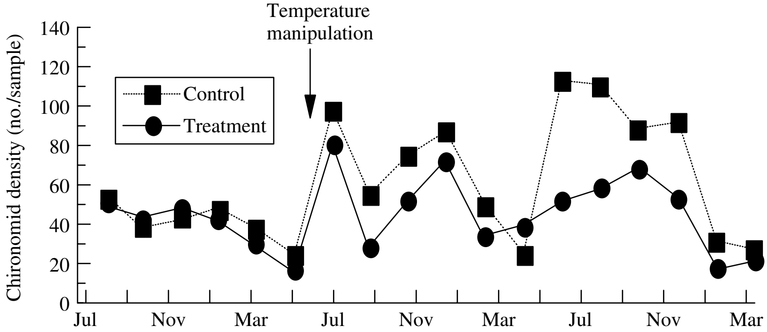

Fig. 7.6. Response of chironomids to a 2–3.5 °C increase in water temperature. Data were collected 1 year before and 2 years after temperature treatments in a first-order stream. (Modified from Figure 6 in Hogg and Williams 1996)

was primarily on life history characteristics (insect emergence, growth, size, sex ratios), but the results also showed a significant reduction in total density of chironomids, especially the coldwater Orthocladiinae (Fig. 7.6). These authors note that changes in life history characteristics were generally more sensitive to increased temperatures than alterations in community structure.

Although most of our discussion has focused on the negative impacts of climate change, increased temperatures can have beneficial effects on some species. Finney *et al.* (2000) used lake sediment records of δ^{15}N and abundance of cladocerans and diatoms to reconstruct sockeye salmon population densities over a 300-year period. Because salmon migrating from the North Pacific to freshwater systems have a strong marine-derived isotopic signature (e.g. high δ^{15}N relative to terrestrial sources), stable N isotopes in lake sediments can be used to track changes in salmon-derived nitrogen. Finney *et al.* (2000) show good agreement between salmon-derived N and abundance of higher trophic levels, indicating the importance of salmon carcasses to productivity in these otherwise oligotrophic systems. More importantly, they report a positive relationship between salmon abundance and documented changes in sea surface temperature from 1750 to about 1850 (Fig. 7.7). Colder than average temperatures generally resulted in below-average salmon abundance. This relationship breaks down over the last few decades, primarily as a result of over-harvesting salmon populations. The study demonstrates the strength of integrating sensitive analytical approaches such as stable isotopes with paleoecological studies to characterize ecological effects of climate change.

Because of the potential interactions between temperature, biogeochemical processes, and hydrologic characteristics, predicting community responses based only on modified thermal regimes may provide misleading results (Clark *et al.* 2001). For example, changes in the magnitude or timing of spring runoff in snowmelt-dominated watersheds (Hauer *et al.* 1997) may alter biogeochemical

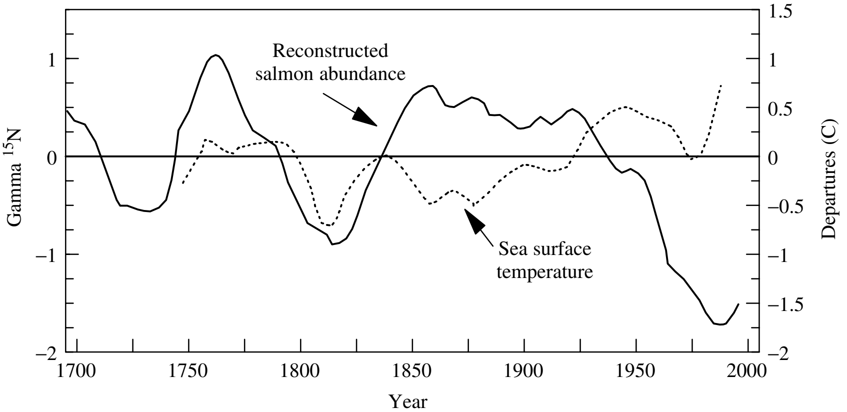

Fig. 7.7. The relationship between salmon abundance and sea surface temperatures. Stable isotope data derived from sediment records were used as an indicator of salmon abundance over the 300-year period. Sea surface temperatures are based on tree ring analyses. There was a positive relationship between salmon abundance and sea surface temperature from about 1700 to 1850. The poor relationship between temperature and salmon abundance in the past few decades is likely a result of commercial harvesting. (Modified from Figure 4 in Finney *et al.* 2000)

cycles and have direct impacts on stream communities. Interactions between riparian vegetation and watershed processes will likely be altered as a result of modified flow regimes. In their review of global change and aquatic ecosystems, Carpenter *et al.* (1992) distinguish between transitional changes and perturbational changes. Transitional changes occur over relatively long time periods (10–100 years) and result from alterations in landscapes, hydrological and geomorphological features, and community persistence. In contrast, perturbational changes occur over relatively short time periods (1–10 years) and are associated with floods, droughts, and temperature extremes. Because hydrologic characteristics, biogeochemical processes, and thermal regimes play a prominent role in determining the distribution and abundance of aquatic organisms, both perturbational- and transitional-scale changes must be considered when predicting impacts of climate change on freshwater communities.

7.2.9 EFFECTS OF CLIMATE CHANGE ON MARINE COMMUNITIES

Elevated ocean temperatures are expected to have significant and diverse impacts on most marine communities (Box 7.2). Effects ranging from increased incidence of disease (Harvell *et al.* 1999) to reduced ecosystem productivity (Roemmich and McGowan 1995) have been associated with warming of ocean waters. Mass mortalities of seagrasses, corals, urchins, and abalone have been attributed to elevated ocean temperatures, resulting in dramatic changes in community composition (Harvell *et al*. 1999). Warmer ocean temperatures may directly influence organisms or make them more susceptible to other stressors. For example, elimination of grazing sea urchins from many Caribbean reefs, which was attributed to an unidentified pathogen, shifted the reefs from a coral-dominated community to an algae-dominated community. In addition to these direct effects, alterations in ocean surface temperatures may have indirect effects on marine food webs. Sanford (1999) speculates that warmer temperatures will have a significant impact on predator–prey interactions that regulate communities in the rocky intertidal zone of southern California. Because the starfish *Pisaster ochraceus*, a keystone predator in this community, is highly sensitive to temperature, community structure of the rocky intertidal zone could be altered by temperature-induced changes in feeding rates.

Box 7.2 The Southern California Bight: a test case of global warming?

The Southern California Bight has been the focus of considerable research into the effects of increased ocean temperatures over the past several decades. Since the 1940s, ocean surface temperatures in this region have increased by approximately 1.5 °C, with much of this increase occurring during 1976–1977 (Holbrook, Schmitt and Stephens 1997). Although it is uncertain if this increase is a result of global climate change or part of a natural cycle, the effects are widespread. The altered temperature regime of the region has been linked to dampened upwelling events, reduced nutrient levels and productivity, loss of species diversity, and alterations in community composition. In short, the Southern California Bight may provide important lessons on how marine ecosystems will respond to global warming.

One of the more significant effects associated with increased temperature in this region is the alteration of upwelling currents and the modification of marine food chains. Upwelling currents off the Pacific Coast of North and South America supply inorganic nutrients from colder, deeper waters to nutrient-poor surface waters. Marine primary producers and the complex food chains they support are highly dependent on this supply of nutrients. Warming trends over the past several decades have increased vertical stratification in areas around the Southern California Bight and reduced the supply of nutrients from upwelling. Roemmich and McGowan (1995) report that over a 43-year period (1951–1993) zooplankton biomass declined by 80% in this region. They attribute this dramatic response to a decrease in inorganic nutrients caused by dampened upwelling. Because of the importance of zooplankton in marine food chains and carbon cycling, this trend could have devastating consequences for coastal marine ecosystems.

Changes in the composition of benthic communities and reef fishes in the Southern California Bight were also associated with increased ocean surface temperatures. Barry *et al*. (1995) reported an increase in abundance of benthic invertebrates with a more southern distribution and a decrease in northern species from the 1930s to 1994. Holbrook, Schmitt and Stephens (1997) observed a 15–25% decrease in total species richness at two sites off Los Angeles, CA in the year immediately after a 1 °C increase in annual seawater temperature. In addition, the proportion of the community consisting of northern species gradually declined and the fraction of southern species increased over a 20-year period. These observations are consistent with predictions that species will shift their geographic distribution in response to increased temperatures. Changes in community composition were accompanied by large reductions in abundance of reef fishes, especially northern species which declined by 88%. These dramatic reductions in abundance are not predicted from current models of climate change (Holbrook, Schmitt and Stephens 1997), and may represent the same long-term trend of lower productivity observed for zooplankton abundance (Roemmich and McGowan 1995). These data underscore the importance of developing a better mechanistic understanding of the relationship between climate change, ecosystem productivity, and community dynamics (Holbrook, Schmitt and Stephens 1997).

Because of their narrow range of temperature tolerance, coral reefs and associated communities are likely to suffer significant damage as a result of moderate global warming (Smith and Buddemeier 1992). The response of coral reefs to global climate change will depend on numerous factors, including the rate of temperature increase, the ability of reef systems to tolerate and adapt to warmer temperatures, and their geographic location. Elevated temperatures during the 1998 El Niño event are a suspected cause of the massive die-offs of corals observed in the Caribbean and other locations. Temperatures exceeding 30 °C triggered reef-building hermatypic corals to expel their zooxanthellae (the symbiotic algae living in corals), a phenomenon known as coral bleaching. During 1998, 46% of the reefs in the Indian Ocean were severely damaged by elevated surface temperatures and 16% of the reefs globally experienced bleaching. In addition to the impacts of elevated temperature, there are also concerns about the direct influence of elevated CO_2 on the process of calcification and reef formation. Although coral reef communities are highly sensitive to contaminants and many other types of anthropogenic stressors, the widespread devastation following the 1998 El Niño event indicates that global climate change is probably the most serious threat.

7.2.10 CONCLUSIONS

In the final chapter of *Biotic Interactions and Global Change*, Kingsolver, Huey and Kareiva (1993) outline a research agenda comprised of eight specific goals designed to help ecologists ‘understand and forecast the consequences of global

Table 7.5. Proposed research agenda for understanding and predicting the consequences of global climate change on communities. (From Kingsolver, Huey and Kareiva 1993)

1. Relate temporal and spatial patterns of global change to likely biotic responses
2. Relate stress responses of individual organisms to changes in fitness, population abundance, species distribution, and interactions
3. Identify the critical rates of environmental change that determine ecological and evolutionary outcomes
4. Understand the reassortment of ecological communities as a source of environmental change
5. Identify sensitive and reliable indicators for current and future ecological research
6. Understand factors that determine changes in the location and nature of ecological transition zones and species margins
7. Develop standards and criteria for simplification of complex models
8. Identify the ecological variables that contribute to important changes in regional or global climate, disturbance regimes, and patterns of habitat fragmentation

environmental change for (1) biological diversity, (2) community integrity, and (3) ecosystem services'. Because these research goals are relevant not only to global change but also to our broader understanding of how communities respond to stressors, it is appropriate to review these eight recommendations (Table 7.5). We feel that the most critical research need for assessing ecological consequences of global change is to identify specific community responses to expected spatial and temporal variation in climate. This will occur only through better integration of basic ecological principles into experimental, monitoring, and modeling studies that focus on climate change. Relating individual responses to fitness, population abundance, and community structure will allow researchers to identify sensitive and ecologically-important indicators of climate change. Research that matches the coarse spatial scale of GCMs with the smaller scale of most ecological investigations is essential for predicting regional responses to climate change. Because effects of climate change will vary among locations and among community types, a rigorous approach for assessing community susceptibility will improve our ability to predict these responses. This approach should distinguish between the direct effects of climate change and the indirect effects associated with alterations in species interactions. Finally, ecologists are only beginning to understand the influence of multiple anthropogenic stressors on species assemblages. Because community composition and ecosystem function will be quite different in a warmer climate, these relationships will likely change. Thus, predicting effects of contaminants on communities will require a better understanding of interactions between global climate change and other anthropogenic stressors.

7.3 STRATOSPHERIC OZONE DEPLETION

Decreasing levels of stratospheric ozone (O_3) have been observed in polar and mid-latitude regions for about two decades (Madronich 1992). There is now conclusive evidence that reduced levels of ozone is a direct result of anthropogenic activities, particularly the release of chlorofluorocarbons (CFCs). Although production and release of CFCs occurred primarily in the northern hemisphere, the greatest reductions in ozone levels have been reported in Antarctica. In September 2000, measurement of the ozone depletion-area using NASA's Total Ozone Mapping Spectrometer showed that the highly publicized 'ozone hole' over Antarctica was the largest ever observed, covering approximately 28 million km^2. Other locations in the southern hemisphere, especially southern Australia and New Zealand, have also reported greatly reduced levels of ozone.

Because ozone limits the penetration of ultraviolet radiation through the earth's atmosphere, lower levels of stratospheric ozone are associated with increased levels of UVR. Recent studies conducted in New Zealand reveal that current levels of ozone during summer are approximately 10–15% less than in the 1970s, resulting in a significant increase in UVR (McKenzie, Connor and Bodeker 1999). Although production and release of CFCs have decreased as a result of international agreements (e.g. the 1987 Montreal Protocol on Substances that Deplete the Ozone Layer), global CFC levels will likely remain elevated because of atmospheric persistence. Therefore, it is anticipated that levels of stratospheric ozone will continue to decline over the next several decades (Smith *et al*. 1992). In addition, there is concern that potential interactions between ozone depletion and global warming may significantly delay the return of stratospheric ozone to pre-industrial levels (Shindell, Rind and Lonergan 1998).

Increased UVR as a result of ozone depletion is a significant environmental hazard and is expected to have negative effects on humans and other organisms. For example, a 1% reduction in ozone is estimated to result in a 3% increase in certain forms of skin cancer in humans. Indeed, there is speculation that the high incidence of skin cancer in New Zealand and Australia is partially a result of elevated levels of UVR. Of the three categories of UVR, UV-B (280–320 nm) is most closely associated with loss of ozone. Ozone depletion has relatively little effect on UV-A (320–400 nm), UV-C (190–280 nm), or photosynthetically active radiation (PAR; 400–700 nm).

As noted above, ozone depletion has most frequently been reported over Antarctica where ambient doses of UV-B have increased approximately 140% per decade (Madronich 1992); however, a similar pattern has been observed in other regions (Kerr and McElroy 1993). Increases of 10–20% UV-B per decade have been reported in temperate regions of the northern and southern hemispheres, and this trend is expected to continue. Spectral measurements of UV-B in Toronto, Canada showed that the intensity of radiation at 300 nm has increased by 35% in winter and 7% in summer since 1989 (Kerr and McElroy 1993). In addition to these latitudinal differences, other factors such as elevation will increase exposure to UVR. For example, Kinzie, Banaszak and Lesser (1998) attributed a significant reduction in photosynthesis in a high elevation (3980 m) lake to UV-B. Thus, despite the focus on Antarctic communities, effects of UV-B radiation are widespread and also likely to impact mid-latitude regions.

Although ozone depletion and associated increases in UV-B are a recent phenomenon, the presence of UV-B has played an important role in the evolution of life on earth. Because of low levels of ozone, UV-B readily penetrated earth's primitive atmosphere and restricted organisms to aquatic habitats for most of their evolutionary history. Migration to terrestrial habitats occurred only after sufficient levels of ozone had accumulated in the atmosphere (Fisher 1965; Cloud 1968). As a consequence of the long-term exposure to UV-B, many organisms evolved protective mechanisms to reduce UV-B effects. For example, the presence of photoprotective pigments, natural sunscreens, and various DNA repair mechanisms allow organisms to survive in habitats saturated with UV-B radiation. Although it is likely that many organisms show some tolerance to UV-B, there is considerable variation among taxa. Differences in the ability of organisms to tolerate UV-B may account for the patterns of community structure observed in some habitats, particularly alpine areas with naturally high levels of exposure.

All wavelengths of UVR are potentially harmful to organisms, but UV-B radiation is of particular concern because of the dramatic increase associated with ozone depletion. Studies conducted with a variety of plants and animals have shown effects of UV-B at all levels of biological organization (Fig. 7.8). At the molecular level, photochemical damage resulting from adsorption of specific

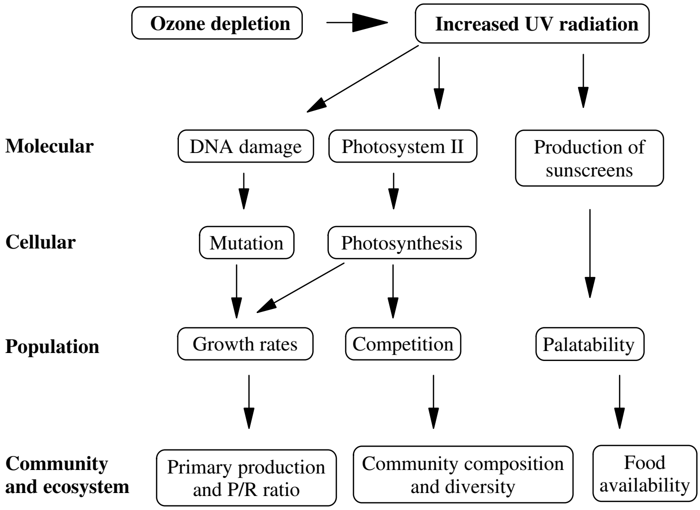

Fig. 7.8. Effects of ozone depletion and increased UV radiation across levels of biological organization. (Modified from Figure 6 in Vincent and Roy 1993)

wavelengths by macromolecules (e.g. DNA, RNA) and inactivation of photosystem II in plants are typical responses to UV-B exposure (Vincent and Roy 1993). Mutagenic effects resulting from DNA damage and reduced photosynthesis due to alteration of light and dark reactions occur at the cellular level. These molecular and cellular alterations affect individual growth rates, community structure, and ecosystem function. Environmentally-relevant, background levels of UV-B radiation are lethal to some taxa, and dramatic changes in primary production, community composition, and trophic structure have been reported following UV-B exposure. The direct and indirect effects of UV-B radiation on communities are diverse, and will be the primary focus of this section.

7.3.1 METHODOLOGICAL APPROACHES FOR MANIPULATING UVR

A variety of approaches, including UV cut-off filters, UV lamps, and more sophisticated solar simulators have been employed in field and laboratory studies to manipulate levels of UVR. UV cut-off filters can either transmit or remove UV-A and UV-B, whereas UV lamps can enhance exposure to different wavelengths of UVR. For logistical reasons, laboratory and microcosm experiments tend to rely on lamps to increase UV-B exposure, whereas field experiments tend to rely on filters to remove natural levels of UV-B. Both approaches have limitations, and there is some concern that differences between field and laboratory studies may be an artifact of different experimental techniques. To expose planktonic organisms to high levels of UV-B in the field, researchers will restrict organisms to shallow, high UV-B habitats. Because this experimental approach limits vertical migration, relevance to natural populations is questionable. Artificial lamps are commonly used in laboratory experiments (Bothwell, Sherbot and Pollock 1994; Kiffney, Little and Clements 1997) and in some field studies (Rader and Belish 1997) to enhance exposure to UV-B. Although this approach allows establishment of dose–response relationships, there are concerns about the unnatural spectral properties of UV lamps (Kelly, Clare and Bothwell 2001).

7.3.2 THE EFFECTS OF ULTRAVIOLET RADIATION ON MARINE AND FRESHWATER PLANKTON

> *The alarmist predictions of immediate and large scale impairment of primary production in response to ozone depletion seem to us to be greatly exaggerated.....* (Vincent and Roy 1993)

> *One of the most important caveats to working with the impact of UV-B radiation on freshwater ecosystems is that complex rather than simple responses are likely to be the rule.* (Williamson 1995)

Negative effects of UV-B radiation have been measured in both freshwater and marine environments. While some researchers feel aquatic communities are resilient to UV-B and that declines in ozone are unlikely to cause large-scale reductions in primary productivity (Vincent and Roy 1993), others suggest that complex responses associated with alterations in community structure and aquatic food webs are likely (Williamson 1995). These indirect effects are often subtle and difficult to predict, but may have important consequences for aquatic communities. In particular, the effects of UV-B radiation on marine phytoplankton and the consequences for oceanic food webs have received considerable attention (Smith *et al*. 1992). In general, marine primary producers (algae and diatoms) are highly sensitive to UV-B. Because much of the global ozone depletion has taken place over Antarctica, there are concerns that enhanced UV-B in this region may have serious consequences for phytoplankton inhabiting the photic zone of the Southern Ocean. More importantly, because Antarctic phytoplankton are a major component of marine food webs in the region, reduced phytoplankton biomass and production may have cascading effects on higher trophic levels.

Despite mounting evidence from the laboratory that UV-B radiation negatively affects phytoplankton, extrapolating these results to natural systems is challenging. Due to the unnatural spectral properties of UV lamps used in laboratory experiments, responses observed under artificial conditions may not reflect responses in the field. Furthermore, because organisms cultured in the laboratory may lack the protective pigments and repair mechanisms found in natural populations, effects of UVR may be exaggerated in laboratory experiments (Mostajir *et al*. 1999). Thus, comprehensive field experiments are essential for understanding the direct and indirect effects of enhanced UV-B. Using combinations of filters to remove different wavelengths of UVR, field experiments have shown that exposure to naturally-occurring levels of UVR significantly affected primary production and community composition (Smith *et al*. 1992; Kinzie, Banaszak and Lesser 1998; Mostajir *et al*. 1999). In an extensive survey of phytoplankton communities in Antarctic waters, Smith *et al*. (1992) related ozone depletion and UV-B levels to phytoplankton production. Measurements were taken inside and outside the ozone depletion zone during a 6-week cruise. UV-B was detected at depths exceeding 60 m, and depth of penetration was greater inside the ozone hole than outside. Ozone-related UV-B inhibition of photosynthesis was observed at depths of 25 m, and primary production was 6–12% lower inside the ozone hole than outside. These results correspond to a 2 to 4% reduction in primary productivity and an estimated loss of 7×10^{12} g of carbon per year over the entire Antarctic marginal ice zone.

7.3.2.1 Direct and Indirect Effects of UV-B Radiation

In a provocative review of the role of UV-B radiation in freshwater ecosystems, Williamson (1995) posed four hypotheses to describe the direct and indirect effects of UV-B on planktonic communities (Table 7.6). These hypotheses are especially relevant to our discussion of community ecotoxicology because they emphasize species interactions and trophic ecology. Because most research on UV-B effects has focused on molecular, cellular, and physiological

Table 7.6. Four hypotheses describing potential direct and indirect effects of increased UV-B radiation on planktonic communities. (From Williamson 1995)

Hypothesis	Description	Ecological concept
Solar ambush	Wavelength-selective changes in solar radiation result in differential abilities of organisms to detect and respond to increased UV-B	Differential tolerance among species will result in variation in community structure
Solar cascade	Differential effects of UV-B across trophic levels will have cascading influences on energy flow	Trophic cascades; top-down versus bottom-up effects
Acid transparency	Effects of UV-B radiation will be greater in anthropogenically acidified lakes than in naturally acidic lakes	Differential responses among communities, stressor interactions
Solar bottleneck	Small zooplankton in clear lakes will experience a 'bottleneck' as a result of intense UV-B in upper surface water and predation pressure from below	Predator–prey interactions, importance of vertical migrations in lakes

responses, Williamson's (1995) description of the potential ecological effects is quite illuminating.

The solar ambush hypothesis proposes that aquatic organisms unable to detect and respond to UV-B may be 'ambushed' by differential wavelength changes in total solar radiation. These wavelength-specific changes occur as a result of differences in elevation, light attenuation, cloud cover, and other factors. According to this hypothesis, sessile or relatively immobile organisms are at high risk because of their inability to respond behaviorally to increased UV-B.

The solar cascade hypothesis highlights the effects of UV-B radiation on trophic interactions in lakes. The influence of top-down and bottom-up trophic regulation in aquatic systems is well established, and the ecotoxicological implications of these interactions are discussed in Chapter 8. According to the solar cascade hypothesis, differential effects of UV-B among trophic levels may have cascading effects on energy flow and community structure. For example, if grazing herbivores are more sensitive to UV-B than phytoplankton, primary production will increase in grazer-limited lakes. The solar cascade hypothesis has been tested in a mesocosm experiment in which microbial and planktonic communities were exposed to natural and enhanced levels of UV-B radiation (Fig. 7.9). Results showed considerable variation in responses to UV-B among trophic levels, and that elimination of predatory ciliates caused an increase in abundance of their prey (bacteria, heterotrophic flagellates, and small phytoplankton). The direct effects of UV-B on ciliates reduced the transfer of energy to higher trophic levels and channeled carbon into the microbial food web.

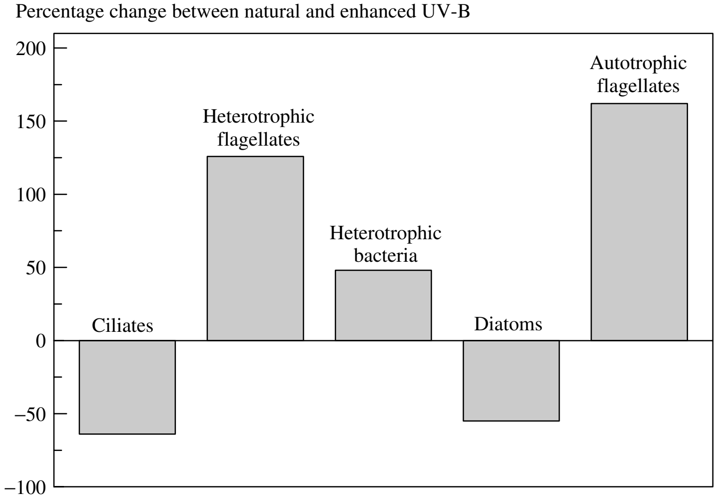

Fig. 7.9. Experimental test of the solar cascade hypothesis in microbial and plankton communities. The figure compares the percentage change in carbon biomass between natural and enhanced UV-B treatments for ciliates, flagellates, bacteria, and diatoms in mesocosms. The decrease in biomass of predatory ciliates resulted in an increase in biomass of flagellates and bacteria, thus channeling more energy into the microbial food web. (Data from Table 2 in Mostajir *et al.* 1999)

The acid transparency hypothesis describes the potential interactions between UV-B and acid deposition in freshwater lakes. Because of lower levels of humic materials, dissolved organic carbon, and other light attenuating substances, UV-B penetration and ecologically significant effects are expected to be greater in acidified lakes. It is possible that alterations in community composition and trophic structure observed in lakes receiving acidic deposition is at least partially a result of greater UV-B exposure.

From an ecological perspective, the most intriguing hypothesis advanced by Williamson (1995) describes the influence of UV-B on predator–prey interactions between large and small zooplankton species in lakes (Fig. 7.10). The solar bottleneck hypothesis proposes that small zooplankton may experience a bottleneck near the surface in clear oligotrophic lakes because of intense UV-B radiation from above and predation pressure by large zooplankton from below. Although small zooplankton could avoid predation and UV-B exposure during most of the year, intense solar radiation in summer months would eliminate this refuge.

7.3.3 RESPONSES OF BENTHIC COMMUNITIES

Most research investigating responses of aquatic ecosystems to UVR has focused on marine and freshwater plankton. The likely explanation for the emphasis

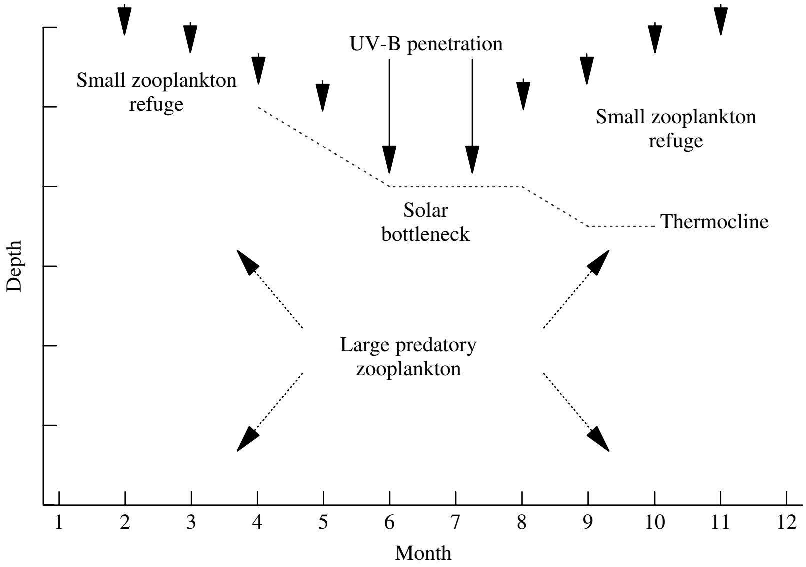

Fig. 7.10. The solar bottleneck hypothesis. Seasonal changes in the depth of the thermocline and penetration of UV-B radiation create a bottleneck for small zooplankton in clear, oligotrophic lakes. Small zooplankton have a refuge from predation in shallow waters during most months of the year. However, deeper penetration of UV-B in summer forces these organisms to deeper water where they are exposed to large predatory zooplankton. (Modified from Figure 1 in Williamson 1995)

on planktonic communities, especially in marine systems, is that rapid attenuation of UVR was expected to limit exposure to benthic communities. However, investigators have recently documented significant alterations in periphyton and benthic macroinvertebrate communities during exposure to UVR. Not only can UVR reach benthic communities in shallow aquatic environments, UVR may actually penetrate sediments and influence microbial photosynthetic communities within these habitats (Garcia-Pichel and Bebout 1996). Unlike planktonic organisms, periphyton communities and some benthic taxa are sessile and unable to avoid exposure to UV-B. Even relatively mobile macroinvertebrate taxa may be exposed to intense UV-B while grazing on periphyton in shallow, clear, lakes and streams.

The pioneering experiments of Bothwell, Sherbot and Pollock (1994) highlighted the complex ecosystem responses to UVR and demonstrated the importance of accounting for indirect effects. In contrast to expectations based on studies of freshwater phytoplankton, accrual of periphyton was actually enhanced in experimental streams receiving UVR. This apparent paradox was explained by lower abundance of grazing chironomids in UVR-treated streams, which allowed algal communities to flourish under conditions of reduced herbivory. Interestingly, the complex trophic response observed in these experiments was similar to that reported for streams exposed to the insecticide malathion (Bothwell, Sherbot and Pollock 1994). It is likely that similar trophic cascades may occur in freshwater systems where herbivores are more sensitive to UVR than primary producers.

7.3.4 RESPONSES OF TERRESTRIAL PLANT COMMUNITIES

Responses of plants to UV-B include reduced growth and biomass, reduced photosynthesis, and increased concentrations of UV-B absorbing compounds, particularly flavonoids (Caldwell *et al.* 1995; van de Staaij *et al.* 1995a,b). Because most research on plant responses to UV-B has been conducted in the laboratory and focused on individual species, the direct application of these studies to natural communities is uncertain (Gehrke 1999). Significant interspecific variation in sensitivity to UV-B has been observed among plant species, suggesting that changes in composition of communities are likely. In a series of field experiments conducted in northern Swedish Lapland, Gehrke (1999) measured responses of two species of bryophytes to enhanced UV-B radiation over a 3-year period. Bryophytes possess a number of unique characteristics that increase their susceptibility to UV-B, including thin leaves that often lack a protective cuticle, reduced photorepair mechanisms, and rootless shoots which cannot buffer against aboveground stress (Gehrke 1999). Differences in these physiological and morphological characteristics between species likely contributed to differences in sensitivity. The authors speculated that UV-B suppressed growth and altered the outcome of competition between sensitive and tolerant species.

Exposure of plants to UV-B may have important consequences for associated belowground communities (e.g. bacteria, mycorrhizal fungi, microarthropods). Because belowground communities play an important role in mineralization, decomposition, and plant nutrition, UV-B may have ecosystem-level effects. Klironomos and Allen (1995) exposed sugar maple (*Acer saccharum*) seedlings to various UVR treatments to measure effects on belowground communities. Although there were no direct effects of UVR on seedlings, large changes in the structure and function of fungal and bacterial communities associated with the roots were attributed to UV-B exposure. Changes in fungal and bacterial populations significantly affected soil microarthropod communities and shifted carbon flow from a mycorrhizal-dominated system to a saprobe/pathogen-dominated system.

7.3.5 BIOTIC AND ABIOTIC FACTORS THAT INFLUENCE UV-B EFFECTS ON COMMUNITIES

7.3.5.1 Dissolved Organic Materials

Dissolved organic materials (DOM) consist of a complex mixture of organic molecules that influence a variety of processes in aquatic ecosystems. Levels of dissolved organic and particulate materials play an important role in moderating effects of UV-B radiation in aquatic ecosystems. In fact, some researchers suggest that changes in DOM may have a greater influence on UVR exposure in aquatic ecosystems than impacts resulting from increased global levels of UVR (Schindler *et al*. 1996). The generally low levels of DOM typical of most marine ecosystems, especially the open ocean, allow UV-B to penetrate deep into the photic zone. In contrast, the much higher levels of UV-B-absorbing materials found in many freshwater ecosystems significantly reduce UV-B penetration in all but the most oligotrophic lakes (Williamson 1995). Because of rapid attenuation of light, UV-B effects in freshwater systems are generally considered to be less than those in marine systems. Nonetheless, some freshwater communities, especially those inhabiting shallow, clear lakes and streams where damaging levels of UV-B may penetrate several meters are at significant risk (Bothwell, Sherbot and Pollock 1994; Williamson 1995; Mostajir *et al*. 1999). In field experiments conducted in a Rocky Mountain stream, Kiffney, Clements and Cady (1997) observed effects of UV-B on benthic communities only after a seasonal decrease in natural levels of DOM.

Interactions between UVR and DOM in aquatic ecosystems are complex. The ability of DOM to attenuate light varies with source (allochthonous versus autochthonous) and chemical composition. For example, DOM derived from terrestrial sources absorbs more UVR than autochthonous materials (McKnight *et al*. 1997). Exposure to UVR can also degrade DOM through a process known as photobleaching (De Haan 1993). Thus, long-term exposure of DOM to UV-B may result in reduced light attenuation and actually enhance UV-B effects in aquatic communities. Because the amount of dissolved and particulate material in some freshwater systems varies with productivity, the trophic status of lakes and streams may also influence light penetration and UV-B effects. Williamson *et al*. (1994) compared responses of zooplankton communities to UV-B radiation in an oligotrophic and a eutrophic lake in Pennsylvania (USA). Experiments showed significant mortality due to UV-B exposure in the oligotrophic lake, whereas communities in the eutrophic lake were protected. Because DOM may have direct effects on microbial productivity and community composition, separating the chemical effects of DOM from the light attenuating influences on UV-B penetration are difficult. Kelly, Clare and Bothwell (2001) used filters containing several concentrations of DOM (0, 2, 5, 8 mg/l) suspended above experimental streams to isolate effects of DOM and UVR on benthic communities. Results showed highly significant increases in abundance of macroinvertebrates with increased DOM concentration and UVR attenuation (Fig. 7.11). A sharp threshold in response of benthic macroinvertebrate grazers was observed between 2 and 5 mg/l, indicating that streams with low levels of DOM (<5 mg/l) may be particularly sensitive to UVR.

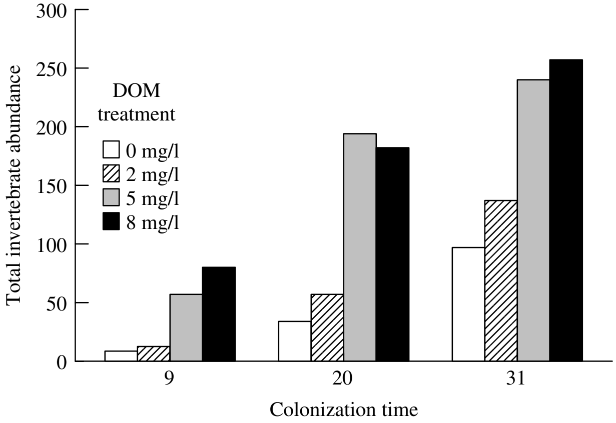

Fig. 7.11. The influence of dissolved organic material on attenuation of UV radiation and colonization by benthic macroinvertebrates in outdoor experimental streams. Filters containing varying concentrations of DOM were suspended above replicate experimental streams to reduce levels of UVR. Note the sharp decrease in macroinvertebrate colonization between 2 and 5 mg/l DOM. (Modified from Figure 5 in Kelly, Clare and Bothwell 2001)

7.3.5.2 Location

Because of spatial variation in UV exposure and species' sensitivity (Hill *et al.* 1997), the ecological effects of UV-B radiation on aquatic ecosystems are likely to differ among geographic regions. Levels of UV-B reaching the earth are affected by a variety of large-scale factors, including cloud cover (Lubin and Jensen 1995), snow depth, elevation (Caldwell, Robberecht and Billings 1980), and latitude. Seasonal changes in day length can also significantly alter exposure to UV-B radiation. Exposure to UV-B in polar regions is especially elevated during the summer due to extended periods of sunshine. Because the intensity of UV-B radiation increases with elevation, communities located at higher altitudes are exposed to greater levels of UV-B than communities at lower elevations. For example, Caldwell, Robberecht and Billings (1980) reported that the biologically effective UVR dose was 25% higher at 3300 m than at 1500 m (40 °N latitude). On a smaller spatial scale, Rader and Belish (1997) showed that effects of ambient and enhanced UV-B on periphyton communities varied among locations, and that effects were greater on communities inhabiting open reaches rather than shaded reaches. Santas, Lianou and Danielidid (1997) showed that depth influenced responses of marine diatom communities to UV-B, and concluded that accurate predictions about UV-B effects cannot be made without accounting for interactions with other environmental factors.

Factors such as elevation and DOM may interact to influence exposure of aquatic communities to UV-B. Because of shallow depth and naturally low levels of DOM, aquatic communities in many alpine habitats are subjected to intense levels of UV-B radiation during summer months (Kiffney, Clements and Cady 1997). In addition, because solar intensity increases significantly with elevation, communities located at higher altitudes are at particular risk from UV-B. Vinebrooke and Leavitt (1996) measured effects of UVR on periphyton in an ultraoligotrophic lake in Banff National Park (Canada). Colonization of periphyton was significantly suppressed under ambient UVR, primarily due to effects on the diatom *Achnanthes minutissima*. Because *A. minutissima* dominates lower elevation lakes with high DOM, Vinebrooke and Leavitt (1996) suggest that this species may be an indicator of UVR effects in western montane lakes.

7.3.5.3 Interspecific and Intraspecific Differences in UV-B Tolerance

Experiments investigating community-level responses to UV-B have revealed considerable variation in tolerance among species. Much of this variation is a result of behavioral, physiological, and morphological adaptations that allow organisms to survive natural UV-B exposure. Variation in tolerance to UV-B among fish species was attributed to an unidentified component in skin tissue that protected fish from UV-B-induced sunburn (Fabacher and Little 1995). Organisms that possess a protective covering, such as a case or shell, may be relatively tolerant to UVR exposure (Hill *et al.* 1997). It is expected that the ability of populations to tolerate UV-B is related to their level of natural exposure, and that populations from high UV-B habitats have greater UV tolerance. For example, organisms in oligotrophic, high elevation lakes and streams produce UV-absorbing compounds and pigments that act as natural sunscreens. Leech and Williamson (2000) define UV-B tolerance as the sum of photoprotection and photorepair processes, which vary with microhabitat and location. Sommaruga and Garcia-Pichel (1999) reported that levels of UV-absorbing compounds in planktonic organisms decreased with depth. Similarly, Gleason and Wellington (1995) observed that survivorship of coral larvae exposed to UV-B decreased with depth of collection, most likely due to lower amounts of UV-B-protective amino acids. Zellmer (1995) compared UV-B tolerance of transparent and heavily melanized *Daphnia* collected from lakes. Significant mortality and lower reproduction were observed in transparent populations, whereas the pigmented populations showed no effects of UV-B exposure. Finally, plants also produce photoprotective compounds in response to UV-B (van de Staaij *et al.* 1995a), and populations exposed to naturally high levels of UVR are generally more efficient at UV-B absorption. However, in contrast to expectations, van de Staaij *et al.* (1995b) found no significant difference in UV-B tolerance between highland populations (where natural levels of UV-B were greater) and lowland populations of a perennial herb.

Since small phytoplankton species (<2.0 μm) often comprise a significant portion of total biomass in plankton communities, understanding size-dependent variation in sensitivity to UV-B is important for predicting ecological effects. Because the protective efficiency of natural sunscreens to phytoplankton decreases with cell size (Laurion and Vincent 1998), we expect that small cells may be more sensitive to UV-B than large cells. Despite the intuitive appeal of the size-dependency hypothesis, it is obvious that other factors will influence tolerance of planktonic communities to UVR. Laurion and Vincent (1998) reported that small phytoplankton were relatively tolerant to UV-B exposure and that interspecific differences were more important than size for predicting effects on phytoplankton. The relationship between organism size and UVR tolerance is further complicated by the presence of visual predators, which often select larger zooplankton species and can modify patterns of vertical migration in the water column. In addition, lake transparency influences tolerance of zooplankton to UV-B and diel migration patterns. Leech and Williamson (2000) developed a conceptual model relating zooplankton body size, lake transparency, and the presence of fish predators to UVR tolerance (Fig. 7.12). The model predicts that body size will be inversely related to tolerance in high UVR lakes with fish predators. Large zooplankton in lakes with fish predators will spend most of the daylight hours in deeper water to avoid predation, thus reducing UVR exposure and the development of tolerance. In contrast, small zooplankton will occupy the upper surface waters in these lakes where they are exposed to intense UVR, thus increasing tolerance. In clear, fishless lakes, the model predicts that zooplankton should be relatively tolerant of UVR and that body size is unimportant. Finally, because of the limited exposure to UVR, zooplankton inhabiting low UVR lakes should show little tolerance. In a series of short-term field experiments to test these predictions, Leech and Williamson (2000) reported that taxonomic variation was more important than body size or lake transparency for predicting UVR tolerance. They speculated that results may change during longer term exposure and that UVR may interact with other stressors to influence zooplankton community structure. Potential interactions between UVR and other stressors will be discussed below.

Some aquatic organisms may avoid exposure to UVR by migrating to deeper water or moving to shaded habitats during periods of intense solar radiation. These behavioral responses are greatly limited in sessile organisms or in species that spend significant amounts of time in shallow water. For example, filter-feeding blackfly larvae are often found attached to the substrate in clear, shallow streams and lake outlets. Donahue and Schindler (1998) observed significant emigration when organisms were exposed to UVR in experimental streams. Some grazing organisms, such as mayflies, chironomids, and caddisflies, are obligate inhabitants of the upper surface of cobble substrate and likely subjected to intense UVR. Kiffney, Little and Clements (1997) measured the drift response of benthic communities to UVR and observed greatest effects on grazing organisms associated with the substrate surface.

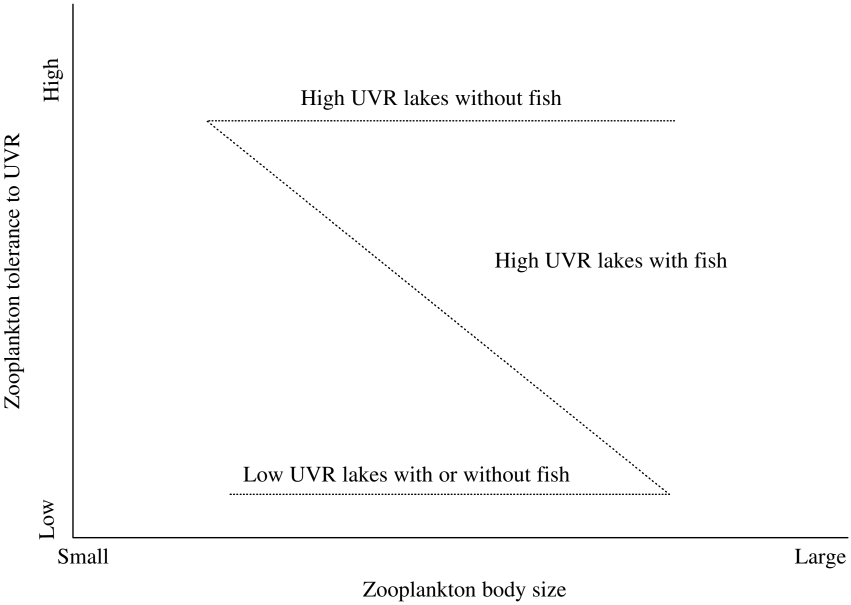

Fig. 7.12. Conceptual model relating zooplankton body size, lake transparency, and the presence of fish predators to UVR tolerance. In high UVR lakes with fish predators, UVR tolerance will be inversely relate to body size. To avoid predation, small zooplankton will generally occupy the lake surface where they are exposed to higher levels of UVR and are expected to develop enhanced tolerance. In contrast, larger zooplankton that occupy deeper sections of the lake receive less natural UVR and are expected to show little tolerance. There is no relationship between body size and tolerance in high UVR lakes without fish because zooplankton of all sizes can migrate freely between the surface and deeper water. These organisms are expected to show greater tolerance than individuals from low UVR lakes because of their greater natural exposure. (Modified from Figure 2 in Leech and Williamson 2000)

7.3.5.4 Interactions with Other Stressors

In addition to the direct effects of UVR on aquatic communities, synergistic interactions between UVR and other anthropogenic stressors may enhance effects and complicate our ability to predict changes observed in the field (Blaustein *et al*. 1995). The increased toxicity of polycyclic aromatic hydrocarbons (PAHs) under UV-B exposure is well documented (Oris and Giesy 1986). Not only are organisms more sensitive to certain PAHs when exposed to UV light, but this increased toxicity persists following exposure (Ankley *et al*. 1994) and may be transferred maternally (Hall and Oris 1991). Unfortunately, because most of the research on interactions between UV-B and PAHs has been conducted in the laboratory, our understanding of community-level phototoxic effects is limited. Long, Saylor and Soule (1995) reported a synergistic interaction between pH and UV-B in amphibians. Mortality of *Rana pipens* was unaffected by low pH or high UV-B exposure; however, significantly greater mortality was observed when organisms were exposed to both stressors. Although the mechanism responsible for this synergistic interaction was not specified, the results are significant because of concerns over global declines of amphibians (Blaustein and Wake 1990). Finally, UVR may increase the bioavailability of certain contaminants by affecting levels of dissolved organic materials (DOM) and by disrupting ligand–contaminant complexes. It is well established that the quality and quantity of DOM greatly influences bioavailability of many contaminants. Exposure to UVR degrades DOM (De Haan 1993), thus increasing light penetration and contaminant bioavailability.

7.4 ACID DEPOSITION

Interest in effects of acid deposition has waned somewhat since the 1970s and 1980s when literally thousands of papers were published describing effects on aquatic and terrestrial ecosystems. Part of the explanation is that modest reductions in atmospheric emissions of SO_2 and particulates from power plants and smelters have significantly improved local conditions. In addition, there are greater concerns for contemporary global stressors such as CO_2 and UV-B radiation. However, acid deposition has significant negative effects on aquatic and terrestrial communities and remains a global environmental problem (Galloway 1995). More importantly, there is a growing awareness that acidic deposition may interact with other atmospheric stressors to affect communities. These interactions will be described in Section 7.5.

7.4.1 DESCRIPTIVE STUDIES OF ACID DEPOSITION EFFECTS IN AQUATIC COMMUNITIES

Acid deposition from anthropogenic sources is a well-established cause of acidification of lakes and streams. In an extensive survey of aquatic ecosystems in the United States, Baker *et al*. (1991) concluded that atmospheric deposition was responsible for acidification of 75% of 1180 acidic lakes and 47% of 4670 acidic streams examined. The spatial distribution of these atmospheric pollutants is determined by a complex interplay of geographic and climatic factors. In particular, patterns of prevailing winds and proximity to industrialized and urban sources greatly influence concentration and deposition. The effects of acidification on aquatic communities has been studied extensively, especially in the northeastern United States, Canada, and Europe (Somers and Harvey 1984; Rosemond *et al*. 1992; Herrmann *et al*. 1993; Juggins, Flower and Battarbee 1996; Lancaster *et al*. 1996; VanSickel *et al*. 1996; Heard *et al*. 1997). A variety of approaches have been employed, including large-scale biomonitoring, whole ecosystem manipulations, and paleolimnological studies (Box 7.3). The most convincing evidence for a relationship between acidification and community structure has been obtained from long-term, experimental studies (e.g. Schindler's long-term acidification studies in the Experimental Lakes Area described in Chapter 4). However, well designed biomonitoring studies conducted at large spatial scales and/or over relatively long time periods have also contributed to our understanding of the ecological effects of acid deposition on aquatic communities. By taking advantage of established gradients in acid deposition downwind from known sources (e.g. smelters, coal-fired power plants), it is possible to quantify effects of acidification at a large spatial scale. Somers and Harvey (1984) described the fish communities from 50 lakes located at varying distances (up to 65 km) downwind from a large point source of SO_2 emissions in Ontario, Canada. Species richness was significantly correlated with distance from the source. Feldman and Connor (1992) used a replicated 'natural experiment' to quantify the relationship between pH and benthic community structure in Shenandoah National Park (VA). Six sites (three acidic and three circumneutral) were selected from 60 candidate streams based on physical, chemical, and habitat conditions. Differences between acidic and non-acidic streams were generally greatest for mayflies. Because their unique experimental design avoids the problem of pseudoreplication (Hurlbert 1984), Feldman and Connor (1992) suggest that their conclusions are broadly applicable to the larger population of acidified streams in the region. In addition to spatially extensive surveys, long-term monitoring data can be used to support hypothesized relationships between pH and community composition. Hall and Ide (1987) related temporal changes in benthic communities collected from two Canadian streams in 1937 and 1985 to increased acidification.

Box 7.3 The role of paleolimnological studies

Additional support for a causal link between acid deposition and acidification of surface waters has been provided by paleolimnological studies. The preservation of certain groups of organisms in lake sediments provides an historical record of community change and, in some instances, can compensate for the lack of long-term data. By dating the strata in sediment cores, the approximate time period when changes in community composition occurred can be identified and related to an hypothesized environmental change (e.g. increased acid deposition during the industrial revolution). Materials commonly used in paleolimnological studies include pollen grains, chironomid head capsules, and diatoms. Most of the paleolimnological research in lentic ecosystems has focused on diatoms, which are well preserved in lake sediments and known to be excellent indicators of water quality. Changes in abundance of pH-sensitive and pH-tolerant taxa over time can indicate the onset of acidification or recovery after reductions of acidic deposition. Comparisons of temporal changes in community composition across broad spatial scales can help identify factors that influence watershed sensitivity to acidification.

Juggins Flower and Battarbee (1996) analyzed long-term temporal patterns (1850–the present) in diatom communities to develop a model of diatom-inferred pH values for 11 lakes in the United Kingdom. Results showed that all lakes were acidified over the past 150 years, but that the timing of acidification varied among lakes. Hall and Smol (1996) compared present day and pre-industrial diatom communities in 54 southern Ontario lakes. An initial relationship between diatom community composition, lake acidity, and total phosphorus (an indicator of shoreline development) was established by sampling present day diatoms in surface sediments. These data were employed to develop a predictive model for water quality based on diatom communities, which was used to estimate long-term changes in pH and total phosphorus. Hall and Smol (1996) conclude that most acidification has occurred during the post-industrial period, probably as a result of atmospheric deposition. Despite increased shoreline development in the lakes, diatom-inferred phosphorus levels actually declined in some lakes. These researchers speculated that lake or watershed acidification may have reduced loading or increased loss of phosphorus.

Most paleolimnological studies of acidification have been limited to relatively short time periods (<150 years) and have focused on anthropogenic sources of lake acidity. However, it is important to note that natural changes in lake acidity will influence communities and may occur over much longer time periods. By characterizing pollen grains, diatoms, and chemical composition of sediment cores, Ford (1990) presents a 10 000-year history of pH changes in two northeastern US lakes. Results showed that a unique combination of geological features (e.g. thin tills derived from base-poor gneisses and schists) predisposed one of these lakes (Cone Pond, New Hampshire) to become acidic over 6500 years ago. These studies highlight the usefulness of paleolimnological data for complementing biomonitoring results and for placing community assessments within the proper historical context.

Biomonitoring studies conducted at relatively large spatial scales (e.g. multiple watersheds) have reported consistent effects on benthic communities (Rosemond *et al*. 1992; Feldman and Connor 1992). In general, acid-sensitive mayflies and stoneflies are replaced by acid-tolerant dipterans and caddisflies at pH values less than 5.5. Interestingly, this is about the same pH level where researchers conducting whole ecosystem manipulations observe significant effects on community structure (see below). It appears that many aquatic organisms are able to tolerate pH excursions to approximately 5.5, but greater levels of acidification generate all-or-none responses. Herrmann *et al*. (1993) reviewed effects of acidification on streams and discussed mechanisms of toxicity to invertebrates. Benthic macroinvertebrate community responses to acidification are quite similar to those observed in circumneutral streams polluted by heavy metals (Clements *et al*. 2000). These results suggest that similar mechanisms may influence toxic effects of acidification and heavy metals on benthic communities (Courtney and Clements 1998). Alternatively, toxic effects on macroinvertebrates observed in acidified streams may be a result of increased metal leaching rather than direct effects of low pH. This possibility highlights one of the key limitations of biomonitoring studies of acidification. Because acidification and metal leaching often co-occur, quantifying the relative importance of these stressors is difficult.

Shifts in phytoplankton and zooplankton communities in response to low pH are well documented. In particular, the reduced species richness of zooplankton has been proposed as an indicator of lake acidification. However, in a comprehensive review of zooplankton responses to acidification, Brett (1989) noted that despite sensitivity of many species to acidification, relationships between community composition and pH in spatially-extensive surveys are often weak. The most likely explanation for the poor explanatory power of pH is that most surveys have focused exclusively on abiotic factors and ignored species interactions. It is well established that fish predation and other trophic interactions have a powerful influence on zooplankton biomass, diversity, and size structure. Because elimination of fish is a common occurrence in acidified lakes, it is not surprising that relationships between community composition and abiotic factors are often weak (Brett 1989). Not only can predation and competition confound relationships between pH and community composition, but acidification may alter the outcome of species interactions (Locke 1992). Separating the direct toxic effects of acidification from changes in trophic structure will require a better understanding of these interactions.

Predicting effects of acid deposition on aquatic communities is also complicated by the ability of some taxa to acclimate or adapt to low pH. Although reduced species richness and shifts in community composition from acid-sensitive to acid-tolerant species are typical responses in acidic lakes and streams, researchers studying naturally acidic environments have reported different results. Winterbourn and Collier (1987) found no relationship between low pH (pH 3.5–5.5) and benthic community structure in naturally acidic streams in New Zealand. In addition to improving our understanding of toxic mechanisms associated with acidification, insights into the process of acclimation and adaptation to low pH are essential for predicting community responses.

7.4.2 EPISODIC ACIDIFICATION

Assessments of acidification in lotic ecosystems have focused primarily on chronic effects that result from relatively long-term changes in pH. However, acute exposure to the combined effects of low pH and metals occurs in some streams during periods of high discharge (Fig. 7.13). This phenomenon, known as episodic acidification, is a short-term decrease in the acid neutralizing capacity (ANC) of a watershed. Episodic acidification is common in the northeastern US and is generally associated with snowmelt and rainfall events.

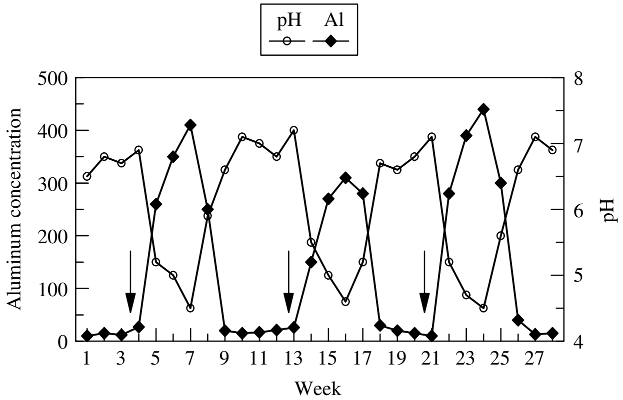

Fig. 7.13. Hypothetical relationship between aluminum concentration and pH during three periods of episodic acidification (indicated by arrows). Decreases in pH as a result of high discharge from rainfall or snowmelt result in rapid increases in Al concentrations. Because of the dynamic relationship between pH, Al, and stream discharge, snapshots of chemical conditions at any point in time are probably inadequate for characterizing ecological integrity

During periods of high discharge, base cations are diluted and materials from upper, more acidic soil layers are flushed into the surrounding watershed. The result is a short-term pulse of solutes, especially H^+ and Al, and a rapid decrease in pH. These episodic events have practical implications for monitoring effects of acidification on streams. Because of the relationship between stream discharge and ANC, assessments of chemical conditions during base flow may provide a relatively poor indication of water quality.

The ecological effects of episodic acidification on aquatic organisms relative to long-term, chronic exposures are not well known. In a series of *in situ* bioassays conducted as part of a large-scale assessment of episodic acidification in the northeastern USA, VanSickle *et al.* (1996) concluded that exposure to Al accounted for most (86–98%) of the observed mortality in native fish species. In a companion study, Baker *et al.* (1996) showed that episodic acidification significantly influenced fish movement, mortality, and community composition. Responses to episodic acidification were similar to those observed in chronically acidified streams, suggesting that short-term acute exposure is an equally important stressor to aquatic organisms.

7.4.3 EXPERIMENTAL STUDIES OF ACID DEPOSITION EFFECTS IN AQUATIC COMMUNITIES

Spatially-extensive surveys of lakes and streams can provide important insight into the relationship between pH and community structure. However, because of the confounding influences of other physical, chemical, and biological factors, these studies only provide a potential explanation for alterations in aquatic communities. Experimental studies have been used extensively to demonstrate effects of acidification on lake and stream communities. In laboratory microcosms, Niederlehner *et al.* (1990) observed that functional measures (e.g. nutrient retention, community respiration) were relatively insensitive to acidification compared with taxonomic measures. The insensitivity of functional measures was also observed by Burton, Stanford and Allan. (1985) who reported that differences in decomposition between treated ($\text{pH} = 4.0$) and control ($\text{pH} = 7.0-7.4$) streams did not occur until 6 months after exposure.

Because acidification of aquatic ecosystems frequently results in increased concentrations of metals, particularly Al, experimental studies are an excellent way to separate the relative importance of these two stressors. Using experimental stream channels, Allard and Moreau (1987) reported that addition of Al (160–520 μg/l) did not increase the effects of acidification ($\text{pH} = 4.0$) on benthic communities. Genter (1995) used a 2×2 factorial design to measure interactive effects of acidification and Al on benthic algal communities in experimental streams. In contrast to results of Allard and Moreau (1987), this study found that aluminum was more toxic than acidification for several taxa. Similar results were reported by Havens and DeCosta (1987) who assessed effects of low pH (5.0) in combination with Al (100–200 μg/l) on zooplankton communities. Results showed little effects of acidification alone; however, the combination of low pH and increased Al significantly impacted most major groups.

Whole-ecosystem manipulations have been conducted in lakes and streams to assess the impacts of acidification on community structure and function. Compared with other chemical and physical stressors such as organochlorines and UV-B radiation, pH is relatively easy to manipulate in the field. Examples of manipulative experiments in lotic systems include studies by Hall and colleagues at Hubbard Brook Experimental Forest (Hall *et al.* 1980, 1985) and by Ormerod *et al.* (1987) in Wales. Although there were no direct effects on brook trout, Hall *et al.* (1980) reported lower diversity and a reduction of food web complexity in an experimentally acidified stream. Ormerod *et al.* (1987) manipulated levels of pH and Al and measured the effects on fish and invertebrate survival and benthic invertebrate drift. Although there were few differences in macroinvertebrate survival between acid and Al treatments, drift of the dominant mayfly (*Baetis rhodani*) increased dramatically during exposure to Al, resulting in reduced density in treated sections.

Details of whole-lake acidification experiments conducted by Schindler and colleagues (Schindler *et al.* 1985; Schindler 1987, 1988) at the Experimental Lakes Area were described in Chapter 4. Biomonitoring and modeling studies conducted by Schindler and colleagues corroborated these experimental findings and showed that significant changes in community composition of phytoplankton, zooplankton, and fish occurred at pH values less than 6.0. Greater levels of acidification (pH approximately 5.0) caused species-specific responses ranging from acute toxicity of H^+ to indirect effects on food chains. Alterations in community composition were generally more sensitive indicators than functional endpoints (e.g. primary production, decomposition, nutrient cycling) (Schindler 1987). In particular, changes in abundance of small, rapidly-reproducing species were the earliest indicators of stress. Although it is likely that these changes in community composition will alter ecosystem processes, functional endpoints alone appear to be inadequate for detecting early signs of acidification stress.

7.4.4 RECOVERY OF AQUATIC ECOSYSTEMS FROM ACIDIFICATION

Reduced emissions of SO_2 and particulates as a result of federal regulations is expected to have a positive influence on physical, chemical, and biological characteristics in aquatic ecosystems. However, our understanding of recovery of lakes and streams from the deleterious effects of acidification is relatively poor. Changes in aquatic communities over time following the removal of a stressor should reflect conditions expected in naturally recovering systems. However, the rate of recovery from acidic deposition will also be influenced by local climate and geology of the watershed. More importantly, studies of recovery from experimental acidification may not adequately predict recovery from atmospheric deposition. Experimental manipulation of pH in lakes and streams generally involves direct acidification of the waterbody, with no treatment of the surrounding watershed. It is likely that recovery rates will be much slower in systems subjected to atmospheric deposition due to loss of buffering capacity from the watershed (Likens, Driscoll and Buso 1996).

A comprehensive assessment of recovery of lentic systems was conducted near Sudbury, Ontario where local emissions of SO_2 and particulates from smelters have been reduced by approximately 90% since the 1970s. Mallory *et al.* (1998) reported chemical characteristics from a 12-year survey of 161 lakes in the region. Most lakes showed significant signs of recovery between 1983 and 1995 due to reductions in sulfur inputs. Physicochemical changes included increased pH and ANC and decreased base cations, metals, and SO_4. However, long-term temporal patterns in recovery were greatly influenced by annual precipitation and lake type. Recovery was greatest during drought years, but conditions deteriorated during wet years, especially in glacial headwaters and lakes located on highly sensitive bedrock.

Despite improvements in water quality as a result of local reductions in atmospheric emissions, acid deposition still affects many aquatic ecosystems. In addition, after several decades of acid deposition many watersheds have lost their natural buffering capacity and are expected to recover only over geological time scales (Likens, Driscoll and Buso 1996). Experimental treatment of streams with lime has been proposed to ameliorate effects of acidic deposition in systems

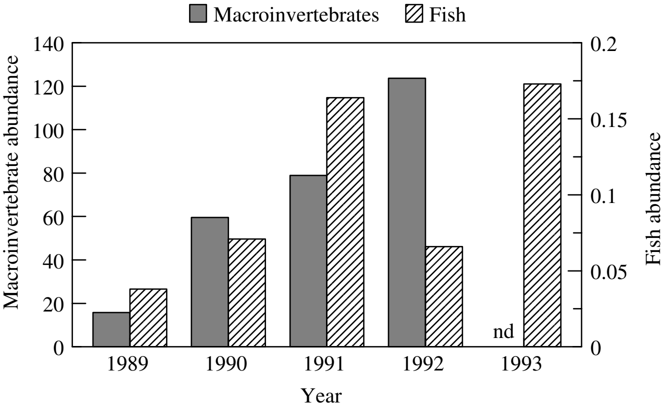

Fig. 7.14. Improvements in macroinvertebrate density and fish abundance (number per m^2) in an acidified stream (Dogway Fork, West Virginia, USA) following treatment with limestone. (Macroinvertebrate data from Table 4 in Clayton and Menendez, 1996. Fish data from Table 5 in Menendez, Clayton and Zurbuch 1996). nd = no data

not expected to recover naturally. Lime treatments in Dogway Fork, a second order stream in West Virginia, significantly increased pH and ANC and reduced Al concentrations (Clayton and Menendez 1996; Menendez, Clayton and Zurbuch 1996). Pre-treatment pH values were generally less than 5.0, whereas a pH of greater than 6.0 was maintained following lime treatments. These improvements in water quality resulted in rapid recovery of fish and macroinvertebrate communities over a 4-year period (Fig. 7.14). Similar results were reported by Simmons, Cieslewicz and Zajicek (1996) in which brook trout density increased significantly following liming treatment of a Massachusetts stream degraded by acid precipitation.

7.4.5 EFFECTS OF ACID DEPOSITION ON FOREST COMMUNITIES

> *Discussion of current forest declines and the possible role of acidic deposition in these declines has been characterized by considerable unsupported claims and speculation in the popular press and even semiscientific publications.* (Pitelka and Raynal 1989)

Few examples of the effects of acidic deposition have received as much attention as the observed correlation between acidification and forest decline. Massive declines in forest health have been reported in Europe and North America over the past several decades, and research efforts initiated in the 1980s to understand the role of acidic deposition have been unprecedented (Pitelka and Raynal 1989). Although forest decline occurs as a result of numerous natural and anthropogenic factors, the simultaneous loss of several acid-sensitive species across broad geographical regions suggests a global cause. In particular, populations of Norway

Spruce (*Picea abies*) in the Bavarian Alps and red spruce (*Picea rubens*) in eastern North America and Canada have been significantly impacted. Ollinger *et al.* (1993) measured broad spatial patterns of major ions associated with precipitation across the northeastern USA. Highly significant increases in SO_4^{2-}, NO_3, and H^+ from east to west were attributed to industrial activities. These authors noted that broad spatial patterns of these atmospheric pollutants were closely correlated with declines in forest health.

The proposed mechanism most likely responsible for the increase in tree mortality is nutrient deficiency resulting from nutrient leaching from soils. The loss of nutrients from forest soils is a typical response to acidification, and a variety of physical, chemical, and biological processes influence leaching. While most research has focused on the role of soil biota (bacteria, fungi, nematodes, microarthropods), the relative importance of different components within the soil community is poorly understood. In a series of microcosm experiments, Heneghan and Bolger (1996) measured various functional attributes of microarthropod assemblages (primarily Acari and Collembola) isolated from soil samples that were exposed to constituents of acid rain (e.g. nitric acid, sulfuric acid, ammonium nitrate). Significant differences in abundance, biomass and trophic composition of microarthropod communities were observed among treatments. More importantly, loss of nutrients, exchangeable cations, and CO_2 production in soils were dependent on microarthropod community composition. These results show that abundance, biomass, and trophic composition of microarthropod communities, independent of soil microbes, play a major role in decomposition and nutrient cycling in forest soils.

Acid deposition is a strong selective force in forest communities and has likely resulted in increased resistance of some species. However, as with other classes of contaminants that we have considered, resistance to a stressor is likely to have some physiological or ecological cost. For example, we expect that resistant populations or species may be at a competitive disadvantage in relatively undisturbed habitats. In situations where pollutant exposure is episodic, there may be a temporal component to patterns of resistance and sensitivity. Taylor, Johnson and Anderson (1994) present a theoretical model showing the relationship between selection coefficients and allocation of carbon resources for growth, maintenance and defense in polluted and pristine environments (Fig. 7.15). In polluted environments, resistant genotypes have a competitive advantage over sensitive genotypes and can allocate greater carbon resources for growth, maintenance, and defense. However, because of the predicted cost of tolerance, these resistant genotypes have a competitive disadvantage in unpolluted environments.

Some researchers are skeptical of the relationship between acidic deposition and forest health. Pitelka and Raynal (1989) argue that because forest decline occurs for numerous reasons, quantifying the relative influence of acidification is not possible without long-term investigations. Despite the difficulties in isolating specific causes of decline, there is strong evidence that the combined effects of

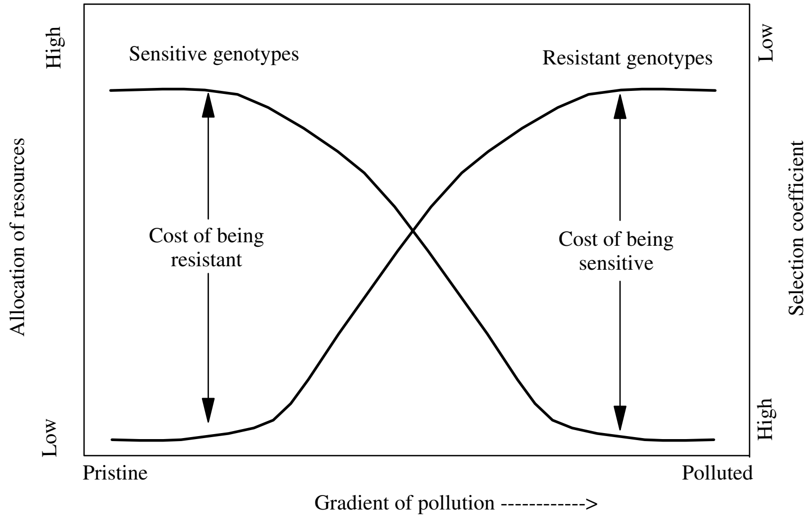

Fig. 7.15. The hypothesized influence of air pollution on allocation of carbon resources and selection coefficients in trees. The figure characterizes the trade-offs between tolerance to stress and allocation of resources along a pollution gradient. In pristine environments, sensitive genotypes have a selective advantage because they can allocate more resources to growth, maintenance, and defense. In contrast, resistant genotypes have an advantage over sensitive genotypes in polluted environments. The differences in performance of these genotypes in pristine and polluted environments is defined as the cost of resistance or the cost of sensitivity. (Modified from Figure 6 in Taylor, Johnson and Anderson 1994. Reproduced by permission of the Ecological Society of America)

atmospheric stressors impact forest communities. In a comprehensive review of air pollution effects on forests, Taylor, Johnson and Anderson (1994) conclude that current levels of atmospheric pollutants are having negative effects on forest ecosystems worldwide. The consequences of changes in community composition on long-term health of forests and the animal communities they support are a significant cause for concern.

7.4.6 INDIRECT EFFECTS OF ACIDIFICATION ON TERRESTRIAL WILDLIFE

Because most terrestrial research on acid deposition has focused on forest communities, our understanding of responses of terrestrial wildlife, particularly birds and mammals, is somewhat limited. Although acidification is assumed to have relatively little direct effect on terrestrial wildlife (Schreiber and Newman 1988), indirect effects due to loss of habitat and prey resources have been reported. Simplification of forest canopy resulting from acidic deposition will reduce habitat complexity and is likely to impact bird communities and other wildlife species.

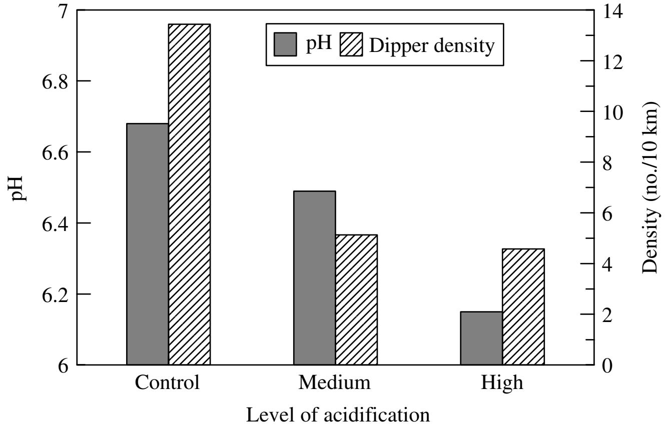

Fig. 7.16. The relationship between pH and abundance of dippers (*Cinclus cinclus*), an obligate riverine predator, in Scotland. Data collected from 27 sites were placed into three categories based on the frequency that pH exceeded a critical threshold. Because dippers are dependent on aquatic prey, standardized counts of dipper abundance may be used to assess the chemical and biological status of streams. (Data from Table 3 in Logie *et al.* 1996)

Indirect effects of acid deposition on a variety of species that consume fish and aquatic invertebrates have been observed (Schreiber and Newman 1988). Reduced abundance of feral mink (*Mustela vison*) populations in Norway has been attributed to the decline of fish in acidified aquatic ecosystems (Bevanger and Albu 1986). The dominant prey species of dippers (*Cinclus cinclus*) in Scottish streams include mayflies, caddisflies, and stoneflies, organisms know to be sensitive to acidification. Because of the dependence of dippers on macroinvertebrates, reductions in prey density due to acidification are likely to impact these bird populations. Buckton *et al.* (1998) reported that dippers were generally absent from acidified streams in Wales due to reduced density of macroinvertebrates. They also note that despite modest improvements in water quality between 1984 and 1995, dipper populations and macroinvertebrates showed no indication of recovery. In a related study, Logie *et al.* (1996) developed a regression model based on census data of dipper abundance to assess the degree of acidification in streams (Fig. 7.16). Results showed that dippers were generally absent or less abundant in watersheds with pH less than 6.5.

7.5 INTERACTIONS AMONG GLOBAL ATMOSPHERIC STRESSORS

Increased levels of CO_2, ozone depletion, and atmospheric deposition of H^+, SO_2 and NO_x occur simultaneously across large spatiotemporal scales. Thus, it is difficult to study the effects of these global atmospheric stressors in isolation or to separate their effects from other disturbances such as contaminants, exotic species, and land use changes. Potential interactions between atmospheric and local stressors will complicate our ability to predict effects of climate change, UV-B, and acidification on communities. Rae and Vincent (1998) report that differential sensitivity among microbial organisms to increased temperature resulted in more complex community responses to UV radiation. In their review of ecosystem responses to global change, Field *et al.* (1992) developed a conceptual framework for interpreting effects of global stressors, separately and in combination, across a variety of terrestrial ecosystems. Their model relates changes in resource availability and utilization to impacts on community composition and ecosystem function. They note the importance of including assessments of land use changes when interpreting responses to global anthropogenic stressors. The most obvious interaction between global climate change and landscape alteration is the rapid rate of deforestation occurring in tropical ecosystems. Because tropical forests are a major carbon sink, deforestation will likely influence global carbon cycles and atmospheric CO_2 levels. Complex interactions between global warming, acidification, and UV-B will also influence microbial production and decomposition. In terrestrial ecosystems, warmer soil temperatures will increase the rate of microbial mineralization and result in greater release of CO_2. However, these increases may be offset in systems subjected to acidification because of the negative effects of low pH on decomposition. Similar interactions among global atmospheric stressors are likely to occur in marine ecosystems. For example, the oceans, also considered a major carbon sink, may be responsible for buffering the planet from increased global temperatures due to anthropogenic emissions of CO_2. The deleterious effects of UV-B radiation on phytoplankton and net primary production in marine ecosystems could therefore influence carbon storage.

Increased levels of atmospheric CO_2 and associated climate change could influence responses of plant communities to air pollutants, but predicting the direction of these responses is difficult. Increased temperature is likely to increase bioavailability and uptake of many pollutants. Taylor, Johnson and Anderson (1994) suggest that effects of atmospheric pollutants on plants will be reduced in a CO_2-enriched world because greater availability of carbon will provide more resources for growth, maintenance, and defense. In addition, increased levels of CO_2 will reduce stomatal transfer and subsequent uptake of airborne toxicants. In contrast, elevated levels of CO_2 may result in greater surface area of leaves, thus providing a larger surface for deposition of pollutants (Bazzaz 1990). Similar complex interactions between climate change and contaminant exposure are likely to occur in aquatic ecosystems. Warmer water temperatures increase uptake rates and bioavailability of many chemicals in lakes and streams. In addition, reduced precipitation and changes in hydrologic characteristics could influence chemical concentrations. For example, decreased precipitation and discharge in northwestern Ontario lakes resulted in dramatically lower renewal rates and increases in concentrations of many chemical solutes (Schindler *et al*. 1990). We expect that similar changes in hydrologic characteristics of other lakes and streams could affect concentrations of contaminants.

Interactions among global atmospheric stressors may indirectly affect responses of aquatic communities to chemical stressors. Because of the well-established influence of dissolved organic material (DOM) on contaminant bioavailability and toxicity in aquatic ecosystems, alterations of DOM could increase or decrease exposure to other stressors. Figure 7.17 shows a conceptual model that describes the predicted influence of acidification, UV radiation, and climate change on the quality (contaminant binding affinity) and quantity of DOM. The model could apply to any class of contaminants where bioavailability and toxicity are influenced by DOM. Acidification and UV-B radiation both decrease the quality and quantity of DOM in aquatic ecosystems (De Haan 1993; Morris and Hargreaves 1997; Williamson *et al*. 1999). Because DOM also reduces light penetration, lower levels will result in greater exposure to UV-B and possibly greater photodegradation of DOM. The direct effects of climate change on DOM will likely be complex and influenced by alterations in riparian vegetation, hydrologic characteristics, and biogeochemical cycles. Studies conducted in subarctic and Canadian shield lakes showed that declines in DOM resulting from climate change increased exposure to UVR (Schindler *et al*. 1996; Pienitz and Vincent 2000). In addition to the direct effects of reduced DOM on aquatic communities,

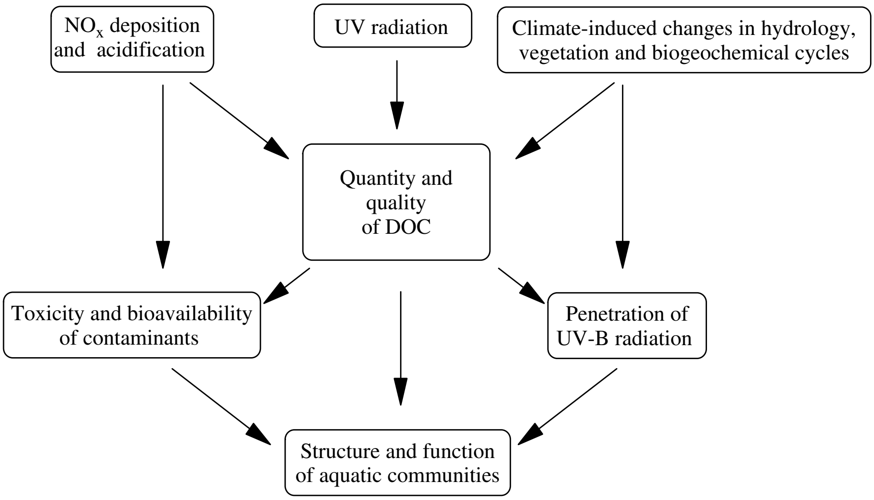

Fig. 7.17. Conceptual model showing the hypothesized influence of climate change, UV radiation, and acidification on aquatic ecosystems. Each of these stressors will directly affect quantity and quality of dissolved organic carbon (DOC), which influences toxicity and bioavailability of contaminants and determines penetration of UV-B radiation

we expect that contaminant bioavailability will be increased in systems with lower DOM. This example illustrates the need to consider not only direct effects of global atmospheric stressors on communities but also their interactions with and influences on other anthropogenic disturbances. Developing a mechanistic understanding of these interactions will be a major research topic over the next several decades.

REFERENCES

Allard M and Moreau G (1987). Effects of experimental acidification on a lotic macroinvertebrate community. *Hydrobiologia* **144**: 37–49.

Allen AS, Andrews JA, Finzi AC, Matamala R, Richter DD and Schlesinger WH (2000). Effects of free-air CO_2 enrichment (FACE) on belowground processes in a *Pinus taeda* forest. *Ecol Appl* **10**: 437–448.

Ankley GT, Collyard SA, Monson PD and Kosian PA (1994). Influence of ultraviolet light on the toxicity of sediments contaminated with polycyclic aromatic hydrocarbons. *Environ Toxicol Chem* **13**: 1791–1796.

Baker JP, VanSickle J, Gagen CJ, DeWalle DR, Sharpe WE, Carline RF, Baldigo BP, Murdoch PS, Bath DW, Kretser WA, Simonin HA and Wigington PJ (1996). Episodic acidification of small streams in the northeastern United States: effects on fish populations. *Ecol Appl* **6**: 422–437.

Baker LA, Herlihy AT, Kaufmann PR and Eilers JM (1991). Acidic lakes and streams in the United States: the role of acidic deposition. *Science* **252**: 1151–1154.

Barnett TP, Pierce DW and Schnur E (2001). Detection of anthropogenic climate change in the world's oceans. *Science* **292**: 270–274.

Barry JP, Baxter CH, Sagarin RD and Gilman SE (1995). Climate-related long-term faunal changes in a California rocky intertidal community. *Science* **267**: 672–675.

Bazzaz FA (1990). The response of natural ecosystems to the rising global CO2 levels. *Ann Rev Ecol Syst* **21**: 167–196.

Bevanger K and Albu O (1986). Decrease in a Norwegian feral mink (*Mustels vison*) population – a response to acid precipitation? *Biol Cons* **38**: 75–78.

Blaustein AR and Wake DB (1990). Declining amphibian populations: a global phenomenon? *Trends Ecol Evol* **5**: 203–204.

Blaustein AR, Edmond B, Kiesecker JM, Beatty JJ and Hokit D G (1995). Ambient ultraviolet radiation causes mortality in salamander eggs. *Ecol Appl* **5**: 740–743.

Boden TA, Kaiser DP, Sepanski RJ and Stoss FW (1994). *Trends '93: A Compendium of Data on Global Change. ORNL/CDIAC65.* Carbon Dioxide Information Analysis Center. Oak Ridge National Laboratory, Oak Ridge, TN.

Boggs CL and Murphy DD (1997). Community composition in mountain ecosystems: climatic determinants of montane butterfly distributions. *Glob Ecol Biogeo Lett* **6**: 39–48.

Bothwell ML, Sherbot DMJ and Pollock CM (1994). Ecosystem response to solar ultraviolet-B radiation: influence of trophic level interactions. *Science* **265**: 97–100.

Bousquet P, Peylin P, Ciais P, Le Quere C, Friedlingstein P and Tans PP (2000). Regional changes in carbon dioxide fluxes of land and oceans since 1980. *Science* **290**: 1342–1346.

Brett MT (1989). Zooplankton communities and acidification processes (a review). *Water Air Soil Pollut* **44**: 387–414.

Buckton ST, Brewin PA, Lewis A, Stevens P and Ormerod SJ (1998). The distribution of dippers, *Cinclus cinclus* (L.), in the acid-sensitive region of Wales, 1984–95. *Freshw Biol* **39**: 387–396.

Burton TM, Stanford RM and Allan JW (1985). Acidification effects on stream biota and organic matter processing. *Can J Fish Aquat Sci* **42**: 669–675.

Caldwell MM, Robberecht R and Billings WD (1980). A steep latitudinal gradient of solar ultraviolet-B radiation in the arctic–alpine life zone. *Ecology* **61**: 600–611.

Caldwell MM, Teramura AH, Tevini M, Bornman JF, Bjorn LO and Kulandaivelu G (1995). Effects of increased solar ultraviolet radiation on terrestrial plants. *Ambio* **14**: 166–173.

Carpenter SR, Fisher SG, Grimm NB and Kitchell JF (1992). Global change and freshwater ecosystems. *Ann Rev Ecol Syst* **23**: 119–139.

Clark ME, Rose KA, Levine DA and Hargrove WW (2001). Predicting climate change effects on Appalachian trout: combining GIS and individual-based modeling. *Ecol Appl.* **11**: 161–178.

Clayton JL and Menendez R (1996). Macroinvertebrate responses to mitigative liming of Dogway Fork, West Virginia. *Restor Ecol* **4**: 234–246.

Clements WH, Carlisle DM, Lazorchak JM and Johnson PC (2000). Heavy metals structure benthic communities in Colorado mountain streams. *Ecol Appl* **10**: 626–638.

Cloud PE (1968). Atmospheric and hydrospheric evolution of primitive earth. *Science* **160**: 729–736.

Courtney LA and WH Clements (1998). Effects of acidic pH on benthic macroinvertebrate communities in stream microcosms. *Hydrobiologia* **379**: 135–145.

Crowley TJ and Berner RA (2001). CO_2 and climate change. *Science* **292**: 870–872.

Davis MB and Shaw RG (2001). Range shifts and adaptive responses to quaternary climate change. *Science* **292**: 673–679.

De Haan H (1993). Solar UV-light penetration and photodegradation of humic substances in peaty lake water. *Limnol Oceangr* **38**: 1072–1076.

DeLucia EH, Hamilton JG, Naidu SL, Thomas RB, Andrews JA, Finzi A, Levine M, Matamala R, Mohan JE, Hendrey GR and Schlesinger WH (1999). Net primary production of a forest ecosystem with experimental CO_2 enrichment. *Science* **284**: 1177–1179.

DeStato III J and Rahel FJ (1994). Influence of water temperature on interactions between juvenile Colorado River cutthroat trout and brook trout in a laboratory stream. *Trans Am Fish Soc* **123**: 289–297.

Dixon RK, Brown S, Houghton RA, Solomon AM, Trexler MC and Wisniewski J (1994). Carbon pools and flux of global forest ecosystems. *Science* **263**: 185–190.

Donahue WF and Schindler DW (1998). Diel emigration and colonization responses of blackfly larvae (Diptera: Simuliidae) to ultraviolet radiation. *Fresh Biol* **40**: 357–365.

Duarte CM and Agusti S (1998). The CO_2 balance of unproductive aquatic ecosystems. *Science* **281**: 234–236.

Fabacher DL and Little EE (1995). Skin component may protect fishes from ultraviolet-B radiation. *Environ Sci Poll Res* **2**: 30–32.

Falkowski P, Scholes RJ, Boyle E, Canadell J, Canfield D, Elser J, Gruber N, Hibbard K, Hogberg P, Linder S, Mackenzie FT, Moore III B, Pedersen T, Rosenthal Y, Seitzinger S, Smetacek V and Steffan W (2000). The global carbon cycle: a test of our knowledge of earth as a system. *Science* **290**: 291–296.

Feldman RS and Connor EF (1992). The relationship between pH and community structure of invertebrates in streams of the Shenandoah National Park, Virginia, USA. *Freshw Biol* **27**: 261–276.

Field CB, Behrenfeld MJ, Randerson JT and Falkowski P (1998). Primary production of the biosphere: integrating terrestrial and oceanic components. *Science* **281**: 237–240.

Field CB, Chapin III FS, Matson PA and Mooney HA (1992). Responses of terrestrial ecosystems to the changing atmosphere: a resource-based approach. *Ann Rev Ecol Syst* **23**: 201–235.

Finney BP, Gregory-Eaves I, Sweetman J, Douglas MSV and Smol JP (2000). Impacts of climatic change and fishing on Pacific salmon abundance over the past 300 years. *Science* **290**: 795–799.

Fisher AG (1965). Fossils, early life, and atmospheric history. *Proc Nat Acad Sci USA* **53**: 1205–1215.

Ford MS (1990). A 10 000-year history of natural ecosystem acidification. *Ecol Monogr* **60**: 57–89.

Galloway JN (1995). Acid deposition: perspectives in time and space. *Water Air Soil Pollut* **85**: 15–24.

Garcia-Pichel F and Bebout BM (1996). Penetration of ultraviolet radiation into shallow water sediments: high exposure for photosynthetic communities. *Mar Eco Prog Ser* **131**: 257–262.

Gehrke C (1999). Impacts of enhanced ultraviolet-B radiation on mosses in a subarctic heath ecosystem. *Ecology* **80**: 1844–1851.

Genter RB (1995). Benthic algal populations respond to aluminum, acid, and aluminum–acid mixtures in artificial streams. *Hydrobiologia* **306**: 7–19.

Gleason DF and Wellington GM (1995). Variation in UVB sensitivity of planula larvae of the coral *Agaricia agaricites* along a depth gradient. *Mar Biol* **123**: 693–703.

Grime JP, Brown VK, Thompson K, Masters GJ, Hillier SH, Clarke IP, Askew AP, Corker D and Kielty JP (2000). The response of two contrasting limestone grasslands to simulated climate change. *Science* **289**: 762–765.

Hall AT and Oris JT (1991). Anthracene reduces reproductive potential and is maternally transferred during long-term exposure in fathead minnows. *Aquat Toxicol* **19**: 249–264.

Hall RJ and Ide FP (1987). Evidence of acidification effects on stream insect communities in central Ontario between 1937 and 1985. *Can J Fish Aquat Sci* **44**: 1652–1657.

Hall RJ and Smol JP (1996). Paleolimnological assessment of long-term water-quality changes in south-central Ontario lakes affected by cottage development and acidification. *Can J Fish Aquat Sci* **53**: 1–17.

Hall RJ, Driscoll CT, Likens GE and Pratt JM (1985). Physical, chemical, and biological consequences of episodic aluminum additions to a stream. *Limnol Oceanogr* **30**: 212–220.

Hall RJ, Likens GE, Fiancé SB and Hendrey GR (1980). Experimental acidification of a stream in the Hubbard Brook Experimental Forest, New Hampshire. *Ecology* **61**: 976–989.

Harrison S (1993). Species diversity, spatial scale, and global change. In *Biotic Interactions and Global Change*, ed. by Kareiva PM, Kingsolver JG and Huey RB, pp. 388–401. Sinauer Associates, Inc., Sunderland, MA.

Harte J and Shaw R (1995). Shifting dominance within a montane vegetation community: results of a climate-warming experiment. *Science* **267**: 876–880.

Harvell CD, Kim K, Burkholder JM, Colwell, R, Epstein PR, Grimes DJ, Hofmann EE, Lipp EK, Osterhaus ADME, Overstreet RM, Porter JW, Smith GW and Vasta GR (1999). Emerging marine diseases – climate links and anthropogenic factors. *Science* **285**: 1505–1510.

Hauer FR, Baron JS, Campbell DH, Fausch KD, Hostetler SW, Leavesley GH, Leavitt PR, McKnight DM and Stanford JA (1997). Assessment of climate change and freshwater ecosystems of the Rocky Mountains, USA and Canada. *Hydrol Proc* **11**: 903–924.

Havens KE and DeCosta J (1987). The role of aluminum contamination in determining phytoplankton and zooplankton responses to acidification. *Water, Air, Soil Pollut.* **33**: 277–293.

Heard RM, Sharpe WE, Carline RF and Kimmel WG (1997). Episodic acidification and changes in fish diversity in Pennsylvania headwater streams. *Trans Am Fish Soc* **126**: 977–984.

Heneghan L and Bolger T (1996). Effects of components of 'acid rain' on the contribution of soil microarthropods to ecosystem function. *J Appl Ecol* **33**: 1329–1344.

Herrmann J, Degerman E, Gerhardt A, Johansson C, Lingdell P and Muniz IP (1993). Acid-stress effects on stream biology. *Ambio* **22**: 298–307.

Hill WR, Dimick SM, McNamara AE and Branson CA (1997). No effects of ambient UV radiation detected in periphyton and grazers. *Limnol Oceanogr* **42**: 769–774.

Hogg ID and Williams DD (1996). Response of stream invertebrates to a global-warming thermal regime: an ecosystem-level manipulation. *Ecology* **77**: 395–407.

Holbrook SJ, Schmitt RJ and Stephens Jr JS (1997). Changes in an assemblage of temperate reef fishes associated with a climate shift. *Ecol Appl* **7**: 1299–1310.

Hurlbert SH (1984). Pseudoreplication and the design of ecological field experiments. *Ecol Monogr* **54**: 187–211.

Jones TH, Thompson LJ, Lawton JH, Bezemer TM, Bardgett RD, Blackburn TM, Bruce KD, Cannon PF, Hall GS, Hartley SE, Howson G, Jones CG, Kampichler C, Kandeler E and Ritchie DA (1998). Impacts of rising atmospheric carbon dioxide on model terrestrial ecosystems. *Science* **280**: 441–442.

Juggins S, Flower RJ and Battarbee RW (1996). Paleolimnological evidence for recent chemical and biological changes in UK acid waters monitoring network sites. *Freshw Biol* **36**: 203–219.

Kareiva PM, Kingsolver JG and Huey RB (1993). *Biotic Interactions and Global Change*. Sinauer Associates, Inc., Sunderland, MA.

Keeling CD and Whorf TP (1998). *Atmospheric CO_2 Concentrations Mauna Loa Observatory, Hawaii, 1958–1997 (revised August 2000). NDP001*. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge, TN.

Kelly DJ, Clare JJ and Bothwell ML (2001). Attenuation of solar ultraviolet radiation by dissolved organic matter alters benthic colonization patterns in streams. *J N Am Benthol Soc* **20**: 96–108.

Kerr JB and McElroy CT (1993). Evidence for large upward trends of ultraviolet-B radiation linked to ozone depletion. *Science* **262**: 1032–1034.

Kiffney PM, Clements WH and Cady TA (1997). Influence of ultraviolet radiation on the colonization dynamics of a Rocky Mountain stream benthic community. *J N Am Benthol Soc* **16**: 520–530.

Kiffney PM, Little EE and Clements WH (1997). Influence of ultraviolet-B radiation on the drift response of stream invertebrates. *Freshw Biol* **37**: 485–492.

Kingsolver JG, Huey RB and Kareiva PM (1993). An agenda for population and community research on global change. In *Biotic Interactions and Global Change*, ed. by Kareiva PM, Kingsolver JG and Huey RB, pp. 480–486. Sinauer Associates, Inc., Sunderland, MA.

Kinzie RA, Banaszak AT and Lesser MP (1998). Effects of ultraviolet radiation on primary productivity in a high altitude tropical lake. *Hydrobiologia* **385**: 23–32.

Klironomos JN and Allen MF (1995). UV-B-mediated changes on below-ground communities associated with the roots of *Acer saccharum*. *Funct Ecol* **9**: 923–930.

Lancaster J, Real M, Juggins S, Monteith DT, Flower RJ and Beaumont WRC (1996). Monitoring temporal changes in the biology of acid waters. *Freshw Biol* **36**: 179–201.

Larson DL (1994). Potential effects of anthropogenic greenhouse gases on avian habitats and populations in the northern great plains. *Am Midl Nat* **131**: 330–346.

Lassiter RR, Box EI, Wiegert RG, Johnston JM, Bergengren J and Suarez LA (2000). Vulnerability of ecosystems of the mid-Atlantic regions, USA, to climate change. *Environ Toxicol Chem* **19**: 1153–1160.

Laurion I and Vincent WF (1998). Cell size versus taxonomic composition as determinants of UV-sensitivity in natural phytoplankton communities. *Limnol Oceanogr* **43**: 1774–1779.

Leech DM and Williamson CE (2000). Is tolerance to UV radiation in zooplankton related to body size, taxon, or lake transparency? *Ecol Appl* **10**: 1530–1540.

Likens GE, Driscoll CT and Buso DC (1996). Long-term effects of acid rain: response and recovery of a forest ecosystem. *Science* **272**: 244–246.

Locke A (1992). Factors influencing community structure along stress gradients: zooplankton responses to acidification. *Ecology* **73**: 903–906.

Logie JW, Bryant DM, Howell DL and Vickery JA (1996). Biological significance of UK critical load accedence estimates for flowing waters: assessments of dipper *Cinclus cinclus* populations in Scotland. *J Appl Ecol* **33**: 1065–1076.

Long LE, Saylor LS and Soule ME (1995). A ph/UV-B synergism in amphibians. *Conserv Biol* **9**: 1301–1303.

Lubin D and Jensen EH (1995). Effects of clouds and stratospheric ozone depletion on ultraviolet radiation trends. *Nature* **377**: 710–713.

Madronich S (1992). Implications of recent total atmospheric total ozone measurements for biologically active ultraviolet radiation reaching the earth's surface. *Geophys Res Let* **19**: 37–40.

Mallory ML, McNicol DK, Cluis DA and Laberge C (1998). Chemical trends and status of small lakes near Sudbury, Ontario, 1983–1995: evidence of continued chemical recovery. *Can J Fish Aquat Sci* **55**: 63–75.

McDonald KA and Brown JH (1992). Using montane mammals to model extinctions due to global change. *Conserv Biol* **6**: 409–415.

McKenzie R, Connor B and Bodeker G (1999). Increased summertime UV radiation in New Zealand in response to ozone loss. *Science* **285**: 1709–1711.

McKnight DM, Harnish R, Wershaw RL, Baron JS and Schiff S (1997). Chemical characteristics of particulate, colloidal, and dissolved organic material in Loch Vale Watershed, Rocky Mountain National Park. *Biogeochemistry* **36**: 99–124.

Menendez R, Clayton JL and Zurbuch PE (1996). Chemical and fishery responses to mitigative liming of an acidic stream, Dogway Fork, West Virginia. *Rest Ecol* **4**: 220–233.

Morris DP and Hargreaves BR (1997). The role of photochemical degradation of dissolved organic carbon in regulating the UV transparency of three lakes on the Pocono Plateau. *Limnol Oceanogr* **42**: 239–249.

Mostajir B, Demers S, deMora S, Belzile C, Chanut JP, Gosselin M, Roy S, Villegas PZ, Fauchot J, Bouchard J, Bird D, Monfort P and Levasseur M (1999). Experimental test of the effect of ultraviolet-B radiation in a planktonic community. *Limnol Oceanogr* **44**: 586–596.

Niederlehner BR, Pontasch KW, Pratt JR and Cairns Jr J (1990). Field evaluation of predictions of environmental effects from a multispecies-microcosm toxicity test. *Arch Environ Contam Toxicol* **19**: 62–71.

Ollinger SV, Aber JD, Lovett GM, Millham SE, Lathrop RG and Ellis JE (1993). A spatial model of atmospheric deposition for the northeastern US. *Ecol Appl* **3**: 459–472.

Oris JT and Giesy Jr JP (1986). Photoinduced toxicity of anthracene to juvenile bluegill sunfish (*Lepomis macrochirus* Rafinesque): photoperiod effects and predictive hazard evaluation. *Environ Toxicol Chem* **5**: 761–768.

Ormerod SJ, Boole P, McCahon CP, Weatherley NS, Pascoe D and Edwards RW (1987). Short-term experimental acidification of a Welsh stream: comparing the biological effects of hydrogen ions and aluminum. *Freshw Biol* **17**: 341–356.

Overpeck J, Hughen K, Hardy D, Bradley R, Case R, Douglas M, Finney B, Gajewski K, Jacoby G, Jennings A, Lamoureux S, Lasca A, MacDonald G, Moore J, Retelle M, Smith S, Wolfe A and Zielinski G (1997). Arctic environmental change of the last four centuries. *Science* **278**: 1251–1256.

Owensby CE, Coyne PI, Ham JM, Auen LM and Knapp AK (1993). Biomass production in a tallgrass prairie ecosystem exposed to ambient and elevated CO_2. *Ecol Appl* **3**: 644–653.

Pacala SW and Hurtt GC (1993). Terrestial vegetation and climate change: integrating models and experiments. In *Biotic Interactions and Global Change*, ed. by Kareiva PM, Kingsolver JG and Huey RB, pp. 57–74. Sinauer Associates Inc., Sunderland, MA.

Petchey OL, McPhearson PT, Casey TM and Morin PJ (1999). Environmental warming alters food-web structure and ecosystem function. *Nature* **402**: 69–72.

Pienitz R and Vincent WF (2000). Effect of climate change relative to ozone depletion on UV exposure in subarctic lakes. *Nature* **404**: 484–487.

Pitelka LF and Raynal DJ (1989). Forest decline and acidic deposition. *Ecology* **70**: 2–10.

Prentice IC, Sykes MT and Cramer W (1991). The possible dynamic response of northern forests to global warming. *Glob Ecol Biogeogr Lett* **1**: 129–135.

Price MV and Waser NM (2000). Responses of subalpine meadow vegetation to four years of experimental warming. *Ecolog Appl* **10**: 811–823.

Rader RB and Belish TA (1997). Effects of ambient and enhanced UV-B radiation on periphyton in a mountain stream. *J Freshw Ecol* **12**: 615–628.

Rae R and Vincent WF (1998). Effects of temperature and ultraviolet radiation on microbial foodweb structure: potential responses to global change. *Freshw Biol* **40**: 747–758.

Robinson CH, Wookey PA, Lee JA, Callaghan TV and Press MC (1998). Plant community responses to simulated environmental change at a high arctic polar semi-desert. *Ecology* **79**: 856–866.

Roemmich D and McGowan J (1995). Climatic warming and the decline of zooplankton in the California current. *Science* **267**: 1324–1326.

Root TL (1988). Environmental factors associated with avian distributional boundaries. *J Biogeogr* **15**: 489–505.

Root TL (1993). Effects of global climate change on North American birds and their communities. In *Biotic Interactions and Global Change*, ed. by Kareiva PM, Kingsolver JG and Huey RB, pp. 280–292. Sinauer Associates Inc., Sunderland, MA.

Root TL and Schneider SH (1993). Can large-scale climatic models be linked with multiscale ecological studies? *Conserv Biol* **7**: 256–270.

Rosemond AD, Reice SR, Elwood JW and Mulholland PJ (1992). The effects of stream acidity on benthic invertebrate communities in the southeastern United States. *Freshw Biol* **27**: 193–209.

Rusek J (1993). Air-pollution-mediated changes in alpine ecosystems and ecotones. *Ecol Appl* **3**: 409–416.

Sanford E (1999). Regulation of keystone predation by small changes in ocean temperature. *Science* **283**: 2095–2997.

Santas R, Lianou C and Danielidis D (1997). UVB radiation and depth interaction during primary succession of marine diatom assemblages of Greece. *Limnol Oceanogr* **42**: 986–991.

Schindler DW (1987). Detecting ecosystem responses to anthropogenic stress. *Can J Fish Aquat Sci* **44** (Suppl 1): 6–25.

Schindler DW (1988). Effects of acid rain on freshwater ecosystems. *Science* **239**: 149–157.

Schindler DW, Bayley SE, Parker BR, Beaty KG, Cruiksjank DR, Fee EJ, Schindler EU and Stainton MP (1996). The effects of climate warming on the properties of boreal lakes and streams in the Experimental Lakes Area, northwestern Ontario. *Limnol Oceanogr* **41**: 1004–1017.

Schindler DW, Beaty KG, Fee EJ, Cruikshank DR, DeBruyn ER, Findlay DL, Linsey GA, Shearer JA, Stainton MP and Turner MA (1990). Effects of climatic warming on lakes of the Central Boreal Forest. *Science* **250**: 967–970.

Schindler DW, Mills KH, Malley DF, Findlay DL, Shearer JA, Davies IJ, Turner MA, Linsey GA and Cruikshank DR (1985). Long-term ecosystem stress: the effects of years of experimental acidification on a small lake. *Science* **228**: 1395–1401.

Schreiber RK and Newman JR (1988). Acid precipitation effects on forest habitats: implications for wildlife. *Cons Biol* **2**: 249–259.

Shindell DT, Rind D and Lonergan P (1998). Increased polar stratospheric ozone losses and delayed eventual recovery owing to increasing greenhouse gas concentrations. *Nature* **392**: 589–592.

Sillett TS, Holmes RT and Sherry TW (2000). Impacts of a global climate cycle on population dynamics of a migratory songbird. *Science* **288**: 2040–2042.

Simmons KR, Cieslewicz PG and Zajicek K (1996). Limestone treatment of Whetstone Brook, Massachusetts. 2. Changes in the brown trout (*Salmo trutta*) and brook trout (*Salvelinus fontinalis*) fishery. *Rest Ecol* **4**: 273–283.

Smith RC, Prezelin BB, Baker KS, Bidigare RR, Boucher NP, Coley T, Karentz D, MacIntyre S, Matlick HA, Menzies D, Ondrusek M, Wan Z and Waters KJ (1992). Ozone depletion: ultraviolet radiation and phytoplankton biology in Antarctic waters. *Science* **255**: 952–959.

Smith SV and Buddemeier RW (1992). Global change and coral reef ecosystems. *Ann Rev Ecol Syst* **23**: 89–118.

Somers KM and Harvey HH (1984). Alteration of fish communities in lakes stressed by acid deposition and heavy metals near Wawa, Ontario. *Can J Fish Aquat Sci* **41**: 20–29.

Sommaruga R and Garcia-Pichel F (1999). UV-absorbing mycosporine-like compounds in planktonic and benthic organisms from a high-mountain lake. *Arch Fur Hydro* **144**: 255–269.

Starfield AM and Chapin III FS (1996). Model of transient changes in arctic and boreal vegetation in response to climate and land use change. *Ecol Appl* **6**: 842–864.

Stokstad E (2001). Myriad ways to reconstruct past climates. *Science* **292**: 658–359.

Stott PA, Tett SFB, Jones GS, Allen MR, Mitchell JFB and Jenkins GJ (2000). External control of 20th century temperature by natural and anthropogenic forcings. *Science* **290**: 2133–2137.

Taylor Jr GE, Johnson DW and Anderson CP (1994). Air pollution and forest ecosystems: a regional to global perspective. *Ecol Appl* **4**: 662–689.

Thomas DW, Blondel J, Perret P, Lambrechts MM and Speakman JR (2001). Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. *Science* **291**: 2598–2600.

Valpine P and Harte J (2001). Plants responses to experimental warming in a montane meadow. *Ecology* **82**: 637–648.

van de Staaij JWM, Ernst WHO, Hakvoort HWJ and Rozema J (1995a). Ultraviolet-B (280–320 nm) absorbing pigments in the leaves of *Silene vulgaris*: their role in UV-B tolerance. *J Plant Physiol* **147**: 75–80.

van de Staaij JWM, Huijsmans R, Ernst WHO and Rozema J (1995b). The effect of elevated UV-B (280–320 nm) radiation levels on *Silene vulgaris*: a comparison between a highland and a lowland population. *Environ Poll* **90**: 357–362.

VanSickle J, Baker JP, Simonin HA, Baldigo BP, Kretser WA and Sharpe WE (1996). Episodic acidification of small streams in the northeastern United States: fish mortality in field bioassays. *Ecol Appl* **6**: 408–421.

Vincent WF and Roy S (1993). Solar ultraviolet-B radiation and aquatic primary productivity: damage, protection, and recovery. *Environ Rev* **1**: 1–12.

Vinebrooke RD and Leavitt PR (1996). Effects of ultraviolet radiation on periphyton in an alpine lake. *Limnol Oceanogr* **41**: 1035–1040.

Vitousek PM (1994). Beyond global warming: ecology and global change. *Ecology* **75**: 1861–1876.

Williamson CE (1995). What role does UV-B radiation play in freshwater ecosystems? *Limnol Oceanogr* **40**: 386–392.

Williamson CE, Hagreaves BR, Orr PS and Lovera PA (1999). Does UV play a role in changes in predation and zooplankton community structure in acidified lakes? *Limnol Oceanogr* **44**: 774–783.

Williamson GE, Zagarese HE, Schulze PC, Hargreaves BR and Seva J (1994). The impact of short-term exposure to UV-B radiation on zooplankton communities in north temperate lakes. *J Plank Res* **16**: 205–218.

Winterbourn MJ and Collier KJ (1987). Distribution of benthic invertebrates in acid, brown water streams in the South Island of New Zealand. *Hydrobiologia* **155**: 277–286.

Zellmer ID (1995). UV-B-tolerance of alpine and arctic *Daphnia*. *Hydrobiologia* **307**: 153–159.

8 Trophic Structure, Food Webs, and Contaminant Transport

> *The empirical patterns are widespread and abundantly documented, but instead of an agreed explanation there is only a list of possibilities to be explored.* (May 1981)
>
> *......there has been little synthesis of the relative roles of different ecological forces in determining population change and community structure. Rather, there is a collection of idiosyncratic systems, with their associated protagonists, in which opposing views on the importance of particular factors are debated.* (Hunter and Price 1992)

8.1 INTRODUCTION

An understanding of trophic interactions and food web structure is critical to the study of basic ecology and ecotoxicology. Early in the history of ecology, feeding relationships were recognized as a fundamental characteristic that defined communities. Trophic interactions provide the fundamental linkages among species that determine the structure of terrestrial and aquatic communities. For some ecologists, the study of food webs and trophodynamics is the central, unifying theme in ecology (Fretwell 1987). Because energy is a common currency required by all living organisms, the study of bioenergetics of individuals, populations, communities, and ecosystems allows researchers to integrate their findings across several levels of biological organization (Carlisle 2000).

Despite the importance of food webs and trophic interactions in basic ecology, ecotoxicologists have not incorporated significant components of basic food web theory into investigations of contaminant effects. This reluctance is ironic because the concern about food chain transport of contaminants in wildlife populations was at least partially responsible for much of the environmental legislation in the early 1960s. Reports of biomagnification of organochlorine pesticides and the subsequent effects on birds of prey (Carson 1962) eventually resulted in the ban of these chemicals.

One important exception to the general neglect of basic food web theory in ecotoxicology is the application of models to predict contaminant fate. Contaminant transport models used in ecotoxicology are analogous to energy flow models derived from the ecological literature. However, quantifying the movement of contaminants through a community is only one of several potential applications of food web theory. An understanding of the ecological factors that determine energy flow in communities, such as food chain length, interaction strength, and connectedness, are also necessary to quantify contaminant fate and effects. For example, studies have shown that trophic structure and food chain length regulate contaminant concentrations in top predators (Rasmussen *et al*. 1990; Bentzen *et al*. 1996; Wong *et al*. 1997 Stemberger and Chen 1998). It is likely that other ecological processes, either directly or indirectly related to trophic structure, will play a role in determining contaminant transport. Recent refinements in transport models have been primarily limited to quantifying the role of physicochemical characteristics that modify contaminant bioavailability. Further improvement of these models will require that ecotoxicologists develop a better understanding of the ecological factors that influence contaminant fate and transport.

Another potential contribution of basic food web theory to ecotoxicology is the measurement of food web structure and function as indicators of contaminant effects. Although the relationship between trophic structure and natural disturbance has been recognized for many years (Odum 1969, 1985), there have been few attempts to determine how food webs respond to contaminants (Carlisle 2000). There is some evidence that food chains are shorter in systems subjected to frequent disturbance, but the mechanistic explanation for this observation has not been determined. Using food web structure and function as indicators of contaminant effects is appropriate for several reasons. Bioenergetic approaches at the level of individuals and populations have a long history in toxicology. Growth is a common endpoint in many toxicological investigations which integrates numerous physiological characteristics. Energetic cost of contaminant exposure may be interpreted within the context of growth and metabolism. For example, recent studies have combined measurements of metabolism, food consumption, and growth into an individual-based bioenergetic model to assess effects of organochlorines (Beyers, Rice and Clements 1999; Beyers *et al*. 1999). Similar approaches could be used to measure the effects of contaminants on flow of energy through a community. Finally, because energy is a common currency in all biological systems, understanding ecological effects of contaminant exposure on communities may help establish mechanistic linkages to lower (individuals, populations) and higher (ecosystems) levels of biological organization.

8.2 BASIC FOOD WEB ECOLOGY

8.2.1 HISTORICAL PERSPECTIVE OF FOOD WEB ECOLOGY

The strength of trophic interactions and the relationship between energy flow and community structure have been topics of considerable interest to ecologists for many years. Charles Elton's (1927) studies of feeding relationships in a tundra community and his representation of trophic levels as an energy pyramid (Fig. 8.1A) focused the attention of ecologists on the importance of food as a 'burning question in animal society'. Subsequent representations of Elton's

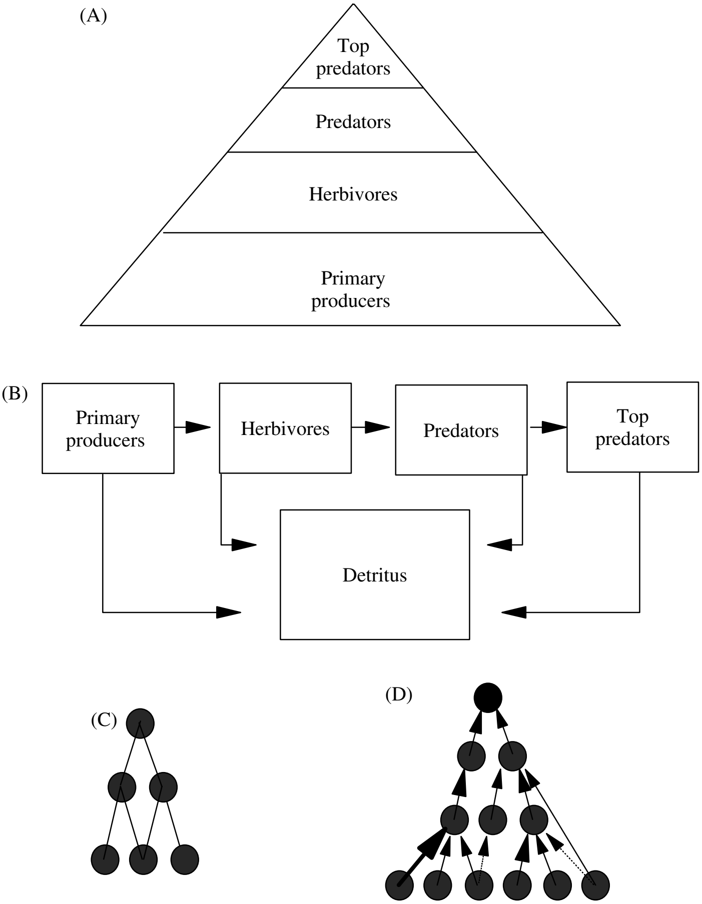

Fig. 8.1. Four different representations of trophic structure and food chains in the ecological literature. (A) Eltonian trophic pyramid showing biomass at each trophic level. (B) Box and arrow diagram showing energy flow through a community. (C) Descriptive food chain showing potential interactions among species. (D) Energetic or interaction food chain showing energy flux or strength of interactions (represented by thickness of the lines) between dominant species in a community

trophic pyramids included biomass and numbers of individuals as the fundamental components.

Ecologists soon recognized that this simple depiction of energy flow treated all species within a trophic level equally and, more importantly, did not account for microbial processes. In addition, there was no attempt to quantify the movement of energy among trophic levels. Raymond Lindeman's (1942) classic paper introduced the 'trophic-dynamic' aspect of natural systems and revolutionized the study of food webs. Based on an extensive analysis of Cedar Bog Lake (MN), this work formalized the concept of energy flow through ecosystems and influenced a generation of systems ecologists. The study of ecology shifted from habitat associations and species lists to a more quantitative analysis of trophic relationships and energy flow. Lindeman also recognized the inherent inefficiency of energy flow in ecological systems, setting the stage for a contentious debate concerning the importance of biotic and abiotic factors that limit the number of trophic levels in communities.

Lindeman's box and arrow diagrams depicting energy flow and cycling of materials through a community were further refined by Eugene P. Odum (1968) (Fig. 8.1B), widely regarded as the father of systems ecology. The emergence of ecosystems ecology in the 1950s also highlighted philosophical differences between holistic and reductionist approaches. While some ecologists felt that understanding complex systems required sophisticated and quantitative analysis of all interacting components, others felt that characteristics of ecosystems transcended those of individual components and could only be investigated by considering emergent properties. These philosophical differences between proponents of holism and reductionism still persist in ecology and ecotoxicology today (Box 1.1, Chapter 1).

8.2.2 DESCRIPTIVE, INTERACTIVE, AND ENERGETIC FOOD WEBS

Food webs depicted in the contemporary ecological literature fall into three general categories: descriptive, interactive, and energetic (Fig. 8.1C, D). Descriptive food webs are probably the most common and are produced by simply characterizing feeding habits of dominant species. Descriptive food webs are analogous to the use of presence–absence data in community monitoring because they provide no information on the relative importance of linkages among species. In contrast, interaction and energetic food webs quantify the importance of linkages among species and energy flow. Interaction food webs are constructed by manipulating the abundance of either predators or prey and measuring responses. Interaction food webs have a long history in experimental ecology, and have been employed to identify keystone species (Paine 1980). The best examples of interaction food webs are from marine rocky intertidal habitats where experimental manipulation is simplified because of the low mobility of species and the essentially two-dimensional nature of the habitat. Energetic-based food webs are constructed by quantifying energy flow between species. This is generally accomplished by characterizing feeding habits and measuring secondary production of dominant species in a community (Benke and Wallace 1997). Either interaction or energetic food webs would be appropriate for assessing contaminant effects; however, it is important to recognize that both approaches are data intensive and require a significant amount of effort to develop.

Because the strength of species interactions are not necessarily related to the amount of energy flow between trophic levels, bioenergetic and interaction approaches can yield different results. For example, relatively little energy flows between kelp and sea urchins in marine ecosystems; however, as described in the following section, removal of sea urchins may have a large impact on kelp populations and associated species. Paine (1980) showed that very different patterns resulted when marine food webs were based on connectedness, energy flow, or interaction strength. Because of potential differences between interaction and energetic food webs, these approaches may have different applications in ecotoxicology. If researchers are interested in modeling the movement of contaminants through a community, an energetic food web may be most appropriate. However, if the purpose of an investigation is to examine the direct and indirect effects of contaminants on community structure, it may also be important to know the strength of species interactions and construct an interaction food web.

The strength of interactions within a food chain may also influence community stability; however, because of the lack of experimental studies and the different approaches employed by theoretical and empirical ecologists to measure interaction strength, the relationship between stability and energy flow is uncertain. de Ruiter, Neutel and Moore (1995) linked material flow descriptions with measures of interaction strength to quantify the influences on stability of terrestrial food webs. Their findings were consistent with previous research that showed relatively small rates of energy flow in a community can have large effects on community stability. Thus, predicting the effects of contaminant-induced alterations in energy flow will not be straightforward because the functional role of a species in a community may not be directly related to its abundance or biomass.

8.2.3 CONTEMPORARY QUESTIONS IN FOOD WEB ECOLOGY

Most contemporary research in food web ecology has focused on two key topics: (1) identifying factors that limit the number of trophic levels; and (2) quantifying the strength of species interactions. One consistent observation in food web research is that most food webs are relatively short, averaging between three and five trophic levels in both aquatic and terrestrial habitats. The length of food chains and the number of trophic levels is assumed to be limited by the inefficient transfer of energy. Ecological systems conform to laws of thermodynamics, and the loss of energy from prey resources to consumers limits the number of possible trophic levels. Based on this argument, we would expect shorter food webs in unproductive systems where resources are limited. We also know that top predators tend to occur in low numbers and are sparsely distributed compared with herbivores and other secondary consumers. In an insightful essay on this topic, Colinvaux (1978) argued that the rarity of large, fierce predators (e.g. tigers, great white sharks) in many ecosystems resulted from the inefficiency of energy transfer from lower trophic levels.

Despite the intuitive appeal and broad theoretical support, few studies of food chains in natural communities have found consistent relationships between productivity and food chain length. Primary productivity may vary by orders of magnitude among communities, but the number of trophic levels remains remarkably consistent. Food chains are not necessarily shorter in unproductive environments (e.g. arctic tundra) compared with productive environments (e.g. tropical rainforests). Ricklefs (1990) estimated the average number of trophic levels based on net primary production, ecological efficiency, and energy available to predators for a variety of communities (Table 8.1). In contrast to theoretical predictions, there was no consistent relationship between net primary productivity and the estimated number of trophic levels.

Hairston, Smith and Slobodkin's (HSS) (1960) revolutionary paper offered an alternative explanation for the relationship between productivity and web structure. According to the HSS model, species interactions (competition, predation) within and between trophic levels determined the structure of food webs. In a three-trophic level system typical of many terrestrial communities, abundance of herbivores was controlled by predators, thus allowing primary producers to compete for resources. Support for this model in terrestrial food webs has been widespread, and predator control of herbivores is proposed as an explanation for the dominance of green plants in most terrestrial ecosystems. A general extension of this argument to other communities suggests that plants are controlled by resources (nutrients, light, space) in systems with an odd number of trophic levels and controlled by herbivores in systems with an even number of trophic levels. In an alternative synthesis of the relationship between energy flow and trophic structure, Hairston and Hairston (1993) observed that the mean number of trophic levels in pelagic (i.e. open water) systems (3.6) is significantly greater than in terrestrial systems (2.6). Based on the relative importance of competition among primary producers in pelagic and terrestrial systems, they provide a compelling argument for the hypothesis that trophic structure determines food web energetics instead of vice versa.

The hypothetical relationship between food chain length and community stability is also somewhat tenuous. Briand and Cohen (1987) reported that the average food chain length in food webs from constant and fluctuating environments was 3.60 and 3.66, respectively. Interestingly, these researchers reported that the complexity and dimensionality of a habitat had a greater influence on food chain length than community stability. In general, two-dimensional habitats (e.g. stream

Table 8.1. Estimated number of trophic levels based on primary production, energy flux to consumers, and ecological efficiencies. (Modified from Table 11.5 in Ricklefs 1990)

Community	Net primary production (Kcal/m^2/year)	Number of trophic levels
Open ocean	500	7.1
Coastal marine	8000	5.1
Temperate grassland	2000	4.3
Tropical forest	8000	3.2

bottoms, rocky intertidal zones) had shorter food chains than three-dimensional habitats (coral reefs; open ocean). Thus far, an adequate mechanistic explanation for this relationship has not been provided. However, results are consistent with the observation that more complex habitats sustain a greater number of species.

Experimental manipulations of food webs provide the most direct tests of the relationship between trophic structure, productivity, and disturbance. Experiments conducted by Power and colleagues (Power 1990; Wootton, Parker and Power 1996) extended the HSS model to aquatic ecosystems and demonstrated the role of disturbance in regulating trophic structure. As predicted by HSS, primary producers were limited by resources (nutrients, space, light) in communities with an odd number of trophic levels, whereas communities with an even number of trophic levels were regulated by herbivores. Disturbance also played a prominent role by controlling abundance of grazers and shifting energy to predatory fish. These results indicate the need to advance from a single species perspective to a community perspective when assessing the effects of disturbance (Wootton, Parker and Power 1996). More importantly, these results demonstrate that disturbance may alter trophic structure and energy flow in food webs by removing key species.

Food chain length and the number of trophic levels of a community may also influence resistance and resilience stability. Mathematical models predict that communities with longer food chains will experience extreme population fluctuations, resulting in a greater probability of extinction of top predators. This hypothesis has important implications for the study of systems subjected to anthropogenic disturbance. For example, we expect that effects of contaminants would be greater in communities with greater trophic complexity and longer food chains.

Food web interactions involving otters and sea urchins in kelp beds of western Alaska provide some insight into how disturbance can dramatically alter trophic structure (Estes *et al*. 1998). The role of otters as a keystone species in marine kelp beds is well established. Otter predation on sea urchins, major consumers of early growth stages of kelp, maintains the structure of kelp forests. Recovery of otter populations following protection from overhunting resulted in recovery of kelp forests along the Pacific Northwest coast. However, a dramatic decline of sea otters over large areas in western Alaska in the 1990s caused increased abundance of urchins and a corresponding decline in kelp abundance (Fig. 8.2). Surprisingly, increased sea otter mortality was attributed to predation by killer whales, which shifted their foraging to coastal areas following reductions in their preferred prey: seals and sea lions. Estes *et al*. (1998) speculated that reduced abundance of seals and sea lions resulted from unexplained declines of forage fish stocks. Thus, addition of a top predator (killer whales) to coastal Alaska converted this three-trophic level system to a four-level system. This spectacular example illustrates the connectance and interdependence of multiple trophic links and the interactions between oceanic and nearshore communities. More importantly, this

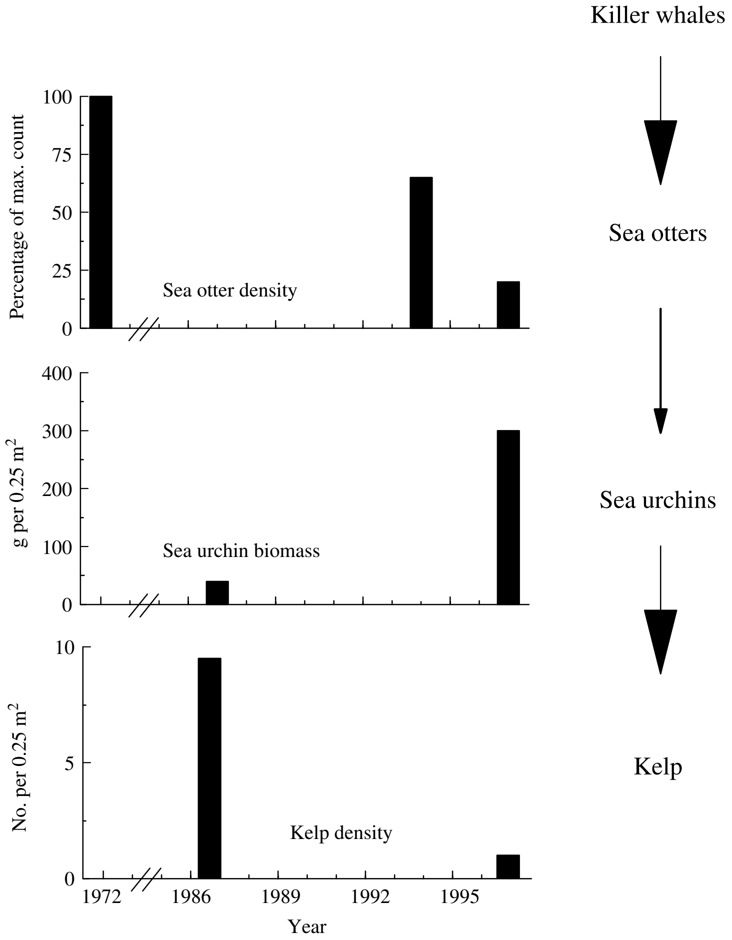

Fig. 8.2. Effects of predation by killer whales on trophic structure of nearshore marine ecosystems in western Alaska. The figure depicts changes in otter abundance, sea urchin biomass, and effects on kelp density following increased predation by killer whales. (Modified from Figure 1 in Estes *et al*. 1998)

study demonstrates the difficulty in predicting indirect effects of reduced prey abundance in natural communities. It is unlikely that researchers could have anticipated that declines in fish forage stocks in the oceanic environment would cause a collapse of coastal kelp beds. Similar ‘ecological surprises’ (sensu Paine, Tegner and Johnson 1998) are likely to occur in systems where important predator or prey species are eliminated as a result of contaminants.

The other major generalizations regarding the structure of food webs are the relatively constant number of species interactions and the ratio of predators to

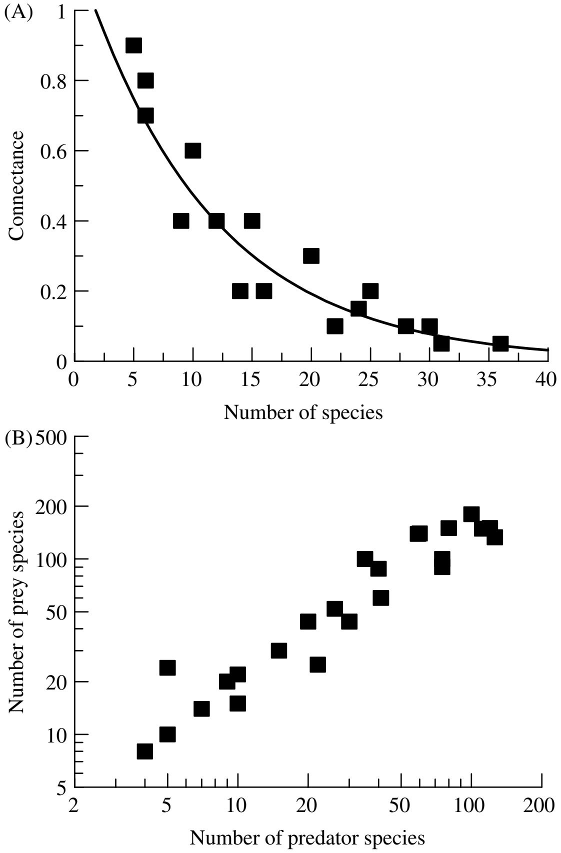

Fig. 8.3. (A) Hypothetical relationship between connectance (number of interactions/number of possible interactions) and the total number of species in a food web. (B) Hypothetical relationship between number of predator species and number of prey species

prey. Food web connectance, defined as the observed number of trophic interactions divided by the total number of possible interactions, generally decreases with species richness (Pimm 1982) (Fig. 8.3A). As a result, each species tends to have on average about two trophic interactions, regardless of the number of species in the community. Similarly, the ratio of predator species to prey species in a community is relatively constant (generally between two and three prey species per predator species), regardless of the total number of species in the community (Jeffries and Lawton 1985) (Fig. 8.3B). Assuming that these theoretical predictions are consistent among communities, connectance and the ratio of predators to prey may prove to be useful endpoints for assessing effects of stressors on food web structure.

8.2.4 TROPHIC CASCADES

The trophic cascade hypothesis (Carpenter and Kitchell 1993) predicts that each trophic level in a community is influenced by trophic levels directly above (e.g. consumers) and directly below (e.g. resources). According to this hypothesis, nutrients determine the potential productivity of a system, but deviations from this potential are due to food web structure. For example, increased abundance of piscivorous fish in a lake can reduce abundance of zooplanktivorous fish, allowing abundance of zooplankton to increase. The resulting increased grazing pressure by zooplankton is predicted to reduce biomass of phytoplankton (see Chapter 1, Fig. 1.1). Researchers conducting large-scale biomanipulation experiments in eutrophic lakes have taken advantage of these relationships and attempted to control primary productivity and eliminate algal blooms by introducing top predators (Box 8.1).

Box 8.1 Biomanipulation experiments to control eutrophication

Experiments conducted in lakes have demonstrated the importance of trophic linkages and the relationship between food web structure and water quality. Lakes provide an ideal habitat to examine trophic interactions because they are well defined, relatively closed systems and are amenable to experimental manipulation. Biomanipulation experiments were initially motivated by the observation that nutrients could account for only a portion of the variation in primary productivity among lakes, which often vary by an order of magnitude in systems with similar levels of nutrients (Carpenter and Kitchell 1993). Introduction of piscivorus fish to Peter Lake, Wisconsin (USA) caused rapid reductions in abundance of zooplanktivorous fish and an increase in herbivore (primarily *Daphnia*) body size. These changes in food web structure resulted in a 37% decrease in primary productivity and a dramatic increase in light penetration. Interestingly, herbivore body size was a better predictor of trophic effects on productivity than abundance.

The observation that primary productivity in lakes is influenced by food web structure provided an opportunity to investigate the relationship between trophic structure and water quality. Despite dramatic improvements in control of point source inputs of nutrients over the past several decades, noxious algal blooms are still a significant problem in many lakes. Cultural eutrophication occurs in systems when grazing herbivores are unable to control abundance of phytoplankton, especially blue-green algae. If introduction of piscivorus fish can reduce predation on herbivores by limiting abundance of zooplanktivorous fish, then grazing pressure on noxious algae is expected to increase. This idea was the impetus for a large-scale biomanipulation experiment conducted in Lake Mendota (WI) during the late 1980s (Kitchell 1992). As was expected, increased stocking of northern pike and walleye in Lake Mendota caused increased abundance of large, grazing zooplankton. However, because of a combination of unexpected events, including unusual weather patterns, greater runoff, and greater fishing pressure, the results of this experiment were mixed. Primary productivity did not respond throughout the experiment as predicted, suggesting that food web interactions were not the sole determinant of primary productivity in Lake Mendota. However, results of this study and others conducted by Kitchell and colleagues demonstrate that predation played a major role in structuring lower trophic levels in lakes.

These experiments highlight the close connection between trophic interactions and energy flow in lentic ecosystems. It is important that ecotoxicologists recognize the significance of these interactions when characterizing food chain transport of contaminants in lake communities. Simple models of contaminant transport generally do not consider direct effects on trophic structure or potential feedback between adjacent trophic levels. In addition, food web manipulations conducted in lakes have generally not included a littoral or benthic component. Because sediments are a major sink for contaminants in most lentic systems, a complete understanding of how trophic structure will influence contaminant transport requires that processes involving sediments should also be considered.

Although there has been strong support for the trophic cascade hypothesis in lakes, the generality of this hypothesis and the relative importance of ‘top-down’ and ‘bottom-up’ effects in other systems have been subjects of considerable debate. Strong (1992) argues that trophic cascades in lakes are an exception and generally restricted to species-poor habitats. He suggests that terrestrial systems and more diverse aquatic communities are characterized by ‘trophic trickles’ rather than cascades. Because predator control is weaker and more diffuse in species-rich communities, the effects of trophic interactions are buffered. More importantly, unlike aquatic systems where manipulative studies are common, the lack of experimental research in terrestrial habitats limits our ability to identify trophic cascades (Strong 1992).

An exception to the general absence of trophic cascades in terrestrial ecosystems is the interaction between moose and wolves on Isle Royale reported in Chapter 7 (McLaren and Peterson 1994). Results of long-term monitoring of wolves and moose have described a tightly coupled predator–prey system. Periods of low wolf and high moose numbers are correlated with intense grazing pressure on balsam fir, the primary forage of moose. These results are especially significant because they provide strong support for top-down control in a non-aquatic, three-trophic level system. However, it is important to note that because boundary conditions are well defined and trophic complexity is low, Isle Royale may represent a relatively unique situation.

Quantifying the relative importance of consumer versus resource control in communities will require a more sophisticated understanding of population dynamics, species interactions, and the abiotic environment. Resource enrichment experiments conducted in a terrestrial, detritus-based food chain showed strong bottom-up limitation of top predators (Chen and Wise 1999). Conversely, Stein, DeVries and Dettmers (1995) reported that food webs in temperate reservoirs were regulated by complex web-like interactions rather than chain-like trophic cascades. The lack of a zooplankton response to introduced piscivorus fish (northern pike) and reduced abundance of planktivores were explained by poor food quality for these grazers. Brett and Goldman (1996) conducted a meta-analysis of 54 different experiments to test the generality of the trophic cascade hypothesis. Meta-analysis is a powerful statistical approach for analyzing patterns and central tendencies of large datasets derived from multiple investigations. Results of this analysis provided strong support for the trophic cascade hypothesis. However, a subsequent analysis of 11 mesocosm experiments showed no relationship between nutrient enrichment and the number of trophic levels (Brett and Goldman 1997). Another meta-analyses of 47 mesocosm experiments and 20 time-series studies conducted in marine habitats demonstrated the importance of nitrogen enrichment and predation on pelagic food webs (Micheli 1999). As expected based on research conducted in freshwater systems, nutrient enrichment increased primary production and addition of planktivorous fish reduced zooplankton abundance. However, unlike patterns observed in lakes and streams, consumer–resource interactions did not cascade through other trophic levels because of the weak interactions between grazers and phytoplankton. As a result, it is unlikely that biomanipulation of marine food chains would have the same effects on algal productivity as that observed in lakes (Micheli 1999).

8.2.5 LIMITATIONS OF FOOD WEB STUDIES

Significant progress has been made in the development of food webs and the quantification of energy flow among trophic levels since the publication of Elton’s energy pyramids in 1927. Because transport of contaminants in a community is often intimately associated with the flow of energy, a better understanding of trophic interactions will improve our ability to predict contaminant fate. However, as with any general ecological model, it is important to recognize the limitations and simplifying assumptions of food webs. Although grouping organisms into broad trophic categories has facilitated the development of mathematical models for estimating energy flow, this representation of food webs is greatly oversimplified. In addition, most studies of food webs either ignore or minimize the importance of omnivory, which may be the dominant mode of feeding for many species. Relatively few consumers feed exclusively on resources from one trophic level. Many consumers are opportunistic generalists that feed on the most abundant, available, or energetically profitable food resources. Thus, pollution-induced alterations in prey communities may shift feeding habits of predators to tolerant prey species with little impact on bioenergetics (Clements and Rees 1997).

Traditional representations of food webs often ignore the role of detritus, which is a major contributor of energy to many aquatic and terrestrial food chains. Experiments conducted by Wallace *et al*. (1997) showed reduced biomass of most functional feeding groups when allochthonous detritus was excluded from a headwater stream. In addition, most characterizations of food webs are limited to a single habitat, and often fail to consider energy flow between adjacent habitats. Experiments conducted by Nakano, Miyasaka and Kuhara (1999) demonstrated the importance of terrestrial arthropods to the trophic structure of a small stream and the linkages between terrestrial and aquatic habitats. Exclusion of terrestrial arthropods shifted feeding habits of predatory fish to aquatic prey and caused significant changes in energy flow and trophic structure.

Food web studies are also limited by the general lack of information on interaction strength among species. Knowing that a particular trophic interaction occurs in a community does not provide any indication of the strength of this interaction. Thus, some assessment of interaction strength, either by manipulative experiments or by analysis of energy flow, is necessary to understand the importance of trophic interactions. In addition, information on seasonal and ontogenetic shifts in trophic interactions should be considered when constructing food webs. Carlisle (2000) developed production-based bioenergetic food webs for reference and metal-polluted streams in the Rocky Mountains, USA (Fig. 8.4). The pathways of major energy flow and relative contribution of prey species to predator biomass differed greatly between streams. There was also significantly more seasonal variation in food web structure in reference streams compared with polluted streams.

Finally, the number of species in natural food webs is usually much greater than the number considered in most published food web studies. Relatively few studies have provided complete food web analyses of all species within a community. If the majority of trophic interactions in a community are relatively weak, it may not be necessary to quantify the importance of all species. However, very different food web characteristics may emerge when all species in a community are included (Polis 1991).

Despite these limitations, analysis of food webs is a productive area of basic ecological research with important applications to ecotoxicology. Changes in the abundance of consumers or their resources often result in strong cascading effects across trophic levels. To predict fate and effects of contaminants, ecotoxicologists must develop a better understanding of these interactions. Reviews of basic food web ecology provide support for the hypothesis that energy flow in communities is regulated by a diverse assortment of biotic and abiotic factors. Ecologists now recognize that the dichotomy between consumer control versus resource control of food webs is artificial, and that top-down and bottom-up factors may operate simultaneously (Menge 1992). The validity of various hypotheses explaining patterns of food web structure in communities can only be evaluated within the context of the quality of data used to construct them. Thus, a major requirement for improving our understanding of trophic ecology is to infuse greater rigor

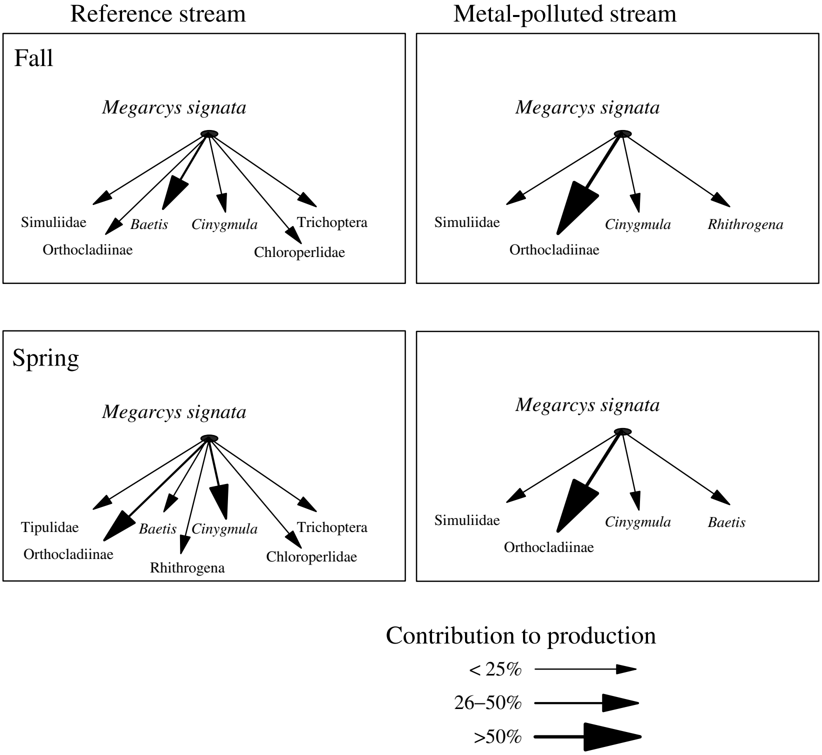

Fig. 8.4. Seasonal changes in energy flow in a reference and metal-polluted stream. The figure shows the relative contribution of each prey species to production of a stonefly predator (*Megarcys signata*). (Modified from Figure 4 in Carlisle 2000)

into the quantification of feeding relationships and construction of food webs (Begon, Harper and Townsend 1990). New methodological approaches, such as the application of stable isotopes to quantify food webs, will improve our ability to estimate contaminant fate and ecological effects.

8.2.6 USE OF RADIOACTIVE AND STABLE ISOTOPES TO CHARACTERIZE FOOD WEBS

Characterizing food webs and quantifying energy flow through communities is labor-intensive. Consequently, relatively few complete food web studies have been published. The application of radioactive tracers, where compounds are labeled using isotopes (usually ^{32}P), provides an indirect measure of the flow of energy through a community. The general approach involves the use of tracers in phosphate solution which are applied directly to primary producers in terrestrial studies or to water in aquatic studies. Consumers are collected at different time intervals to follow movement of the materials. Based on the assumption that energy flow between trophic levels can be estimated by the movement of organic material, tracer studies have verified traditional food web methods in terrestrial and aquatic ecosystems (Odum 1968). Results of tracer studies indicate that materials are rapidly assimilated by herbivores, whereas uptake by predators and decomposers requires more time. Studies conducted in aquatic habitats showed that most of the energy is dissipated within a few weeks; however, organic materials incorporated into bottom sediments may persist for many years.

One of the most significant methodological developments in the study of food webs is the application of stable isotopes to characterize feeding habits and quantify energy flow. Over the past 20 years studies have shown a strong relationship between stable isotope ratios of consumers and those of their diet. Stable isotope ratios, particularly $^{13}C/^{12}C$ and $^{15}N/^{14}N$, are determined by a variety of geochemical, meteorological, and biological characteristics that vary among habitats and trophic groups. Thus, isotopic analyses of organisms can provide a unique signature that is representative of their habitat and feeding habits. By comparing stable isotope ratios of predators and prey across different communities, it is possible to obtain time-integrated estimates of energy flow, trophic position, and carbon sources for major consumers (Fig. 8.5). Stable isotope studies have

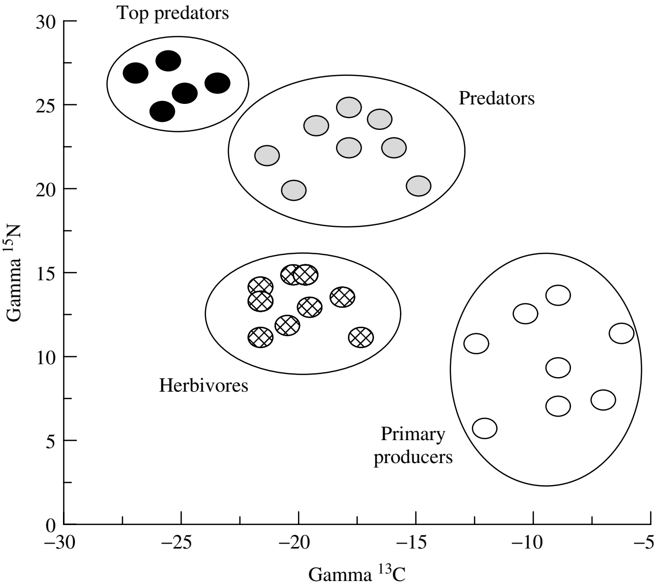

Fig. 8.5. Example of the use of stable isotopes to characterize food webs. Variation in stable isotopes of N reflect trophic levels, whereas variation in stable isotopes of C reflect food sources

been used to assess effects of disturbances on food web structure and energy flow and to investigate the food web consequences of introduced species on native species (Vander Zanden, Casselman and Rasmussen 1999). The application of these approaches to the study of contaminant transport is described in Section 8.3.10.

8.3 APPLICATIONS OF FOOD WEB ECOLOGY TO COMMUNITY ECOTOXICOLOGY

Food web investigations have a relatively long history in ecotoxicological research. Rachel Carson's *Silent Spring* (1962) placed bald eagles and other birds of prey at the top of Elton's trophic pyramid and introduced the lay public to the concept of biomagnification. Since the publication of Carson's influential book, literally hundreds of studies have reported concentrations of contaminants across trophic levels and attempted to relate trophic position to biomagnification. Because of the difficulty in developing reliable food web models, researchers are keenly aware that predicting food chain transport requires more than an understanding of the physicochemical properties of contaminants. The structure of food webs and the dynamics of energy and contaminant flow vary greatly among locations. Consequently, predictive models have become increasingly sophisticated as investigators attempt to quantify the influence of ecological factors, such as feeding habits, food chain length, and habitat characteristics, on contaminant transport and biomagnification. The inclusion of these ecological factors into transport models represents a major improvement in our understanding of how contaminants are distributed in ecological systems. However, knowing the concentration of contaminants in a particular species or trophic level tells little about the consequences of exposure. The next logical step in the refinement of food web models is to relate predicted tissue concentrations to ecologically significant effects.

Another important application of food web ecology to ecotoxicology is to understand how contaminants directly and indirectly influence food web structure. This topic has received considerably less attention in the ecotoxicological literature than the study of contaminant transfer and biomagnification. Because elimination of individual species may have far reaching consequences for trophic structure and energy flow, an understanding of trophic responses to contaminants is essential for predicting contaminant distribution within a community. The remainder of this chapter will examine applications of food web ecology to community ecotoxicology. The first section will review traditional approaches for assessing biomagnification of contaminants in food webs and the attempts to improve these models by integrating basic ecological concepts. The last part of this chapter will focus on direct effects of contaminants on food web structure.

8.3.1 BIOCONCENTRATION, BIOACCUMULATION, BIOMAGNIFICATION, AND FOOD CHAIN TRANSFER

The traditional application of food web ecology to ecotoxicological research has been to quantify uptake and transport of contaminants between biotic and abiotic compartments. Inconsistent usage of terms such as bioconcentration, bioaccumulation, and biomagnification has caused some confusion in the literature, especially in aquatic communities (Dallinger *et al.* 1987). Here, we define bioconcentration as the uptake of contaminants directly from water. Bioconcentration factors (BCFs) are calculated as the ratio of chemical concentration in the organism to the concentration in water. Bioaccumulation is defined as the uptake of chemicals from either biotic (food) or abiotic (sediment) compartments, and bioaccumulation factors (BFs) are calculated as the ratio of the concentration in organisms to the concentration in these compartments. Biomagnification refers specifically to the increase in contaminant concentration with trophic level (after adjusting for lipid content of the organism). If biomagnification occurs, we would expect that lipid-based concentrations should increase with trophic level. Although the highest levels of contaminants such as PCBs and other lipophilic chemicals are frequently measured in top predators, biomagnification is a complex phenomenon influenced by many physicochemical, physiological, and ecological factors (Moriarty, Hanson and Freestone 1984; Moriarty and Walker 1987). In addition to feeding habits, factors such as metabolism, growth rates, and habitat preferences of predators and prey may regulate contaminant transfer to higher trophic levels.

8.3.2 LIPIDS INFLUENCE THE PATTERNS OF CONTAMINANT DISTRIBUTION AMONG TROPHIC LEVELS

The positive relationship between the concentration of lipophilic chemicals and trophic level is a consistent pattern reported in the literature. However, the precise mechanistic explanation for this phenomenon is not well understood. The relationship between chemical concentration and trophic level may be explained by the increased levels of lipids measured in organisms at higher trophic levels. Kiriluk *et al.* (1995) observed a significant positive relationship between lipid content and trophic position in a pelagic food web. Similar results were reported by Rasmussen *et al.* (1990) for lake trout. Various statistical approaches, such as analysis of covariance (ANCOVA), have been employed to estimate the influence of lipid content and food chain length on organochlorine concentrations in fish (Bentzen *et al.* 1996). Kidd *et al.* (1998) observed a strong positive relationship between food chain length and organochlorine concentration after accounting for lipid content in fish from subarctic lakes. The strength of the relationship between contaminant concentration and trophic position will also be influenced by lipophilicity of the chemicals (Fig. 8.6). In general, more lipophilic chemicals show stronger relationships between concentration and trophic level (Kiriluk *et al.* 1995).

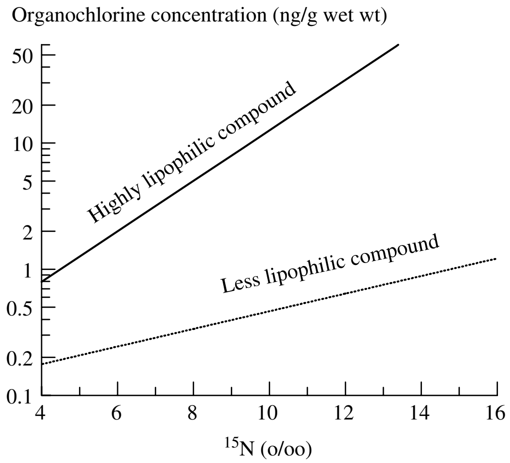

Fig. 8.6. Hypothetical relationship between trophic position (as indicated by stable isotope N value) and organochlorine concentration in fish for highly lipophilic and less lipophilic compounds. It is expected that highly lipophilic compounds will have a greater potential for biomagnification than less lipophilic chemicals

8.3.3 RELATIVE IMPORTANCE OF DIET AND WATER IN AQUATIC SYSTEMS

Much of the debate regarding the significance of food chain transfer of contaminants in aquatic systems focuses on the relative importance of food and water pathways. For many lipophilic organic contaminants, especially PCBs and other organochlorines, accumulation from food is generally considered the primary route of exposure. Although sophisticated models have been developed to predict bioconcentration from water, models that ignore aqueous exposure can still accurately predict contaminant levels in fish (Jackson and Schindler 1996). In contrast, attempts to predict chemical concentrations in predators based only on physiological features of organisms and physicochemical characteristics of contaminants are fraught with uncertainty (Owens, Swanson and Birkolz 1994; Russell, Gobas and Haffner 1999). Failure to account for food chain transport will significantly underestimate concentrations of organochlorines and other lipophilic chemicals (Zaranko, Griffiths and Kaushik 1997). Indeed, contemporary models describing fate and transport of highly lipophilic contaminants generally include a food chain component and account for input from sediment (Fig. 8.7). Morrison *et al*. (1997) developed and field-validated a model to predict transfer of PCBs in a pelagic food chain. Results showed that 95% of the observed concentrations in invertebrates and fish were within a factor of 2 × the predicted concentrations. The close agreement between measured and predicted concentrations suggests that the model ultimately may be useful for assessing effects

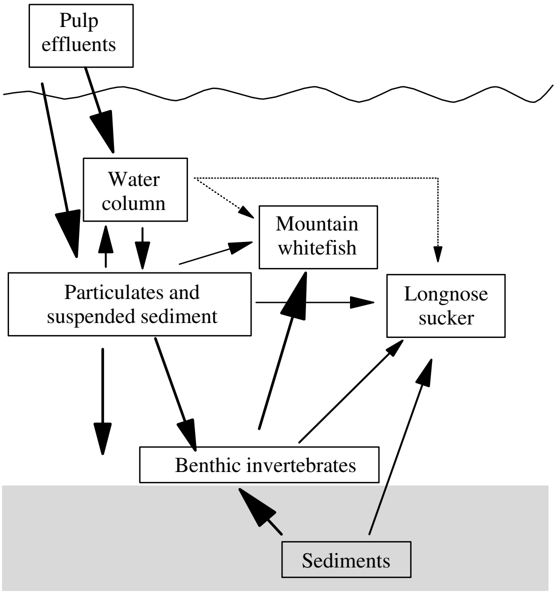

Fig. 8.7. Food chain model showing transport of contaminants in an aquatic ecosystem. The size of the arrows indicates the relative importance of each pathway. (Modified from Figure 6 in Owens, Swanson and Birkolz 1994)

of PCBs on aquatic organisms. Mathematical models developed by Thomann (1981) that quantify the relative importance of exposure from diet and water are discussed in Section 8.3.5.1.

Unlike the situation for many lipophilic organic contaminants, the relative importance of aqueous and dietary exposure to heavy metals is uncertain. Most of the evidence derived from laboratory studies indicates that uptake from water is a more important route of exposure than food, particularly for fish. However, some investigators have suggested that dietary uptake may also contribute significantly to total body burdens of heavy metals (see review by Dallinger *et al*. 1987). For example, Hatakeyama and Yasuno (1987) reported that 90% of cadmium (Cd) accumulation in the guppy, *Poecilia reticulata*, was derived from feeding on contaminated chironomids. Similarly, Dallinger and Kautzky (1985) demonstrated that rainbow trout accumulated metals primarily through the diet, particularly when levels in the water were low. Munger and Hare (1997) measured the relative importance of diet and water as sources of Cd uptake for the predatory insect *Chaoborus* in a laboratory food chain. They reported no significant difference in organisms exposed to Cd in food alone versus Cd in food and water, indicating that uptake from water was relatively unimportant.

Although food chain transfer of most metals is probably a less serious issue than for lipophilic organic contaminants, dietary exposure should not be ignored when assessing ecological risk of heavy metals. Dietary exposure to heavy metals is especially contentious because water quality criteria are based exclusively on aqueous exposure and assume no effects from dietary uptake. Because concentrations of metals in certain biotic and abiotic compartments may be very high, relatively inefficient transfer of metals through food chains can result in harmful levels. Several researchers have reported that despite low transfer efficiencies for some metals, dietary exposure may have negative effects on organisms (Woodward *et al.* 1994, 1995; Farag *et al.* 1998). This point was demonstrated convincingly in a series of laboratory experiments in which rainbow trout were fed benthic invertebrates collected from a metal-contaminated stream (Woodward *et al.* 1994). Fish consuming metal-contaminated prey showed reduced growth and greater mortality compared with fish feeding on organisms collected from an unpolluted stream. Results of this study were complicated by potential differences in nutritional quality between contaminated and uncontaminated prey (Mount *et al.* 1994). However, these findings suggest that dietary exposure should not be ignored when assessing ecological risk of heavy metals.

8.3.4 ENERGY FLOW AND CONTAMINANT TRANSPORT

Quantitative approaches developed to measure energy flow in communities can also be employed to estimate the movement of contaminants across trophic levels and between biotic and abiotic compartments. Odum's box and arrow diagrams showing energy and materials flow among trophic levels are the forerunners of contemporary contaminant transport models. Although ecotoxicologists have done a reasonable job quantifying contaminant concentrations in biotic and abiotic compartments, validation of transport models requires accurate estimates of transfer rates between trophic levels. Because these estimates are typically obtained from laboratory studies, there is some uncertainty concerning their relevance to conditions in the field. Jackson and Schindler (1996) used a long-term monitoring program to estimate transfer efficiencies of PCBs from prey fishes to salmonids in Lake Michigan. Despite significant temporal changes in concentrations of PCBs in prey, transfer efficiencies remained relatively constant over the 15-year study. These findings demonstrate that temporal changes in PCB levels in top predators are determined primarily by concentrations in prey species. Thus, the steady decline in PCB levels in Lake Michigan salmonids over the past 20 years (Stow *et al.* 1995) is a direct result of reduced inputs and lower PCB concentrations in prey species.

Russell, Gobas and Haffner (1999) employed multivariate analyses to investigate the relationship between trophic level and organochlorine concentrations in a Detroit River food chain. Lipid-based concentrations of organochlorines increased with trophic level, supporting the hypothesis that these chemicals were biomagnified through the food chain. In addition to an increase in concentration with trophic level, principal component analysis (PCA) showed that the specific constituents of organochlorines varied among trophic groups. Results of PCA also showed good resolution of community composition, suggesting the possibility that quantification of contaminant distributions among trophic levels may be a useful tool for assessing community structure.

8.3.5 MODELING CONTAMINANT MOVEMENT IN FOOD WEBS

8.3.5.1 Models for Discrete Trophic Levels

Trophic exchange of contaminants can be defined with a simple model that includes contaminant concentration, biomass in the trophic level of interest, biomass consumed from the lower trophic level, contaminant bioavailability, and the fraction of contaminant excreted daily (Ramade 1987) by organisms in the trophic level of interest. To begin developing such a model, the bioaccumulation factor (BF) is defined as the ratio of the contaminant concentration (C) at trophic level $n + 1$ and the concentration in the next lowest trophic level, n:

$$\text{Bioaccumulation factor} = BF_{n,n+1} = \frac{C_{n+1}}{C_n}$$

Rearranging this equation, the concentrations in the two trophic levels can be defined.

$$C_{n+1} = BF_{(n,n+1)}C_n$$

The bioaccumulation factor for transfer $n \rightarrow n + 1$ can be described in more detail by inclusion of the weight of organisms in level $n + 1$ (b_n), the weight of level n organisms consumed (a_n), the fraction of contaminant absorbed from ingested food (f_n), and the fraction of accumulated contaminant that is excreted daily (k_n).

$$BF_{n,n+1} = \frac{a_n f_n}{b_n k_n}$$

Substituting this more detailed version of $BF_{n,n+1}$ into the relationship between C_n and C_{n+1} given above, the following model is generated:

$$C_{n+1} = \left[\frac{a_n f_n}{b_n k_n}\right] C_n$$

This model can be easily expanded to predict the concentration at level C_{n+2} by adding the explicit form of $BF_{n+1,n+2}$ into this model.

$$C_{n+2} = \left[\frac{a_{n+1} f_{n+1}}{b_{n+1} k_{n+1}}\right]\left[\frac{a_n f_n}{b_n k_n}\right] C_n$$

Generalizing this approach, one could theoretically predict the concentration in any trophic level (r) knowing the contaminant concentration at the lowest level (C_0) and the variables a_i, f_i, b_i and k_i for each trophic level.

$$C_r = \left[\prod_{i=1}^{r} \frac{a_i f_i}{b_i k_i}\right] C_0$$

Close inspection of this model reveals a general lack of realism as well as its conceptual parsimony. Considerable information is needed to parameterize this model, but more importantly the trophic sequence is based on overly simplified exchanges. Species only feed on those prey in the next lowest trophic level and are only consumed by species at the next highest trophic level. This might be adequate in some situations, but it is inadequate for modeling many food webs.

Thomann (1981) expanded this steady-state approach by including organism growth rate and uptake of contaminants from water. Organism growth was incorporated because any increase in body mass has an apparent dilution effect on contaminant concentration. Inclusion of uptake from water allowed comparison of the relative importance of food and water sources. A food chain transfer number (f) serves this purpose.

$$f = \frac{\alpha C}{k} + G$$

In this equation, $\alpha =$ the chemical absorption efficiency (f_i in the simple BF model above), $C =$ the specific consumption (weight-specific consumption rate in units of mass of prey/(mass of predator × day), $k =$ excretion rate (k_i in the BF model above), and $G =$ net organism growth rate. Thomann (1981) generalized that significant food chain transfer was indicated if $f > 1$, but uptake of contaminants from water was more important than food sources if $f < 1$. Applying this rule to PCBs, ^{239}Pu and ^{137}Cs data, he concluded that PCB and radiocesium concentrations in top predators were predominantly determined by food sources but accumulated plutonium came primarily from water sources. Thomann (1981) also added explicit details to this steady-state model for predicting water → phytoplankton, phytoplankton → zooplankton, zooplankton → small fish, and small fish → large fish transfers of contaminants. Later (Thomann 1989), this approach was focused on predicting transfer of organic chemicals in food chains by relating relevant model parameters to the octanol–water partition coefficient (K_{ow}). Trophic transfer in simple aquatic systems was predicted to be insignificant if $\log_{10} K_{ow} < 5$. Food chain transfer was important for top predators in aquatic systems if $\log_{10} K_{ow}$ was between 5 and 7.

8.3.5.2 Models Incorporating Omnivory

A major shortcoming of the approaches described above is the assumption that no species feeds on more than one trophic level. Although unrealistic in many cases, this assumption allows a level of accuracy in predicting trophic transfer of some contaminants. After noting that such an approach was insufficient to define trophic transfer in a pelagic food web, Cabana and Rasmussen (1994) expanded trophic models to include ‘omnivory’. Here, omnivory means that a species is feeding on food items coming from several trophic levels. Although the approach is similar to that described above, matrix formulation accommodates the increased number of trophic exchanges. In this approach, fractions of the total amount of the ith level's diet coming from specific trophic levels (j) are designated ρ_{ij}. Obviously, all ρ_{ij} fractions sum to 1 in order to include the entire diet of level i. The total ration to the ith level (C_i) is defined as follows.

$$C_i = \sum_{1}^{j} \rho_{ij} C_j$$

The fractions of the ith level's diet coming from the different sources (j levels) can be placed into a matrix with the subdiagonal reflecting the fractions for the simple level 1 → level 2, level 2 → level 3, level 3 → level 4, etc. transfers. The fractions entered below the subdiagonal are those for the transfers not accommodated in Thomann's model (e.g. level 1 → level 3 and level 2 → level 4 transfers). The following relationship describes a vector of the total rations for all trophic levels i in a trophic scheme with four levels.

$$C_i = \begin{bmatrix} C_1 \\ C_2 \\ C_3 \\ C_4 \end{bmatrix} \begin{bmatrix} 0 & 0 & 0 & 0 \\ \rho_{21} & 0 & 0 & 0 \\ \rho_{31} & \rho_{32} & 0 & 0 \\ 0 & \rho_{42} & \rho_{43} & 0 \end{bmatrix}$$

Such a matrix was called an omnivory matrix by Cabana and Rasmussen (1994). The food chain model reduces to the simple one described by Thomann if fractions for all matrix elements are 0 except those in the subdiagonal. There are more complex exchanges in the omnivory matrix illustrated above because neither ρ_{31} nor ρ_{42} are equal to 0.

Using matrix notation and omitting accumulation for all sources except food, Cabana and Rasmussen (1994) redefined Thomann's steady-state model as the following,

$$\mathbf{B} = \boldsymbol{\alpha}\mathbf{C}[(\mathbf{K} + \mathbf{G})\mathbf{I}]^{-1}$$

where, for the different trophic levels, $\mathbf{B}$ = a vector of bioaccumulation factors, $\boldsymbol{\alpha}$ = a vector of assimilation (chemical absorption) efficiencies, $\mathbf{C}$ = a vector of rations, $\mathbf{K}$ = a vector of excretion rates, $\mathbf{G}$ = a vector of growth rates, and $\mathbf{I}$ = the identity matrix. They expanded this formulation to include exchanges other than those depicted in the matrix subdiagonal (e.g. ρ_{42} and ρ_{43}) in the example above. The following matrix-formulated model predicts a vector of contaminant concentrations ($\boldsymbol{\nu}$) expected for the i trophic levels in a food web incorporating omnivory.

$$\boldsymbol{\nu}(\boldsymbol{\rho}\boldsymbol{\nu}\mathbf{I})^{-1} = \boldsymbol{\alpha}\mathbf{C}[(\mathbf{K} + \mathbf{G})\mathbf{I}]^{-1}$$

In this model, $\boldsymbol{\rho}$ is the omnivory-adjusted mean dietary concentration for each trophic level.

A major challenge to applying this approach is to obtain estimates of elements in the omnivory matrix. Some estimates of the trophic position must be obtained that include the possibility that species are feeding at various lower levels. In Section 8.3.10, a technique will be described that can be applied to these estimates.

8.3.6 FEEDING HABITS, HABITAT ASSOCIATIONS, AND PREY TOLERANCES

Species-specific feeding habits, habitat associations, and tolerance of prey will greatly influence food chain transfer and levels of contaminants in top predators. For example, differences in organochlorine concentrations among waterfowl species from the Great Lakes were directly related to consumption of zebra mussels (*Dreissena polymorpha*), an introduced species that has dramatically altered food chains in this region (Mazak *et al.* 1997). Variation in contaminant concentrations within populations were also explained by the proportion of zebra mussels in the diet. Similarly, differences in feeding habits between populations of small mammals also accounted for large variation in Hg bioaccumulation (Fig. 8.8). Higher levels of contamination in prey and greater transfer efficiency resulted in a 20 × higher concentration of Hg in insectivorous mammals (short-tail shrew) compared with omnivorous mammals (white-footed mouse) (Talmage and Walton 1993). Finally, several investigations have reported that concentrations of contaminants in aquatic systems are often higher in small prey organisms compared with larger individuals (van Hattum, Timmermans and Govers 1991;

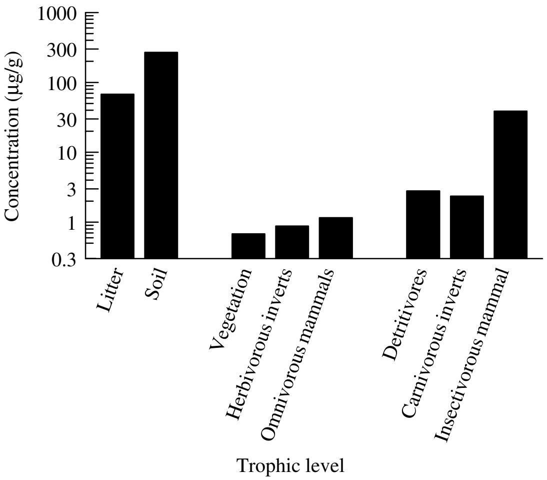

Fig. 8.8. Hg concentrations (μg/g wet weight) in soil, litter, vegetation, invertebrates, and small mammals (kidney tissue) collected from a terrestrial field site at Oak Ridge National Laboratory. Dietary differences and variation in transfer coefficients were hypothesized to account for the differences in Hg levels between omnivorous and insectivorous mammals. (Data from Figure 1 in Talmage and Walton 1993)

Kiffney and Clements 1993). Thus, predators that select smaller prey species, such as juveniles and early life stages, may be at greater risk from contaminant exposure (Farag *et al.* 1998).

Habitat associations of prey species will contribute to variation in contaminant levels among predators. Contaminated habitats are typically characterized by reduced species diversity and a shift in community composition from sensitive to tolerant species. Prey species directly associated with the most contaminated compartments in these systems (e.g. sediments) are likely to have significantly elevated levels of chemicals. Several investigators have shown that feeding habits of predators at impacted sites may be modified to include these tolerant and highly contaminated prey species (Jeffree and Williams 1980; Clements and Livingston 1983; Livingston 1984). For example, in streams polluted by mining effluents, Jeffree and Williams (1980) reported that fish switched from pollution-sensitive to pollution-tolerant prey. As described above, these shifts in feeding habits are likely to influence contaminant levels in top predators.

Pollution-tolerant species employ a variety of mechanisms to detoxify contaminants, including increased excretion, storage, and compartmentalization. The specific method of detoxification employed by prey species in polluted environments may influence bioavailability and food chain transfer. In particular, organisms that store or compartmentalize contaminants may pose a significant risk to predators. This phenomenon, called the ‘food chain effect’, has been reported for species inhabiting metal-polluted environments (Dallinger *et al.* 1987). In a laboratory study, fish fed Cd-contaminated mussels accumulated approximately 2× higher metal levels than fish fed Cd-contaminated chironomids, despite greater metal concentrations in the chironomids (Langevoord *et al.* 1995). These differences were related to differences in detoxification mechanisms between the two species. Wallace, Lopez and Levinton (1998) showed that metal-tolerant oligochaetes accumulated 4× more Cd than non-resistant organisms when exposed in the laboratory. However, because of differences in regulatory mechanisms employed by resistant and non-resistant prey (storage in metal rich granules versus metallothionein), metals in non-resistant oligochaetes were more bioavailable to predators.

8.3.7 TRANSPORT FROM AQUATIC TO TERRESTRIAL COMMUNITIES

While the majority of studies investigating food chain transport of contaminants have focused on invertebrates and fish, a few researchers have attempted to quantify movement from aquatic systems to avian and mammalian predators. Fairchild *et al.* (1992) estimated that as much as 2% of 2378-tetrachlorodibenzofuran (TCDF) in sediments are exported annually by emerging insects, posing a significant risk to terrestrial predators (primarily birds and bats). Froese *et al.* (1998) measured transport of PCBs from emerging aquatic insects to tree swallows in Saginaw Bay, Michigan. Relative concentrations of PCB congeners were markedly different between sediments, benthic invertebrates, and swallows, possibly reflecting metabolic differences among trophic levels. Muir, Norstrom and Simon (1988) measured PCBs and other organochlorines in a marine food chain consisting of arctic cod (*Boreogadus saida*), ringed seals (*Phoca hispida*), and polar bears (*Ursus maritimus*). In addition to increased concentrations with trophic level, major differences in the constituents of PCBs and chlordane-related compounds were observed among species. Elevated levels of organochlorines in bald eagles collected from Lake Superior were attributed to consumption of highly contaminated gulls (Kozie and Anderson 1991), which feed predominately on fish. Finally, food chain transport and biomagnification of PCBs have likely contributed to the decline of otter *(Lutra lutra)* populations in western Europe (Leonards *et al*. 1997). In addition to significant biomagnification of PCBs, results of multivariate analyses showed changes in the distribution of PCB congeners among trophic levels and enrichment of the most toxic constituents in otters (Fig. 8.9).

8.3.8 FOOD CHAIN TRANSFER OF CONTAMINANTS FROM SEDIMENTS

Because sediments are an important sink for contaminants in aquatic ecosystems, models of contaminant transport should include a sediment compartment.

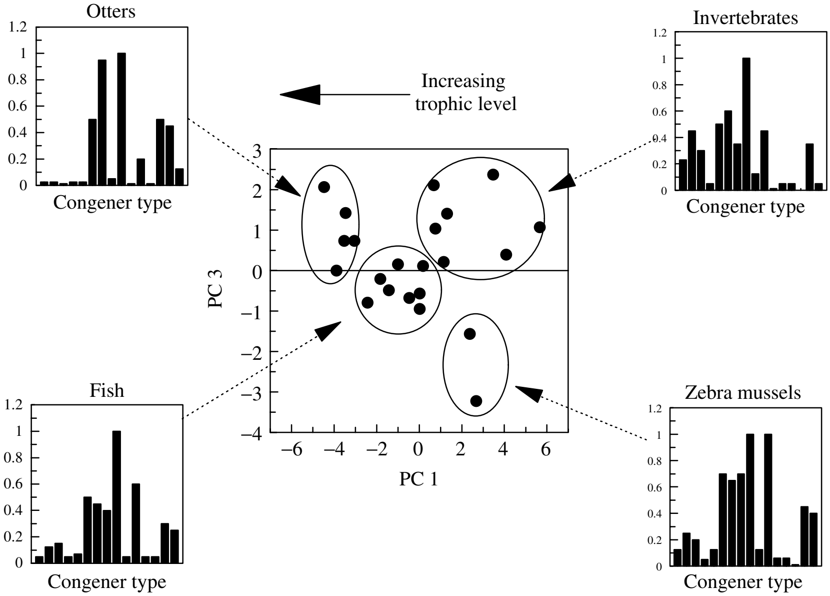

Fig. 8.9. Results of principal component analysis showing the relationship between trophic level and patterns of PCB constituents in a marine food web. (Modified from Figure 4 in Leonards *et al.* 1997)

Concentrations of contaminants in sediments are often several orders of magnitude greater than in overlying water, and benthic organisms associated with sediments may influence the transport of these contaminants. In addition to their role in food chain transport of contaminants to higher trophic levels, the activities and movements of benthic organisms may indirectly affect bioconcentration and bioaccumulation. For example, Reynoldson (1987) reported that 0.2–7.4 g/m^2/year PCBs are ingested by oligochaete worms in contaminated sections of the Detroit River. Similarly, Evans, Noguchi and Rice (1991) estimated that 30% of the PCBs deposited annually in Lake Michigan sediments are recycled by amphipods. Vertical migration of the invertebrate planktivore *Mysis relicta* transports sediment contaminants back to the water column where they are available to higher trophic levels (Bentzen *et al.* 1996). Bioturbation, defined as the reworking of sediments resulting from various activities of benthic organisms, releases sediment contaminants into overlying water where they are bioconcentrated by other organisms and transferred to higher trophic levels. Ciarelli *et al.* (1999) observed that activities of amphipods in sediments resulted in significant transfer of polycyclic aromatic hydrocarbons to filter-feeding mussels (Fig. 8.10). Finally, consumption of contaminated sediments, either directly or incidentally, can result in elevated concentrations in predators. DiPinto and Coull (1997) estimated the transfer of PCBs in a simple benthic food chain (sediments → copepods → fish). Approximately 33% of the PCB Arochlor 1254 accumulated by copepods was transferred to fish. Interestingly, PCB levels in predators foraging on clean prey in contaminated sediments were 5 × greater than in fish feeding on contaminated prey in clean sediments. These results suggest that incidental ingestion of sediments is a significant route of exposure in benthic-feeding fish.

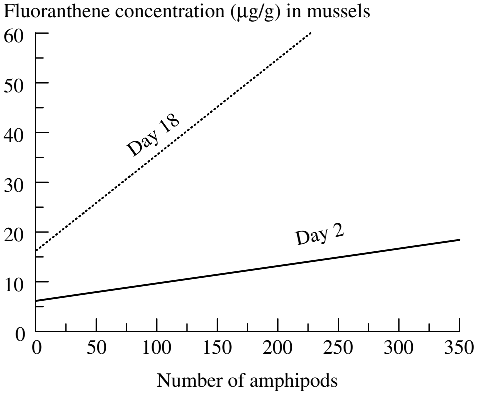

Fig. 8.10. The influence of bioturbation by benthic invertebrates on concentration of fluoranthene in filter-feeding mussels. The figure shows results after 2 and 18 days exposure. (Modified from Figure 4 in Ciarelli *et al.* 1999)

8.3.9 ECOLOGICAL INFLUENCES ON FOOD CHAIN TRANSPORT OF CONTAMINANTS

Most studies that describe uptake and food chain transport of contaminants usually do not focus on the ecology of these systems, but simply report tissue concentrations in biotic and abiotic compartments. More recently, researchers have recognized that ecological characteristics of communities influence contaminant transfer and the concentrations in upper trophic levels. Because food web interactions strongly influence energy flow and biogeochemical cycling, understanding the relative importance of consumer versus resource control is important for predicting chemical transport. For example, the concentration of lipophilic contaminants in top predators will be influenced by food web interactions and the relative strength of top-down versus bottom-up controls. The development of new techniques to quantify feeding preferences, such as stable isotope analyses, allows investigators better to characterize relationships between trophic level and contaminant concentrations. In addition, the larger spatial scale of many contemporary food web studies provides an opportunity to investigate how landscape features influence food chain transport of chemicals. Quantifying the relative importance of ecological factors on contaminant transport is greatly improved by making comparisons across communities. For example, studying contaminant levels in systems that lack point source discharges allows investigators to isolate the relative importance of ecological and habitat features. The best examples of this research have been conducted in remote systems where atmospheric deposition is the primary source of contamination (Rasmussen *et al*. 1990; Larsson, Collvin and Meyer 1992; Berglund *et al*. 1997; Kidd *et al*. 1995, 1998). Better integration of ecological and landscape concepts into kinetic and bioenergetic models will allow for a more comprehensive understanding of contaminant transport in communities.

8.3.9.1 Food Chain Length and Complexity

Understanding the relative importance of ecological factors such as food chain length, primary and secondary productivity, and linkage strength will help explain the large amount of variability in contaminant concentrations often observed in predators collected from different ecosystems. The early work by Rasmussen *et al*. (1990) stimulated a significant amount of interest in the relationship between food web structure and contaminant transport. Rasmussen *et al*. classified lakes into three types based on the presence of invertebrate planktivores (*Mysis*) and pelagic forage fish. Trout collected from lakes with long food chains (i.e. more trophic levels) generally had higher PCB levels than fish from lakes with simple food chains (Fig. 8.11). Similar results were reported by Kidd *et al*. (1995) in which elevated levels of toxaphene in fish collected from a subarctic lake were attributed to an ‘exceptionally long’ food chain. These findings have important implications for systems where food webs are altered by exotic species.

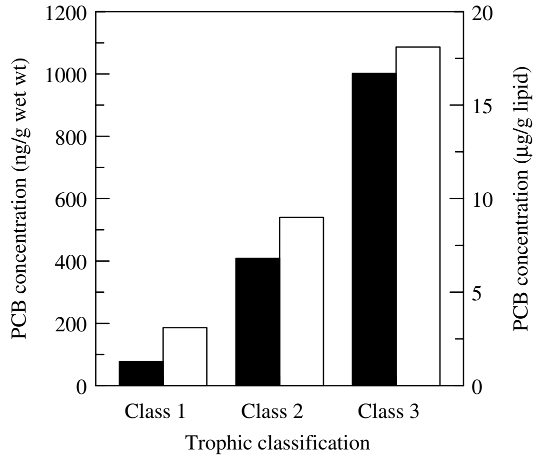

Fig. 8.11. Influence of trophic structure on concentrations of PCBs in lake trout from central Ontario lakes. Data are shown as total PCBs (solid bars) and after correcting for lipid content (open bars). Class 1 lakes with short food chains lack *Mysis* and pelagic forage fish. Class 2 lakes with intermediate length food chains lack *Mysis* but have pelagic forage fish. Class 3 lakes with long food chains have both *Mysis* and pelagic forage fish. (Data from Table 1 in Rasmussen *et al.* 1990)

Introduced species that lengthen food chains may increase levels of persistent chemicals in top predators (Kidd *et al.* 1995), especially if these species link contaminated benthic habitats to pelagic consumers.

The complexity of food webs and the presence of key species may also influence concentrations of contaminants in top predators. Wong *et al.* (1997) attributed high rates of Hg transport from benthic communities to fish in an Ontario lake to the presence of piscivorus fish. These top predators reduced abundance of benthic-feeding fish, resulting in greater biomass of macroinvertebrates. Presence of the invertebrate planktivore *Mysis relicta* was found to regulate food chain transport of organic contaminants (DDT, PCBs) in pelagic food webs (Bentzen *et al.* 1996). Stemberger and Chen (1998) observed a negative relationship between metal levels in fish tissue and the number of trophic links. They speculated that complex food webs contain a large number of lateral or horizontal links that do not terminate in top predators, resulting in reduced metal transfer within the community.

Although most studies relating levels of contaminants to food chain length have been conducted in aquatic habitats, recent evidence suggests that trophic complexity will also influence bioaccumulation and biomagnification in terrestrial species. Differences in food chain structure may explain why concentrations of organochlorines and other lipophilic contaminants are often higher in aquatic mammalian predators (e.g. mink, otters) compared with terrestrial predators.

Bremle, Larsson and Helldin (1997) speculated that the shorter food chains typical of terrestrial systems may account for lower levels of PCBs in pine marten (a forest-dwelling mustelid) compared with those in aquatic predators. Similarly, the elevated levels of organochlorines and mercury measured in bald eagles from the Aleutian Archipelago supports the hypothesis that food chain length influences bioaccumulation and biomagnification. Levels of contaminants were greater and reproductive success was lower in eagles that consumed fish-eating seabirds compared with eagles that fed directly on fish (Anthony *et al*. 1999).

8.3.9.2 Primary Productivity

Levels of organochlorines in phytoplankton and the potential transport of these chemicals to higher trophic levels are influenced by primary productivity (Taylor *et al*. 1991; Larsson, Collvin and Meyer 1992; Hanten, Neumann and Ward 1998). In general, productive lakes have higher rates of sedimentation and greater biomass dilution, resulting in lower contaminant transfer. Larsson, Collvin and Meyer (1992) reported significant variation in concentrations of PCBs and DDE in predatory fish from 61 Scandinavian lakes, despite similar inputs of pollutants. In general, levels of persistent chemicals decreased with lake productivity and concentration of humic substances. These researchers speculated that lower levels of chemicals in more productive lakes resulted from higher growth rates of fish (and corresponding growth dilution) and faster turnover of phytoplankton.

Although studies of lentic systems have generally shown a negative relationship between productivity and contaminant levels in top predators, food chain transfer of contaminants in streams may be quite different. Streams differ from lakes and large rivers in several important ways, including major physical structuring forces (flow versus thermal stratification), sources of energy (allochthonous versus autochthonous), major primary producers (periphyton versus phytoplankton), and factors that control primary productivity (light versus nutrients). As a consequence, the ecological factors that regulate contaminant transport in lotic and lentic communities may be quite different. In contrast to results observed in lakes, Berglund *et al*. (1997) reported that levels of organochlorines in brown trout from streams increased with primary productivity. Differences between lotic and lentic systems were attributed to spiraling of pollutants, a shift from heterotrophic to autotrophic production, and the greater influence of watershed area on streams.

The relationship between phytoplankton biomass and levels of contaminants in higher trophic levels has important implications for the biomanipulation experiments described above (Box 8.1). If the introduction of piscivorus fish to lakes results in lower abundance of planktivores and greater abundance of zooplankton as predicted by the trophic cascade hypothesis (Carpenter and Kitchell 1993), we may expect organochlorine concentrations in top predators to increase (Taylor *et al*. 1991). Other potential conflicts exist between managing fisheries for maximum sustainability and controlling PCB levels in sport fishes (Fig. 8.12). The

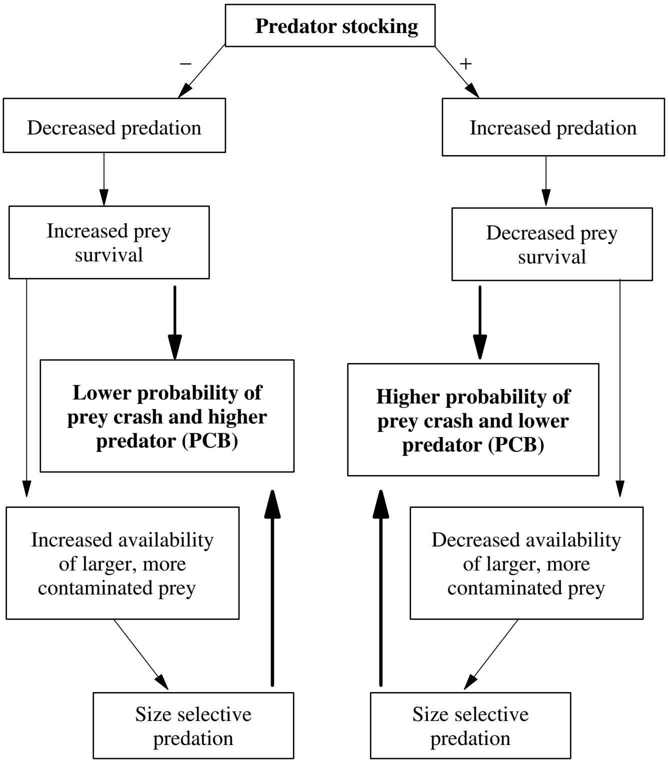

Fig. 8.12. Trade-off between managing a sustainable Great Lakes salmon fishery and maintaining PCB concentrations below the consumption advisory. (Modified from Figure 1 in Jackson 1997. Reproduced by permission of the Ecological Society of America)

sport fisheries in the Great Lakes is an approximately $10 billion per year industry. Thus, understanding the relationship between PCB levels in top predators and sport fishery management has major socioeconomic implications. Because of size-selective predation, stocking programs for salmonids and other predators may influence size structure and growth rates of prey (Jackson 1997). Lower stocking rates of salmonids would most likely reduce predation pressure and result in older, more contaminated prey species. Although higher stocking rates would result in less contaminated prey, increased predation pressure would increase the probability of a prey population crash. Jackson (1997) developed an age-structured model for Lake Ontario that considered the trade-offs between managing the Great Lakes for a sustainable fishery and the potential problems associated with elevated PCBs in top predators. Results of this model showed that small changes in stocking levels had significant effects on PCB concentrations in predators and the probability of a crash in prey communities.

8.3.9.3 Landscape Features

Large-scale, comparative studies have documented the influence of landscape features such as watershed area, land use, and hydrologic characteristics on food web structure and contaminant transport. Macdonald *et al.* (1993) reported greater bioavailability of PCBs in shallow lakes compared with deep lakes, and speculated that food web processes were more important determinants of contaminant transport in these larger systems. Similarly, Hanten, Neumann and Ward (1998) observed that watershed and hydrological characteristics explained a significant amount of variation in Hg concentrations in fish from 46 Connecticut (USA) lakes. In contrast, Paterson *et al.* (1998) found no relationship between lake size and levels of PCBs in zooplankton and fish. However, because organic carbon content decreased with lake size, levels of PCBs in sediment expressed on an organic carbon basis were greater in larger lakes.

Land use within a watershed may interact with trophic characteristics to influence contaminant transport. Berglund *et al.* (1997) reported that the percentage of land in agriculture was positively associated with higher levels of nutrients and higher concentrations of organochlorines in top predators. Evers *et al.* (1998) attributed variation in Hg concentrations measured in the common loon (*Gavia immer*) to large-scale geographic patterns of anthropogenic deposition. However, variation within a region was explained primarily by geochemical variables and lake morphology. Long-term (100-year) trends in Hg contamination were documented by comparing concentrations in bird communities collected from the North Atlantic (Monteiro and Furness 1997). Using museum specimens from the late 1800s, these researchers showed that concentrations of mercury in mesopelagic birds (those feeding on mesopelagic fish) were generally higher and increased more over the 100-year period compared with concentrations in epipelagic birds (Fig. 8.13). Although increased Hg over time in epipelagic birds was consistent with increases observed in global Hg concentrations, levels in mesopelagic birds were considerably greater. Differences between these two groups were attributed to the greater production of methylmercury in low-oxygen, mesopelagic seawater.

A spatially extensive survey of PCB concentrations in herring gull eggs collected from the Great Lakes showed that levels have declined significantly between 1974 and 1996 (Hebert 1998). However, concentrations appear to have stabilized over the past 10 years (Fig. 8.14). Interestingly, much of the annual variation in PCB concentrations resulted from the effects of winter severity on gull feeding and migration behavior. Previous studies demonstrated that winter severity influenced PCB concentrations in gulls by altering the proportion of fish in the diet (Hebert, Shutt and Norstrom 1997). In a more recent study, Hebert (1998) speculated that extreme winters forced gulls to migrate farther south where they fed in more contaminated locations. This study illustrates the importance of accounting for behavioral characteristics of animals when assessing long-term patterns in contaminant accumulation.

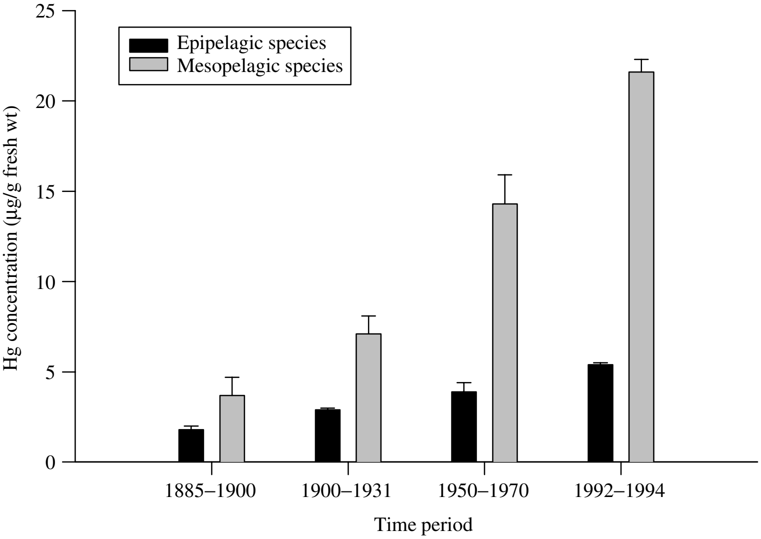

Fig. 8.13. Long-term increase in mean (+ SE) Hg concentration in epipelagic (Cory's shearwater) and mesopelagic (Bulwer's petrel) seabirds in the North Atlantic. Mesopelagic birds feed on more contaminated prey. (Data from Table 1 in Monteiro and Furness 1997)

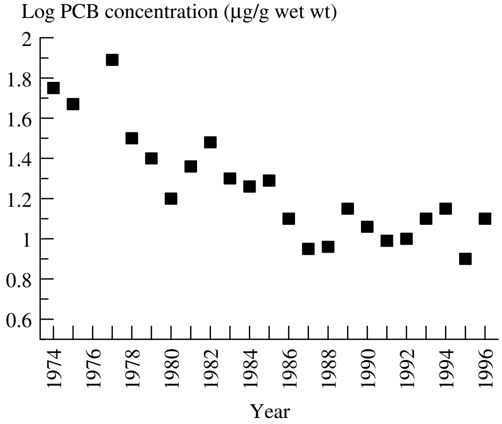

Fig. 8.14. Temporal patterns in PCB concentrations ($\log_{10}$) in herring gull eggs collected from Double Island, Lake Huron (USA). The data show that PCB levels have declined significantly since 1974, but that concentrations have stabilized around 10 µg/g wet weight. Some of the annual variation resulted from the effects of winter severity on migration patterns. (Data from Table 4 in Hebert 1998)

8.3.10 APPLICATION OF STABLE ISOTOPES TO STUDY CONTAMINANT FATE AND EFFECTS

The same problems and limitations associated with characterizing food webs for basic ecological studies also complicate ecotoxicological investigations. In particular, obtaining reliable estimates of biomagnification of contaminants is difficult because trophic levels are often poorly defined. Dietary analyses of consumers only provide a snapshot of feeding habits, and often omit important seasonal and ontogenetic changes. Indeed much of the variability associated with estimating biomagnification of different compounds results from the uncertainty of assigning organisms to trophic levels. The use of stable isotopes improves quantitative assessment of food chain transfer of contaminants by treating trophic position as a continuous variable (Box 8.2). Instead of simply characterizing a predator as a secondary or tertiary consumer, stable isotope analyses provide a quantitative and time integrated measure of trophic position. Because $\delta^{15}N$ values are enriched with trophic position, the relative degree of omnivory in a predator can also be quantified.

Box 8.2 Stable isotopes and contaminant transport

Food web structure influences the distribution and partitioning of lipophilic chemicals and may account for significant variation in contaminant concentrations within ecosystems (Rasmussen *et al*. 1990). By linking stable isotope analyses with models of contaminant transport, it is possible to examine the relationship between trophic ecology of a system and movement of contaminants through food chains. Broman *et al*. (1992) used stable isotopes of C and N to characterize pelagic and littoral food chains and to estimate biomagnification of polychlorinated dibenzo-p-dioxins (PCDDs). Levels of $\delta^{15}N$ in pelagic and littoral food chains increased from phytoplankton → seston → grazers → top predators, reflecting known trophic differences among these groups. Results showed that the total concentration of PCDDs and PCDFs decreased, whereas concentrations of the more toxic constituents increased with trophic level (Fig. 8.15). Comparison of the slopes of the relationship between contaminant concentration and trophic level (as determined by $\delta^{15}N$) for the different PCDD isomers provide an estimate of the biomagnification potential.

Kiriluk *et al*. (1995) employed a similar approach to assess biomagnification of DDE, mirex, and PCBs in a pelagic food web. Stable isotope signatures for C and N characterized this food web and defined lake trout as the top predator in the system. Results showed that $\delta^{15}N$ increased with trophic level and was significantly correlated with contaminant concentrations within the major groups. Similar to the results of Broman *et al*. (1992), these researchers concluded that the slope of the relationship between $\delta^{15}N$ and organochlorine

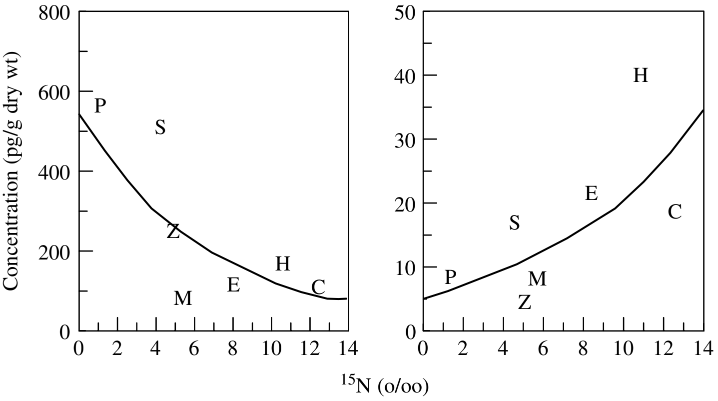

Fig. 8.15. Relationship between trophic position (as indicated by stable isotopes of N) and total concentration of 2378-substituted PCDD/Fs (left panel) and toxic content of the 2378-substituted PCDD/Fs (right panel). P, phytoplankton; S, seston; Z, zooplankton; M, mussels; E, eider ducks; H, herring; C, cod. (Modified from Figure 3 in Broman *et al.* 1992)

concentration (*b*) was an indication of biomagnification potential. This study also demonstrated the role of omnivory in aquatic food chains and showed that omnivory may be important in top predators. Considerable variation in δ^{15}N was measured among individual lake trout, reflecting the opportunistic feeding habits of these fish.

Quantification of food web structure using stable isotopes may also help clarify relationships between long-term changes in food webs and contaminant concentrations. Gradual declines in levels of persistent organochlorines and other contaminants in fish from the Great Lakes have been observed for the past 20 years (Stow *et al.* 1995). It is uncertain how much of this decline reflects reduced levels of contamination versus long-term alterations in food web structure. Stable isotope analyses may allow researchers to quantify the relative importance of reduced concentrations of organochlorines and changes in trophic structure (Kiriluk *et al.* 1995).

Great advantage has been taken of the fact that stable, naturally-occurring nitrogen isotopes are excreted at different rates by organisms. The heavy isotope (^{15}N) is not excreted as readily as the lighter ^{14}N by any species, regardless of its specific excretory biochemistry and physiology. Differential isotopic excretion leads to differential isotopic retention. A consumer will ingest a source of nitrogen slightly enriched with ^{15}N relative to atmospheric N, the ultimate source to all trophic levels. During the lifetime of that organism, ^{14}N will be excreted more readily than ^{15}N, and the enrichment of ^{15}N relative to ^{14}N during an organism's life will further shift this isotopic ratio in favor of ^{15}N. The consequence of this process is a gradual enrichment of ^{15}N relative to ^{14}N with each trophic exchange. Quantifying the degree of ^{15}N enrichment relative to ^{14}N produces an index of trophic status that readily incorporates omnivory.

The δ^{15}N metric is the most common way of expressing ^{15}N enrichment relative to ^{14}N. The ratio of ^{15}N and ^{14}N in a sample (e.g. fish tissue) is compared with the same ratio in the atmosphere using the following equation.

$$\delta^{15}\mathrm{N} = 1000\left[\frac{(^{15}\mathrm{N}_{\mathrm{tissue}})/(^{14}\mathrm{N}_{\mathrm{tissue}})}{(^{15}\mathrm{N}_{\mathrm{air}})/(^{14}\mathrm{N}_{\mathrm{air}})} - 1\right]$$

The units for δ^{15}N are parts per thousand (‰ or per mill). The average δ^{15}N increase with each trophic exchange is 3.4‰ (Minawaga and Wada 1984; Cabana and Rasmussen 1994), but it can vary from 1.3 to 5.3‰ (Minawaga and Wada 1984). A species feeding at several trophic levels will have a δ^{15}N value lower than would be predicted if omnivory was not occurring. Cabana and Rasmussen (1994) related δ^{15}N to ρ_{ij} values (the fraction of the ith's level diet coming from trophic level j) with lake trout (*Salvelinus namaycush*) as the apex predator using matrix algebra: $\boldsymbol{\delta}\ ^{15}\mathbf{N} - 3.4 = \boldsymbol{\rho\delta}\ ^{15}\mathbf{N}$. Assuming that the average increase in δ^{15}N is 3.4‰ per trophic exchange in these lakes, the realized δ^{15}N for a lake trout feeding at different trophic levels is estimated by accounting for the fraction of the diet consumed from the different levels.

Numerous studies have related δ^{15}N quantitatively to contaminant concentration in various species occupying different positions in a food web (Rasmussen *et al.* 1990; Hesslein *et al.* 1991; Broman *et al.* 1992; Rolff *et al.* 1993; Cabana *et al.* 1994; Kidd *et al.* 1995). Instead of relating changes in δ^{15}N to ρ values, statistical models are constructed relating δ^{15}N to contaminant concentration. These statistical models can be linear (e.g. linear fit of Figure 3 of Cabana and Rasmussen 1994), but application of an exponential model is more common.

$$\text{Concentration} = \mathrm{e}^{a+b\delta^{15}\mathrm{N}}$$

This model can be fit to data directly with non-linear regression methods or with linear regression methods after transformation of concentrations to a log scale.

$$\ln \text{Concentration} = a + b\delta^{15}\mathrm{N}$$

The a and b in the above model are the intercept and slope derived by linear regression. (See Newman (1993) about the importance of correcting the back-transformation bias that appears while converting results of linearized exponential models back to the original exponential form.) As a good example of applying linear regression after concentration transformation, Kidd *et al.* (1995) related total toxaphene concentration to δ^{15}N in the pristine Laberge Lake (Canada) with the following model, $\log_{10}$ of total toxaphene (ng/g wetweight) $= 0.23(\delta^{15}$N per mill) − 0.33. Relative to the same fish species in lakes nearer to toxaphene sources, trout (*S. namaycush*), burbot (*Lota lota*), and lake whitefish (*Coregonus clupeaformis*) had very high toxaphene tissue concentrations due to their more piscivorus habits in Laberge Lake. The δ^{15}N and gut content analysis of these species from several lakes supported this notion. The longer than normal food chain was the only reason for the relatively elevated toxaphene concentrations in Laberge Lake.

The term b is described by some authors as the biomagnification power (Broman *et al*. 1992; Rolff *et al*. 1993). If $b > 0$, the transfer of a contaminant is more efficient than the trophic transfer of biomass and biomagnification of the contaminant will occur. If $b < 0$, the transfer of a contaminant is less efficient than the trophic transfer of biomass and contaminant concentrations will decrease with an increase in trophic position (δ^{15}N). Finally, if $b = 0$, the transfer of a contaminant through trophic levels is the same as that for biomass and there will be no discernible change in concentration with increase in δ^{15}N. The a in the model is related to the amount of contaminant available at the base of the food chain (Rolff *et al*. 1993). However, there will be a bias in this estimate if the linearizing transformation was used to fit the data to the model and no bias correction was made (Newman 1993).

8.4 EFFECTS OF CONTAMINANTS ON FOOD CHAINS AND FOOD WEB STRUCTURE

Although there has been significant progress in the development and testing of food web theory over the past 20 years, investigators generally have not considered contaminant-induced alterations in food web structure as endpoints in ecotoxicological investigations. The limited application of basic food web ecology to ecotoxicological research is partially a result of the logistical difficulties and uncertainty associated with constructing food webs. New technical approaches, such as stable isotope analyses and bioenergetic modeling, will likely increase the integration of food web theory into ecotoxicology.

General patterns of food web structure described in the basic ecological literature provide some insight into how communities may respond to anthropogenic stress. The number of trophic levels, the connectance of food webs, and the strength of interactions are likely to be affected by exposure to contaminants. For example, one of the most consistent observations at contaminated sites is reduced species richness and simplification of community structure. Loss of species will probably be accompanied by a reduced number of trophic levels and a reduced degree of connectance. Contaminated sites also tend to be characterized by a disproportionate loss of larger, longer-lived species and a switch to smaller, more opportunistic taxa. The loss of keystone and other important predators from these systems will likely have cascading effects on lower trophic levels. Finally, because the stability of food chains is often influenced by external forces, factors such as disturbance may decouple food chains and weaken trophic cascades.

8.4.1 INTERSPECIFIC DIFFERENCES IN CONTAMINANT SENSITIVITY

Interspecific differences in sensitivity to contaminants are well established, and the effects of contaminant exposure on food webs will depend on these differences. Contaminant-induced elimination of a sensitive but ecologically important species from a food web would have significant consequences for trophic levels above and below. Currently, there is little evidence indicating that any one trophic level will be more or less sensitive to contaminants than another. However, because of the potential for biomagnification of lipid-soluble contaminants, we expect that top predators will be more susceptible to lipophilic contaminants than their prey. For example, the extremely high sensitivity and susceptibility of mink (*Mustela vison*) to organochlorines, especially PCBs, is well established (Peterle 1991). Because these organisms are considerably more sensitive to organochlorines than their prey (primarily fish), PCBs could eliminate this top predator resulting in significant effects on lower trophic levels.

The relative influence of species loss on consumer or resource trophic levels will depend on a number of factors, including the importance of top-down versus bottom-up regulation. In many ways, contaminant-induced mortality is similar to the effects of a selective predator (Carman, Fleeger and Pomarico 1997). According to the trophic cascade hypothesis, removal of a top predator in a three-trophic level system regulated by top-down forces would result in decreased biomass of primary producers. In contrast, the loss of a top predator in a four-trophic level system would result in an increase in producer biomass. Similarly, elimination of an important grazer would result in increased primary producer biomass but reduced predator biomass.

8.4.2 INDIRECT EFFECTS OF CONTAMINANT EXPOSURE ON FEEDING HABITS

Exposure to contaminants may have both direct and indirect effects on feeding relationships and trophic interactions. Altered prey behavior following exposure to pesticides may increase vulnerability to predation, thus increasing predator exposure to contaminants. Schauber, Edge and Wolff (1997) reported that deer mice (*Peromyscus maniculatus*) consumed more insects immediately following application of insecticides, suggesting that these organisms opportunistically selected dead or dying prey. Selective predation and the ability of predators to switch to contaminated prey will greatly complicate our ability to predict effects of contaminants on trophic interactions.

Elimination or reduction of prey resources will cause predators to shift to alternative prey species and may have important energetic consequences for predators.

Experimental studies investigating effects of large-scale insecticide sprays have provided an unprecedented opportunity to evaluate responses of bird predators to reductions in prey abundance. These studies also demonstrate the important linkage between evolutionary ecology and ecotoxicology. Because many avian species are adapted to take advantage of seasonal increases in insect abundance, the application of pesticides often coincides with critical life-history periods. The greatest exposure and potential for loss of prey resources occurs when adults are caring for their young. Surprisingly, despite large reductions in prey abundance following application of pesticides, some studies have shown relatively little indirect impact on insectivorous birds (Powell 1984; Adams *et al*. 1994; Howe *et al*. 1996). These results suggest that either prey resources are superabundant in these systems or that predators are able to switch to alternative prey.

The opportunistic feeding habits of many predators may allow them to compensate for contaminant-induced reductions in abundance of preferred prey. Clements and Rees (1997) examined the effects of heavy metals on prey abundance and feeding habits of brown trout (*Salmo trutta*). Prey communities at an unpolluted station were dominated by metal-sensitive mayflies (Ephemeroptera) and black flies (Diptera: Simuliidae), whereas those at a polluted site were dominated by metal-tolerant chironomids (Diptera: Chironomidae) and caddisflies (Trichoptera). Differences in prey community composition were reflected in the feeding habits of brown trout, which consumed primarily chironomids and caddisflies at the metal-polluted station. Despite these alterations in prey communities, the mean biomass of prey consumed by brown trout was actually greater at the polluted site. These results are consistent with the hypothesis that a predator's feeding habits are flexible and can shift to take advantage of locally abundant prey resources. Similar results were reported by Wipfli and Merritt (1994) for invertebrate predators. Experimental treatment of two streams with the black fly larvicide B.t.i. (*Bacillus thuringiensis* var *israelensis*) resulted in a switch to alternative, less preferred prey species. The ability to utilize alternative prey varied among species, as effects of prey reduction were greater for specialized predators than for generalized predators.

8.4.3 ALTERATIONS IN ENERGY FLOW AND TROPHIC STRUCTURE

Energy flow and trophic structure of communities may be altered by exposure to contaminants if important functional groups are eliminated. Experimental and descriptive studies conducted in Rocky Mountain streams have shown that grazing mayflies are highly sensitive to heavy metals and usually eliminated from polluted streams (Clements *et al*. 2000). These organisms are generally replaced by metal-resistant groups, resulting in a shift in energy flow and greater utilization of detritus by other consumers. Carlisle (2000) used stable isotopes to characterize the food webs of stream communities impacted by heavy metals. As expected, isotopic analysis of food web structure showed a greater reliance on detritus in the metal-polluted stream and a greater utilization of periphyton in the unpolluted stream. These findings are in agreement with Odum's (1985) predictions that stressed ecosystems tend to be more detritus-based compared with unstressed ecosystems.

Exposure of meiofaunal communities to diesel fuel in sediment microcosms resulted in significantly increased algal biomass due to lower grazing pressure by hydrocarbon-sensitive copepods (Carman, Fleeger and Pomarico 1997). These researchers observed a similar pattern of reduced grazing pressure and increased algal biomass in a field study. Although stimulation of algae by hydrocarbons has been reported previously, this was the first study to demonstrate the role of grazers. Clearly, consideration of multiple trophic levels is necessary to understand mechanisms by which natural communities respond to contaminants.

A long-term series of studies conducted by Wallace and colleagues in the Coweeta Experimental Forest demonstrated significant alterations in food chains and energy flow after experimental introductions of the larvicide methoxychlor (Wallace, Webster and Cuffney 1982; Wallace *et al.* 1987, 1989). Catastrophic drift following methoxychlor treatments resulted in a 90% reduction in total abundance and biomass of stream invertebrates. Changes in abundance of dominant prey taxa also caused shifts in feeding habits of predators. More importantly, the elimination of shredders (organisms that consume leaf litter) reduced leaf decomposition rates and the amount of particulate organic material transferred downstream.

Alterations in trophic structure observed in contaminated systems may depend on specific characteristics of the food web. In simple two-trophic level systems (producers and herbivores), toxic substances may modify trophic structure by reducing abundance of important grazers, resulting in an increase in primary producers (Webber *et al.* 1992). In a three-trophic level system exposed to the insecticide esfenvalerate, Fairchild *et al.* (1992) reported that increased biomass of primary producers resulted from lower predation by bluegill on grazing zooplankton. Whole ecosystem acidification studies conducted by Schindler and colleagues (Schindler *et al.* 1985) have shown that elimination of mysids (*Mysis relicta*) and fathead minnows (*Pimephales promelas*), major prey organisms in the lake's pelagic food web, had significant effects on lake trout condition. Interestingly, abundance of lake trout and changes in ecosystem processes (primary productivity, decomposition, nutrient cycling) were less sensitive to acidification than food web alterations.

Because species interactions in natural communities are often subtle, experimental manipulation of both contaminants and consumers may be necessary to understand consumer–resource dynamics. In experimental rockpools, Koivisto, Arner and Kautsky (1997) manipulated levels of Cd, grazers, and predators to measure interactions between chemical stressors and trophic structure. Results showed that Cd directly reduced phytoplankton and zooplankton abundance, but did not alter trophic interactions. In contrast, reduction of herbivores by predators resulted in increased phytoplankton productivity, demonstrating top-down control of this system.

Although most research on contaminant-induced alterations in trophic structure has been limited to aquatic systems, a few investigators have examined food web responses in soil communities (Parker *et al.* 1984; Parmelee *et al.* 1993, 1997). Organisms inhabiting soil communities control important ecosystem processes such as decomposition and mineralization. Because soil microfaunal communities are often naturally diverse and consist of large numbers of organisms (10^4 to $10^6/m^2$), effects on multiple species at several trophic levels can be investigated at ecologically realistic spatial and temporal scales (Parmelee *et al.* 1993). When integrated with microbial assays and measures of functional characteristics (soil respiration, decomposition), soil microcosm experiments provide a relatively complete assessment of contaminant effects.

A major challenge of working with soil fauna, especially meiofauna, is the difficulty in identifying certain taxonomic groups. This limitation can be partially resolved by categorizing organisms based on guilds or functional feeding groups (e.g. fungivore, bacterivore, herbivore, omnivore-predator) instead of relying on traditional taxonomic measures. Parmelee *et al.* (1993) observed considerable variation in sensitivity to contaminants among trophic groups, and noted that reduced abundance of predators resulted in increased abundance of herbivores (Fig. 8.16). Similar results were reported in desert soil communities treated with insecticides (Parker *et al.* 1984). The large amount of variation among feeding groups demonstrates the importance of understanding trophic structure when assessing ecological impacts on soil communities.

Finally, it should be noted that complete removal of species is not necessary to disrupt the structure and function of food webs. Significantly reduced abundance

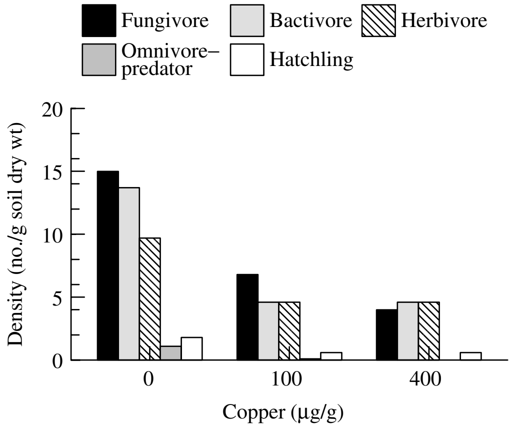

Fig. 8.16. Responses of nematode functional groups to copper in soil microcosms. (Modified from Figure 1 in from Parmelee *et al.* 1997)

of predators or prey could influence lower or higher trophic levels. As noted above, many vertebrate predators are capable of switching to alternative prey when abundance of preferred prey drops below a particular threshold. Because contaminants influence either the ability of predators to capture prey or the ability of prey to escape predation (Chapter 2), species-specific differences in relative sensitivity will ultimately influence how food webs are affected by these stressors.

8.4.4 THE DEVELOPMENT AND APPLICATION OF BIOENERGETIC FOOD WEBS IN ECOTOXICOLOGY

Carlisle (2000) has proposed a bioenergetic approach for assessing impacts of contaminants on communities that combines population measures of secondary

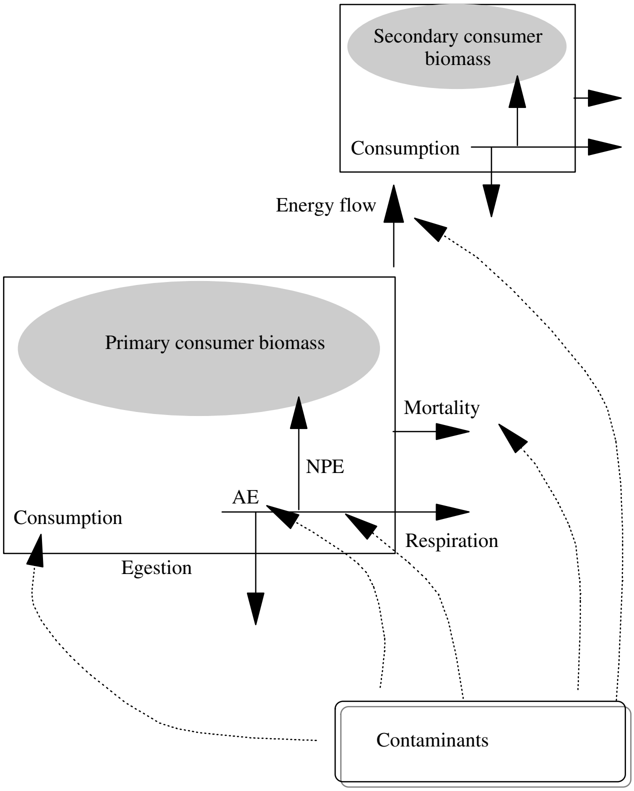

Fig. 8.17. Model describing the potential effects of contaminants on bioenergetics. Solid lines show the flow of energy within and between trophic levels. Dashed lines show the aspects of production that are likely to be affected by contaminants. AE, assimilation efficiency; NPE, net production efficiency. (Modified from Figure 3 in Carlisle 2000)

production with energetic food webs. Just as growth integrates numerous physiological processes in individual organisms, secondary production integrates important population processes and is a useful endpoint in ecotoxicological investigations. This approach assumes that exposure to contaminants will modify population energetics directly by effects on growth, mortality, production efficiency, and assimilation efficiency. Indirect effects include alterations in feeding behavior, quality/quantity of resources, and susceptibility to predation (Fig. 8.17). Using data collected from Rocky Mountain streams impacted by heavy metals, Carlisle (2000) measured community-level production in a guild of aquatic insects and linked these estimates using energetic food webs. Results showed that metals significantly reduced secondary production of several species, primarily through reduced abundance, and that these changes had cascading effects on predators. This bioenergetic food web approach is an important step in linking observed toxicological effects on population growth and production to ecologically significant responses at higher levels of organization.

8.5 SUMMARY

In summary, a significant amount of empirical and theoretical research has been devoted to understanding the structure and function of food webs in basic ecology. The historical application of food web theory in ecotoxicology has been limited primarily to predicting the flux of contaminants through food chains and estimating potential exposure to top predators. More recently, ecotoxicologists have developed a better understanding of how ecological characteristics (e.g. primary production, food chain length, trophic complexity) influence transport of contaminants through food chains. However, there has been relatively little effort devoted to predicting the direct effects of contaminants on food chain structure or using food web characteristics as endpoints in ecotoxicological assessments. We see this as an important area for future research in community ecotoxicology. If food is the ‘burning question’ in animal communities as suggested by Elton (1927), the field of ecotoxicology would benefit from a greater understanding of how contaminants directly and indirectly influence food chain structure.

REFERENCES

Adams JS, Knight RL, McEwen LC and George TL (1994). Survival and growth of nestling Vesper Sparrows exposed to experimental food reductions. *Condor* **96**: 739–748.

Anthony RG, Miles AK, Estes JA and Isaacs FB (1999). Productivity, diets, and environmental contaminants in nesting bald eagles from the Aleutian Archipelago. *Environ Toxicol Chem* **18**: 2054–2062.

Begon M, Harper JL and Townsend CR (1990). *Ecology: Individuals, Populations and Communities*. Blackwell Scientific Publications, Cambridge, MA.

Benke AC and Wallace JB (1997). Trophic basis of production among riverine caddisflies: implications for food web analysis. *Ecology* **78**: 1132–1145.

Bentzen E, Lean DRS, Taylor WD and Mackay D (1996). Role of food web structure on lipid and bioaccumulation of organic contaminants by lake trout (*Salvelinus namycush*). *Can J Fish Aquat Sci* **53**: 2397–2407.

Berglund O, Larsson P, Bronmark C, Greenberg L, Eklov A and Okla L (1997). Factors influencing organochlorine uptake in age-0 brown trout (*Salmo trutta*) in lotic environments. *Can J Fish Aquat Sci* **54**: 2767–2774.

Beyers DW, Rice JA and Clements WH (1999). Evaluating biological significance of chemical exposure to fish using a bioenergetics-based stressor-response model. *Can J Fish Aquat Sci* **56**: 823–829.

Beyers DW, Rice JA, Clements WH and Henry CJ (1999). Estimating physiological cost of chemical exposure: integrating energetics and stress to quantify toxic effects in fish. *Can J Fish Aquat Sci* **56**: 814–822.

Bremle G, Larsson P and Helldin JO (1997). Polychlorinated biphenyls in a terrestrial predator, the pine marten (*Martes martes L.*). *Environ Toxicol Chem* **16**: 1779–1784.

Brett MT and Goldman CR (1996). A meta-analysis of the freshwater trophic cascade. *Proc Natl Acad Sci USA* **93**: 7723–7726.

Brett MT and Goldman CR (1997). Consumer versus resource control in freshwater pelagic food webs. *Science* **275**: 384–386.

Briand F and Cohen JE (1987). Environmental correlates of food chain length. *Science* **238**: 956–960.

Broman D, Naf C, Rolff C, Zebuhr Y, Fry B and Hobbie J (1992). Using ratios of stable nitrogen isotopes to estimate bioaccumulation and flux of polychlorinated dibenzo-p-dioxins (PCDDs) and dibenzofurans (PCDFs) in two food chains from the northern Baltic. *Environ Toxicol Chem* **11**: 331–345.

Cabana G and Rasmussen, JB (1994). Modeling food chain structure and contaminant bioaccumulation using stable nitrogen isotopes. *Nature* **372**: 255–257.

Cabana G, Tremblay A, Kalff J and Rasmussen JB (1994). Pelagic food chain structure in Ontario lakes: a determinant of mercury levels in lake trout (*Salvelinus namacush*). *Can J Fish Aquat Sci* **51**: 381–389.

Carlisle DM (2000). Bioenergetic food webs as a means of linking toxicological effects across scales of ecological organization. *J Aquat Ecosys Stress Recov* **7**: 155–165.

Carman KR, Fleeger JW and Pomarico SM (1997). Response of a benthic food web to hydrocarbon contamination. *Limnol Oceanogr* **42**: 561–571.

Carpenter SR and Kitchell JF (1993). *The Trophic Cascade in Lakes*. Cambridge University Press, Cambridge, UK.

Carson R (1962). *Silent Spring*. Houghton Mifflin, Boston, MA.

Chen B and Wise DH (1999). Bottom-up limitation of predaceous arthropods in a detritus based terrestrial food web. *Ecology* **80**: 761–772.

Ciarelli S, van Straalen NM, Klap VA and van Wezel AP (1999). Effects of sediment bioturbation by the estuarine amphipod *Corophium volutator* on fluoranthene resuspension and transfer into the mussel (*Mytilus edulis*). *Environ Toxicol Chem* **18**: 318–328.

Clements WH and Livingston RJ (1983). Overlap and pollution-induced variability in the feeding habits of filefish (Pisces: Monocanthidae) from Apelike Bay, Florida. *Copeia* **1983**: 331–338.

Clements WH and Rees DE (1997). Effects of heavy metals on prey abundance, feeding habits, and metal uptake of brown trout in the Arkansas River, Colorado. *Trans Am Fish Soc* **126**: 774–785.

Clements WH, Carlisle DM, Lazorchak JM and Johnson PC (2000). Heavy metals structure benthic communities in Colorado mountain streams. *Ecol Appl* **10**: 626–638.

Colinvaux P (1978). *Why Big Fierce Animals Are Rare. An Ecologist's Perspective*. Princeton University Press, Princeton, NJ.

Dallinger R and Kautzky H (1985). The importance of contaminated food for the uptake of heavy metals by rainbow trout (*Salmo gairdneri*): a field study. *Oecologia* **67**: 82–89.

Dallinger R, Prosi F, Segner H and Back H (1987). Contaminated food and uptake of heavy metals by fish: a review and a proposal for further research. *Oecologia* **73**: 91–98.

de Ruiter PC, Neutel A and Moore JC (1995). Energetics, patterns of interaction strengths, and stability in real ecosystems. *Science* **269**: 1257–1260.

DiPinto LM and Coull BC (1997). Trophic transfer of sediment-associated polychlorinated biphenyls from meiobenthos to bottom-feeding fish. *Environ Toxicol Chem* **16**: 2568–2575.

Elton C (1927). *Animal Ecology*. Macmillan, New York, NY.

Estes JA, Tinker MT, Williams TM and Doak DF (1998). Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* **282**: 473–476.

Evans MS, Noguchi GE and Rice CP (1991). The biomagnification of polychlorinated biphenyls, toxaphene, and DDT compounds in a Lake Michigan offshore food wed. *Arch Environ Contam Toxicol* **20**: 87–93.

Evers DC, Kaplan JD, Meyer MW, Reaman PS, Braselton WE, Major A, Burgess N and Scheuhammer AM (1998). Geographic trend in mercury measured in common loon feathers and blood. *Environ Toxicol Chem* **17**: 173–183.

Fairchild JF, La Point TW, Zajicek JL, Nelson MK, Dwyer FJ and Lovely PA (1992). Population, community, and ecosystem-level responses of aquatic mesocosms to pulsed doses of a pyrethroid insecticide. *Environ Toxicol Chem* **11**: 115–129.

Farag AM, Woodward DF, Goldstein JN, Brumbaugh W and Meyer JS (1998). Concentrations of metals associated with mining waste in sediments, biofilm, benthic macroinvertebrates, and fish from the Coeur d'Alene River Basin, Idaho. *Arch Environ Contam Toxicol* **34**: 119–127.

Fretwell SD (1987). Food chain dynamics: the central theory of ecology? *Oikos* **50**: 291–301.

Froese KL, Verbrugge DA, Ankley GT, Niemi GJ, Larsen CP and Giesy JP (1998). Bioaccumulation of polychlorinated biphenyls from sediments to aquatic insects and tree swallow eggs and nestlings in Saginaw Bay, Michigan, USA. *Environ Toxicol Chem* **17**: 484–492.

Hairston Jr NG and Hairston Sr NG (1993). Cause–effect relationships in energy flow, trophic structure, and interspecific interactions. *Am Nat* **142**: 379–411.

Hairston Sr NG, Smith FE and Slobodkin LB (1960). Community structure, population control, and interspecific competition. *Am Nat* **94**: 421–425.

Hanten RP, Neumann RM and Ward SM (1998). Relationships between concentrations of mercury in largemouth bass and physical and chemical characteristics of Connecticut lakes. *Trans Am Fish Soc* **127**: 807–818.

Hatakeyama S and Yasuno M (1987). Chronic effects of Cd on the reproduction of the guppy (*Poecilia reticulata*) through Cd-accumulated midge larvae (*Chironomus yoshimatsui*). *Ecotox Environ Safety* **14**: 191–207.

Hebert CE (1998). Winter severity affects migration and contaminant accumulation in northern Great Lakes Herring Gulls. *Ecol Appl* **8**: 669–679.

Hebert CE, Shutt JL and Norstrom RJ (1997). Dietary changes cause temporal fluctuations in polychlorinated biphenyl levels in Herring Gull eggs from Lake Ontario. *Environ Sci Technol* **31**: 1012–1017.

Hesslein RH, Capel MJ, Fox DE and Hallard KA (1991). Stable isotopes of sulfur, carbon, and nitrogen as indicators of trophic level and fish migration in Lower MacKenzie River Basin, Canada. *Can J Fish Aquat Sci* **48**: 2258–2265.

Howe FP, Knight RL, McEwen LC and George TL (1996). Direct and indirect effects of insecticide applications on growth and survival of nestling passerines. *Ecol Appl* **6**: 1314–1324.

Hunter MD and Price PW (1992). Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* **73**: 724–732.

Jackson LJ (1997). Piscivores, predation, and PCBs in Lake Ontario's pelagic food web. *Ecol Appl* **7**: 991–1001.

Jackson LJ and Schindler DE (1996). Field estimates of net trophic transfer of PCBs from prey fishes to Lake Michigan salmonids. *Environ Sci Technol* **30**: 1861–1865.

Jeffree RA and Williams NJ (1980). Mining pollution and the diet of the purple-striped gudgeon *Mogurnda mogurnda* Richardson (Eleotridae) in the Finniss River, Northern Territory, Australia. *Ecol Monogr* **50**: 457–485.

Jeffries MJ and Lawton JH (1985). Predator–prey ratios in communities of freshwater invertebrates: the role of enemy free space. *Freshw Biol* **15**: 105–112.

Kidd KA, Schindler DW, Muir DCG, Lockhart WL and Hesslein RH (1995). High concentrations of toxaphene in fishes from a subarctic lake. *Science* **269**: 240–242.

Kidd KA, Schindler DW, Hesslein RH and Muir DCG (1998). Effects of trophic position and lipid on organochlorine concentrations in fishes from subarctic lakes in Yukon Territory. *Can J Fish Aquat Sci* **55**: 869–881.

Kiffney PM and Clements WH (1993). Bioaccumulation of heavy metals by benthic invertebrates at the Arkansas River, Colorado, USA. *Environ Toxicol Chem* **12**: 1507–1517.

Kiriluk RM, Servos MR, Whittle DM, Cabana G and Rasmussen JB (1995). Using ratios of stable nitrogen and carbon isotopes to characterize the biomagnification of DDE, mirex, and PCB in a Lake Ontario pelagic food web. *Can J Fish Aquat Sci* **52**: 2660–2674.

Kitchell JF (1992). *Food Web Management – a Case Study of Lake Mendota*. Springer-Verlag. New York, NY.

Koivisto S, Arner M and Kautsky N (1997). Does cadmium pollution change trophic interactions in rockpool food webs? *Environ Toxicol Chem* **16**: 1330–1336.

Kozie KD and Anderson RK (1991). Productivity, diet, and environmental contaminants in bald eagles nesting near the Wisconsin shoreline of Lake Superior. *Arch Environ Contam Toxicol* **20**: 41–48.

Langevoord M, Kraak MHS, Kraal MH and Davids C (1995). Importance of prey choice for Cd uptake by carp (*Cyprinus carpio*) fingerlings. *J N Am Benthol Soc* **14**: 423–429.

Larsson P, Collvin L and Meyer G (1992). Lake productivity and water chemistry as governors of the uptake of persistent pollutants in fish. *Environ Sci Technol* **26**: 346–352.

Leonards PEG, Zierikzee Y, Brinkman UATh, Cofino WP, van Straalen NM and van Hattum B (1997). The selective dietary accumulation of planar polychlorinated biphenyls in the otter (*Lutra lutra*). *Environ Toxicol Chem* **16**: 1807–1815.

Lindeman RL (1942). The trophic-dynamic aspect of ecology. *Ecology* **23**: 399–418.

Livingston RJ (1984). Trophic response of fishes to habitat variability in coastal seagrass systems. *Ecology* **65**: 1258–1275.

Macdonald CR, Metcalfe CD, Balch GC and Metcalfe TL (1993). Distribution of PCB congeners in seven lake systems: interactions between sediment and food-web transport. *Environ Toxicol Chem* **12**: 1991–2003.

May RM (1981). Patterns in multi-species communities. In *Theoretical Ecology*, ed. by May RM, pp. 197–227. Blackwell Scientific Publications, Boston, MA.

Mazak EJ, MacIsaac HJ, Servos MR and Hesslein R (1997). Influence of feeding habits on organochlorine contaminant accumulation in waterfowl on the Great Lakes. *Ecol Appl* **7**: 1133–1143.

McLaren BE and Peterson RO (1994). Wolves, moose, and tree rings on Isle Royale. *Science* **266**: 1555–1558.

Menge BA (1992). Community regulation: under what conditions are bottom-up factors important on rocky shores? *Ecology* **73**: 755–765.

Micheli F (1999). Eutrophication, fisheries, and consumer–resource dynamics in marine pelagic ecosystems. *Science* **285**: 1396–1398.

Minawaga M and Wada E (1984). Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between ^{15}N and animal age. *Geochem Cosm Acta* **48**: 1135–1140.

Monteiro LR and Furness RW (1997). Accelerated increase in mercury contamination in north Atlantic mesopelagic food chains as indicated by time series of seabird feathers. *Environ Toxicol Chem* **16**: 2489–2493.

Moriarty F and Walker CH (1987). Bioaccumulation in food chains – a rational approach. *Ecotox Environ Safety* **13**: 208–215.

Moriarty F, Hanson HM and Freestone P (1984). Limitations of body burden as an index of environmental contamination: heavy metals in fish *Cottus gobio* L. from the River Ecclesbourne, Derbyshire. *Environ Pollut* **34**: 297–320.

Morrison HA, Gobas FAPC, Lazar R, Whittle DM and Haffner GD (1997). Development and verification of a benthic/pelagic food web bioaccumulation model for PCB congeners in western Lake Erie. *Environ Sci Technol* **31**: 3267–3273.

Mount DR, Barth AK, Garrison TD, Barten KA and Hockett JR (1994). Dietary and waterborne exposure of rainbow trout (*Oncorhynchus mykiss*) to copper, cadmium, lead and zinc using a live diet. *Environ Toxicol Chem* **13**: 2031–2041.

Muir CG, Norstrom R and Simon M (1988). Organochlorine contaminants in arctic marine food chains: accumulation of specific polychlorinated biphenyls and chlordane-related compounds. *Environ Sci Technol* **22**: 1071–1979.

Munger C and Hare L (1997). Relative importance of water and food as cadmium sources to an aquatic insect (*Chaoborus punctipennis*): implications for predicting Cd bioaccumulation in nature. *Environ Sci Technol* **31**: 891–895.

Nakano S, Miyasaka H and Kuhara N (1999). Terrestrial–aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. *Ecology* **80**: 2435–2441.

Newman MC (1993). Regression analysis of log-transformed data: statistical bias and its correction. *Environ Toxicol Chem* **12**: 1129–1133.

Odum EP (1968). Energy flow in ecosystems: a historical review. *Amer Zool* **8**: 11–18.

Odum EP (1969). The strategy of ecosystem development. *Ecology* **164**: 262–270.

Odum EP (1985). Trends expected in stressed ecosystems. *BioScience* **35**: 419–422.

Owens JW, Swanson SM and Birkolz DA (1994). Bioaccumulation of 2,3,7,8-tetrachlorodibenzo-p-dioxin, 2,3,7,8-tetrachlorodibenzofuran and extractable organic chlorine at a bleached-kraft mill site in a northern Canadian river system. *Environ Toxicol Chem* **13**: 343–354.

Paine RT (1980). Food webs: linkage, interaction strength and community infrastructure. *J. Anim Ecol* **49**: 667–685.

Paine RT, Tegner MJ and Johnson EA (1998). Compounded perturbations yield ecological surprises. *Ecosystems* **1**: 535–545.

Parker LW, Santos PF, Phillips J and Whitford WG (1984). Carbon and nitrogen dynamics during the decomposition of litter and roots of a Chihuahuan desert annual. *Lepidium lasiocarpum. Ecol Monogr* **54**: 339–360.

Parmelee RW, Phillips CT, Checkai RT and Bohlen PJ (1997). Determining the effects of pollutants on soil faunal communities and trophic structure using a refined microcosm system. *Environ Toxicol Chem* **16**: 1212–1217.

Parmelee RW, Wentsel RS, Phillips CT, Simini M and Checkai RT (1993). Soil microcosm for testing effects of chemical pollutants on soil fauna communities and trophic structure. *Environ Toxicol Chem* **12**: 1477–1486.

Paterson MJ, Muir DCG, Rosenberg B, Fee EJ, Anema C and Franzin W (1998). Does lake size affect concentrations of atmospherically derived polychlorinated biphenyls in water, sediment, zooplankton, and fish? *Can J Fish Aquat Sci* **55**: 544–553.

Peterle TJ (1991). *Wildlife Toxicology*. Van Nostrand Reinhold, New York, NY.

Pimm SL (1982). *Food Webs*. Chapman and Hall, London, UK.

Polis GA (1991). Complex trophic interactions in deserts: an empirical critique of food-web theory. *Am Nat* **138**: 123–155.

Powell GVN (1984). Reproduction by an altricial songbird, the red-winged blackbird, in fields treated with the organophosphate insecticide fenthion. *J Appl Ecol* **21**: 83–95.

Power ME (1990). Effects of fish in river food webs. *Science* **250**: 811–814.

Ramade F (1987). *Ecotoxicology*. John Wiley and Sons, New York, NY

Rasmussen JB, Rowan DJ, Lean DRS and Carey JH (1990). Food chain structure in Ontario lakes determines PCB levels in lake trout (*Salvelinus namaycush*) and other pelagic fish. *Can J Fish Aquat Sci* **47**: 2030–2038.

Reynoldson TB (1987). Interactions between sediment contaminants and benthic organisms. *Hydrobiologia* **149**: 53–66.

Ricklefs RE (1990). *Ecology* (3rd edn). W.H. Freeman and Company, New York, NY.

Rolff C, Broman D, Näf C and Zebühr Y (1993). Potential biomagnification of PCDD/Fs – new possibilities for quantitative assessment using stable isotope trophic position. *Chemosphere* **27**: 461–468.

Russell RW, Gobas PAPC and Haffner DG (1999). Role of chemical and ecological factors in trophic transfer of organic chemicals in aquatic food webs. *Environ Toxicol Chem* **18**: 1250–1257.

Schauber EM, Edge WD and Wolff JO (1997). Insecticide effects on small mammals: influence of vegetation structure and diet. *Ecol Appl* **7**: 143–157.

Schindler DW, Mills KH, Malley DF, Findlay DL, Shearer JA, Davies IJ, Turner MA, Linsey GA and Cruikshank DR (1985). Long-term ecosystem stress: the effects of years of experimental acidification on a small lake. *Science* **228**: 1395–1401.

Stein RA, DeVries DR and Dettmers JM (1995). Food-web regulation by a planktivore: exploring the generality of the trophic cascade hypothesis. *Can J Fish Aquat Sci* **52**: 2518–2526.

Stemberger RS and Chen CY (1998). Fish tissue metals and zooplankton assemblages of northeastern lakes. *Can J Fish Aquat Sci* **55**: 339–352.

Stow CA, Carpenter SR, Eby LA, Amrhein JF and Hesselberg RJ (1995). Evidence that PCBs are approaching stable concentrations in Lake Michigan fishes. *Ecol Appl* **5**: 248–260.

Strong DR (1992). Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology* **73**: 747–754.

Talmage SS and Walton BT (1993). Food chain transfer and potential renal toxicity of mercury to small mammals at a contaminated terrestrial field site. *Ecotoxicology* **2**: 243–256.

Taylor WD, Carey JH, Lean DRS and McQueen DJ (1991). Organochlorine concentrations in the plankton of lakes in southern Ontario and their relationship to plankton biomass. *Can J Fish Aquat Sci* **48**: 1960–1966.

Thomann RV (1981). Equilibrium model of fate of microcontaminants in diverse aquatic food chains. *Can J Fish Aquat Sci* **38**: 280–296.

Thomann RV (1989). Bioaccumulation model of organic chemical distribution in aquatic food chains. *Environ Sci Technol* **23**: 699–707.

van Hattum B, Timmermans KR and Govers HA (1991). Abiotic and biotic factors influencing *in situ* trace metal levels in macroinvertebrates in freshwater ecosystems. *Environ Toxicol Chem* **10**: 275–292.

Vander Zanden MJ, Casselman JM and Rasmussen JB (1999). Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature* **401**: 464–467.

Wallace JB, Cuffney TF, Lay CC and Vogel D (1987). The influence of an ecosystem-level manipulation on prey consumption by a lotic dragonfly. *Can J Zool* **65**: 35–40.

Wallace JB, Eggert SL, Meyer JL and Webster JR (1997). Multiple trophic levels of a forested stream linked to terrestrial litter inputs. *Science* **277**: 102–104.

Wallace JB, Lugthart GJ, Cuffney TF and Schurr GA (1989). The impact of repeated insecticidal treatments on drift and benthos of a headwater stream. *Hydrobiologia* **179**: 135–147.

Wallace JB, Webster JR and Cuffney TF (1982). Stream detritus dynamics: regulation by invertebrate consumers. *Oecologia* **53**: 197–200.

Wallace WG, Lopez GR and Levinton JS (1998). Cadmium resistance in an oligochaete and its effect on cadmium trophic transfer to an omnivorous shrimp. *Mar Ecol Prog Ser* **172**: 225–237.

Webber EC, Deutsch WG, Bayne DR and Seesock WC (1992). Ecosystem-level testing of a synthetic pyrethroid insecticide in aquatic mesocosms. *Environ Toxicol Chem* **11**: 87–105.

Wipfli MS and Merritt RW (1994). Disturbance to a stream food web by a bacterial larvicide specific to black flies: feeding responses of predatory macroinvertebrates. *Freshw Biol* **32**: 91–103.

Wong AHK, McQueen DJ, Williams DD and Demers E (1997). Transfer of mercury from benthic invertebrates to fishes in lakes with contrasting fish community structures. *Can J Fish Aquat Sci* **54**: 1320–1330.

Woodward DF, Brumbaugh WG, DeLonay AJ, Little EE and Smith CE (1994). Effects on rainbow trout of a metals-contaminated diet of benthic invertebrates from the Clark Fork River, Montana. *Trans Am Fish Soc* **123**: 51–62.

Woodward DF, Farag AM, Bergman HL, Delonay AJ, Little EE, Smith CE and Barrows FT (1995). Metals-contaminated benthic invertebrates in the Clark Fork River, Montana: effects on age-0 brown trout and rainbow trout. *Can J Fisheries Aquat Sci* **52**: 1994–2004.

Wootton JT, Parker MS and Power ME (1996). Effects of disturbance on river food webs. *Science* **273**: 1558–1561.

Zaranko DT, Griffiths RW and Kaushik NK (1997). Biomagnification of polychlorinated biphenyls through a riverine food web. *Environ Toxicol Chem* **16**: 1463–1471.

9 Conclusions

9.1 GENERAL

The study of community ecology is primarily concerned with understanding how biotic and abiotic factors influence patterns of distribution, abundance, and species diversity. Deriving mechanistic explanations for patterns observed in nature, including the lognormal distribution of abundance, species–area relationships, and the spatial changes that occur across latitudinal or elevational gradients, has occupied the attention of community ecologists for several decades. Our treatment of community ecotoxicology has attempted to explain how communities will respond to one major abiotic factor: contaminants. Direct effects of contaminants may result in reduction or elimination of local populations and are generally easier to interpret than indirect effects. An autecological understanding of life-history characteristics and species-specific sensitivity to contaminants may be sufficient for predicting direct effects on populations. In contrast, indirect effects of contaminants are often subtle and difficult to predict without conducting manipulative experiments. Our poor understanding of the indirect effects of contaminants on communities is surprising, especially given the prominent role that research on species interactions (e.g. competition, predation, mutualism) has played in basic ecology. If ecotoxicologists accept the notion that species interactions are important in regulating natural communities, then focused research should be directed at understanding the influence of contaminants on these interactions.

9.2 SOME PARTICULARLY KEY CONCEPTS

9.2.1 IMPROVEMENTS IN EXPERIMENTAL TECHNIQUES

One of the greatest challenges in community ecotoxicology is separating contaminant-induced changes in species diversity and composition from variation due to natural factors. While observational studies can provide critical support for hypotheses concerning relationships between contaminants and community responses, some researchers feel that experiments are the only way to demonstrate causation. The lack of true replication and random assignment of treatments to experimental units limits the use of inferential statistics in most observational studies. The recent emphasis on experimental approaches for assessing the effects of contaminants is seen as a major development in community ecotoxicology. If the ability to test hypotheses with critical experiments truly defines the maturity of a science (Popper 1972), we suggest that experimental approaches should play an increasingly important role in ecotoxicology.

Our enthusiasm for experimental approaches is somewhat tempered by recognition of the important trade-offs between replication and ecological realism. Some ecologists argue that the degree of control afforded by small-scale experiments does not compensate for the lack of realism (Carpenter 1996). We feel that the importance of spatiotemporal considerations for predicting how communities will respond to contaminants should be treated like any other scientific hypothesis (Resetarits and Fauth 1998). Thus, an emerging area of research in microcosm and mesocosm testing is to identify those key ecological processes that must be accurately reproduced in order to obtain an adequate representation of nature.

Another major research goal for community ecotoxicology should be to determine the context dependency of community responses to contaminants. Because communities from different locations will vary naturally in diversity, abundance, and history of disturbance, effects of stressors on these communities are also likely to differ. Experimental approaches may be the only way to investigate context-dependent responses to contaminants. Relatively simple experimental designs allow researchers to manipulate several variables simultaneously and investigate the importance of direct and indirect effects. The US EPA's decision to abandon mesocosm testing for pesticide registration is seen by many as a missed opportunity to improve our understanding of context-dependent responses and indirect effects (Pratt *et al*. 1997; Taub 1997).

Finally, while improvements in experimental approaches have strengthened our ability to demonstrate causation, ecotoxicological experiments should not be conducted without an appreciation of natural history or in isolation from underlying ecological theory. We do not consider descriptive and experimental approaches as opposing ends of a continuum, but rather advocate a research program in which well-designed experiments are integrated with observational and theoretical approaches. When small-scale experiments are linked with observational studies, ecotoxicologists will gain a more realistic understanding of how communities respond to contaminants and other stressors.

9.2.2 USE OF MULTIMETRIC AND MULTIVARIATE APPROACHES TO ASSESS COMMUNITY-LEVEL RESPONSES

Community-level data used to assess effects of contaminants range from simple lists that reflect the presence or absence of species to more sophisticated compilations that include abundance, trophic structure, life-history characteristics, and measures of species-specific sensitivity. Because the occurrence of an indicator species is influenced by numerous factors other than contaminants, presence–absence data alone are insufficient for assessing all but the most severe forms of pollution. Although there has been significant progress in biomonitoring research since the development of the Saprobien system of classification, most community-level assessments rely on the assumption that species vary in their sensitivity to a particular stressor and that community responses will reflect this variation. Multimetric and multivariate approaches are particularly useful for community-level studies because they reduce the typically complex, multidimensional data to readily interpretable patterns. Unfortunately, the complex and often unwieldy statistical algorithms of many multivariate approaches are considered major obstacles to their widespread application. The new generation of software packages designed to perform multivariate analyses has increased the use of these approaches; however, the widespread availability of 'point-and-click' software does not eliminate the obligation of users fully to understand the output. Multimetric approaches are computationally simple, but are data intensive and often require a comprehensive understanding of ecology and natural history. These approaches have been especially effective for assessing impacts of contaminants in aquatic systems. The development of multimetric indices for other taxonomic groups, particularly those in terrestrial communities, is seen as an important research need.

Although they developed independently, multimetric and multivariate approaches are complementary and can be used together to assess biological integrity (Reynoldson *et al*. 1997). For example, output from multivariate analyses could be used to identify sensitive metrics in a multimetric index. Conversely, multivariate analyses could be conducted using traditional metrics from a multimetric index. By selecting metrics that respond to different classes of stressors, results of multivariate analyses may be useful for identifying specific stressors in systems receiving multiple perturbations.

9.2.3 DISTURBANCE ECOLOGY AND COMMUNITY ECOTOXICOLOGY

One of the most significant contributions of basic ecology to ecotoxicology is the application of disturbance theory in the study of community responses to contaminants. Disturbance is considered a major regulator of community structure and has been the subject of intense debate for several decades. Assuming that responses to natural and anthropogenic disturbance are somewhat analogous, theoretical and empirical studies of resistance and resilience may help ecotoxicologists predict effects of contaminants. Rapport's Ecosystem Distress Syndrome (Rapport, Regier and Hutchinson 1985) provides an important framework for understanding how communities respond to and recover from natural and anthropogenic disturbances.

Basic research in disturbance ecology may also help explain the significant variation in responses to contaminants observed among communities. If diversity in some communities is enhanced under moderate levels of contaminant stress, as predicted by the intermediate disturbance hypothesis, we would not expect that concentration–response relationships between contaminants and species diversity to be linear. In addition, communities subjected to natural disturbance may be preadapted to anthropogenic stressors, thus reducing their sensitivity to contaminants.

The ability of communities to tolerate contaminants forms the basis of the pollution-induced community tolerance (PICT) hypothesis (Blanck and Wangberg 1988). In contrast to community composition, which can vary significantly due to natural factors, increased community tolerance for a particular contaminant is considered a direct result of exposure.

It is likely that the same biological factors that determine the rate of recovery from natural disturbance will also determine how quickly communities recover from exposure to contaminants. Thus, an understanding of colonization abilities of dominant species, proximity of colonists, and life-history characteristics may help ecotoxicologists predict recovery times following remediation. Because of natural changes in community composition and species turnover over time, there remains considerable uncertainty in our ability to identify specific endpoints of recovery. For example, we know that some measures of recovery, such as number of species, can quickly return to pre-disturbance conditions despite persistent differences in community composition. Similarly, because of redundancy in many communities, functional measures may recover faster than structural measures. Our understanding of recovery is further complicated by the uncritical acceptance of equilibrium theories and our failure to recognize the role of historic events. The community conditioning hypothesis (Landis, Matthews and Matthews 1996; Matthews, Landis and Matthews 1996) acknowledges that communities are a reflection of their unique history. Because this history may include exposure to contaminants and other anthropogenic disturbances, traditional models of recovery based on equilibrium conditions may not apply.

Finally, throughout this volume we have attempted to make a strong case for the importance of long-term research. The National Science Foundation's Long Term Ecological Research (LTER) programs have contributed significantly to our understanding of basic ecology. Unfortunately, there are relatively few examples where long-term studies have been conducted to assess recovery from contaminants. Bruce Wallace's research on responses of headwater streams to pesticides (Wallace, Webster and Cuffney 1982) and David Schindler's long-term research on acidification in lakes (Schindler 1988) described in Chapter 4 are two of the more prominent examples. We suggest that a national program monitoring responses to anthropogenic disturbance, analogous to NSF's LTER program, would greatly enhance our understanding of biotic and abiotic factors that determine recovery.

9.2.4 AN IMPROVED UNDERSTANDING OF TROPHIC INTERACTIONS

Few topics in basic community ecology are as relevant to understanding ecotoxicological effects of contaminants as food webs and trophic interactions. Quantitative approaches used by ecologists to measure energy flow have been modified to estimate potential transport of contaminants. The primary focus of this effort has been on measuring the concentrations of contaminants in organisms and attempting to quantify contaminant transport among biotic and abiotic compartments. What is generally lacking from many ecotoxicological investigations has been a critical understanding of the ecological factors that influence contaminant transport. In addition to information on physicochemical properties of contaminants (e.g. molecular structure, lipophilicity), ecotoxicologists now realize that predicting contaminant transport also requires an understanding of ecological characteristics (e.g. feeding habits, food chain length and complexity, and habitat use). Our ability to quantify the importance of ecological factors on contaminant transport has been greatly improved by the application of stable isotopes analyses. Few advances in the study of food webs have had as great an impact on our understanding of feeding relationships. Time-integrated estimates of energy flow, trophic position, and carbon sources can be obtained by comparing the unique isotopic signatures of consumers and resources.

Despite the broad interest in quantifying contaminant transport in ecotoxicological investigations, relatively few studies have considered the effects of contaminants on trophic structure or used food web characteristics as endpoints in assessments of ecological integrity. We feel that understanding the effects of contaminants on food web length, complexity, and trophic structure is a significant research need in ecotoxicology. The ecological effects of contaminants on trophic structure and the transport of contaminants to higher trophic levels is dependent on the number of trophic levels and whether the system is regulated by top-down or bottom-up factors. These ecological factors have important applications for the management of sport fisheries. Because contaminant transfer is greatly influenced by food chain length and other aspects of trophic structure (Rasmussen *et al*. 1990), size-selective stocking and other fisheries management programs may influence contaminant levels in game species (Jackson 1997).

The most important research limitation in food web ecotoxicology has been the inability to relate concentrations of contaminants measured in different trophic levels with biologically important effects. Bioenergetic approaches may provide the conceptual framework to quantify biologically significant responses associated with contaminant uptake. Because energy is a common currency that unifies all biological systems (Carlisle 2000), studying the effects of contaminants on energy flow provides an opportunity to integrate responses across levels of organization. Integrating contaminant transport models with bioenergetic models will allow researchers to link exposure with ecologically significant effects.

9.2.5 INTERACTIONS BETWEEN CONTAMINANTS AND GLOBAL ATMOSPHERIC STRESSORS

Although generally not included in discussions of ecotoxicology, global climate change, increased UV-B radiation, and acidic deposition represent three of the most serious threats to ecological communities. Assessing the direct effects of these stressors is complicated by their large geographic extent, which requires extrapolation across broad spatial and temporal scales. Evidence that global climate change, increased UV-B radiation, and acidification are directly related to anthropogenic emissions has been obtained from a variety of sources. However, the direct and indirect effects on aquatic and terrestrial communities are largely uncertain. The coarse spatial scale of most general circulation models (GCMs) limits our ability accurately to predict regional responses to climate change. For example, although global declines of amphibians have been related to increased levels of UV-B (Blaustein and Wake 1990) and the worldwide degradation of forest health has been attributed to acidification (Ollinger *et al.* 1993), there is tremendous uncertainty in these relationships.

Because of the pervasive and widespread distribution of global atmospheric stressors, ecotoxicologists cannot continue to study the effects of contaminants in isolation. Interactions between atmospheric and local stressors complicate our ability to predict effects of climate change, UV-B, and acidification on communities. It is quite likely that increased temperatures will have a significant influence on physiochemical characteristics of contaminants and also influence community responses to contaminants. In addition, the structure of communities and their susceptibility to contaminants will most likely change in a warmer climate. Synergistic interactions between UV-B radiation and polycyclic aromatic hydrocarbons (Oris and Giesy 1986) and between acidification and heavy metals (Genter 1995) are well documented. To predict effects of contaminants on communities simultaneously subjected to increased temperature, greater UV-B radiation, and/or increased acidification will require a better appreciation for the impacts of multiple stressors. Currently, our ability to predict interactive effects of multiple stressors on natural systems is greatly limited. It is likely that interactions among stressors will be common in natural systems, and therefore community ecotoxicologists should anticipate the 'ecological surprises' resulting from these interactions (Paine, Tegner and Johnson 1998).

9.3 CONCLUDING REMARKS

We hope that our treatment of community ecotoxicology has convinced the reader of the importance of understanding how contaminants may affect distribution, abundance, and species diversity. Within the context of the hierarchical arrangement of living systems, communities are intermediate between populations and ecosystems. Although the responses of individual species to contaminants will influence patterns of diversity and abundance in nature, community responses often transcend those observed in populations. Recognition of the emergent properties of communities and higher levels of biological organization remains a significant point of contention between proponents of reductionism and holism (Odum 1984). The emergence of ecotoxicology as a distinct discipline within the field of toxicology was at least partially a result of criticism of traditional reductionist approaches such as laboratory toxicity tests (Cairns 1983, 1986). Until ecotoxicologists develop a better appreciation for the importance of species interactions and indirect effects of contaminants, extrapolation of laboratory results based on responses of single species will remain tenuous.

Predicting the indirect effects of contaminants on species interactions and trophic structure has been a major theme in our discussion of community ecotoxicology. Experience has shown that population surveys of charismatic or economically-important species often provide an incomplete picture of how communities will respond to or recover from anthropogenic disturbance (Wiens *et al*. 1996). Similarly, functional characteristics such as primary productivity, nutrient cycling, and detritus processing, the endpoints typically included in ecosystem-level studies, are often insensitive to anthropogenic stressors (Schindler 1987). Because the endpoints evaluated in community-level assessments are generally sensitive, ecologically significant, and socially relevant, communities are an appropriate focus for ecotoxicological investigations.

REFERENCES

Blanck H and Wangberg S (1988). Induced community tolerance in marine periphyton established under arsenate stress. *Can J Fish Aquat Sci* **45**: 1816–1819.

Blaustein AR and Wake DB (1990). Declining amphibian populations: a global phenomenon? *Trends Ecol Evolut* **5**: 203–204.

Cairns Jr J (1983). Are single species toxicity tests alone adequate for estimating environmental hazard? *Hydrobiologia* **100**: 47–57.

Cairns Jr J (1986). The myth of the most sensitive species. *BioScience* **36**: 670–672.

Carlisle DM (2000). Bioenergetic food webs as a means of linking toxicological effects across scales of ecological organization. *J Aquat Ecosys Stress Recov* **7**: 155–165.

Carpenter SR (1996). Microcosm experiments have limited relevance for community and ecosystem ecology. *Ecology* **77**: 677–680.

Genter RB (1995). Benthic algal populations respond to aluminum, acid, and aluminum–acid mixtures in artificial streams. *Hydrobiologia* **306**: 7–19.

Jackson LJ (1997). Piscivores, predation, and PCBs in Lake Ontario's pelagic food web. *Ecol Appl* **7**: 991–1001.

Landis WG, Matthews RA and Matthews GB (1996). The layered and historical nature of ecological systems and the risk assessment of pesticides. *Environ Toxicol Chem* **15**: 432–440.

Matthews RA, Landis WG and Matthews GB (1996). The community conditioning hypothesis and its application to environmental toxicology. *Environ Toxicol Chem* **15**: 597–603.

Odum EP (1984). The mesocosm. *BioScience* **34**: 558–562.

Ollinger SV, Aber JD Lovett GM, Millham SE, Lathrop RG and Ellis JE (1993). A spatial model of atmospheric deposition for the northeastern US. *Ecol Appl* **3**: 459–472.

Oris JT and Giesy Jr JP (1986). Photoinduced toxicity of anthracene to juvenile bluegill sunfish (*Lepomis macrochirus* Rafinesque): photoperiod effects and predictive hazard evaluation. *Environ Toxicol Chem* **5**: 761–768.

Paine RT, Tegner MJ and Johnson EA (1998). Compounded perturbations yield ecological surprises. *Ecosystems* **1**: 535–545.

Popper KR (1972). *The Logic of Scientific Discovery* (3rd edn). Hutchinson, London, UK.

Pratt JR, Melendez AE, Barreiro R and Bowers NJ (1997). Predicting the ecological effects of herbicides. *Ecol Appl* **7**: 1117–1124.

Rapport DJ, Regier HA and Hutchinson TC (1985). Ecosystem behavior under stress. *Am Nat* **125**: 617–640.

Rasmussen JB, Rowan DJ, Lean DRS and Carey JH (1990). Food chain structure in Ontario lakes determines PCB levels in lake trout (*Salvelinus namaycush*) and other pelagic fish. *Can J Fish Aquat Sci* **47**: 2030–2038.

Resetarits Jr WJ and Fauth JE (1998). From cattle tanks to Carolina bays: the utility of model systems for understanding natural communities. In *Experimental Ecology: Issues and Perspectives*, ed. by Resetarits Jr WH and Bernardo J, pp. 133–151. Oxford University Press, Inc., New York, NY.

Reynoldson TB, Norris RH, Resh VH, Day KE and Rosenberg DM (1997). The reference condition: a comparison of multimetric and multivariate approaches to assess water-quality impairment using benthic macroinvertebrates. *J N Am Benthol Soc* **16**: 833–852.

Schindler DW (1987). Detecting ecosystem responses to anthropogenic stress. *Can J Fish Aquat Sci* **44** (Suppl 1): 6–25.

Schindler DW (1988). Experimental studies of chemical stressors on whole lake ecosystems. *Verh Internat Verin Limnol* **23**: 11–41.

Taub FB (1997). Are ecological studies relevant to pesticide registration decisions? *Ecol Appl* **7**: 1083–1085.

Wallace JB, Webster JR and Cuffney TF (1982). Stream detritus dynamics: regulation by invertebrate consumers. *Oecologia* **53**: 197–200.

Wiens JA, Crist TO, Day RH, Murphy SM and Hayward GD (1996). Effects of the *Exxon Valdez* oil spill on marine bird communities in Prince William Sound. *Ecol Appl* **6**: 828–841.

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