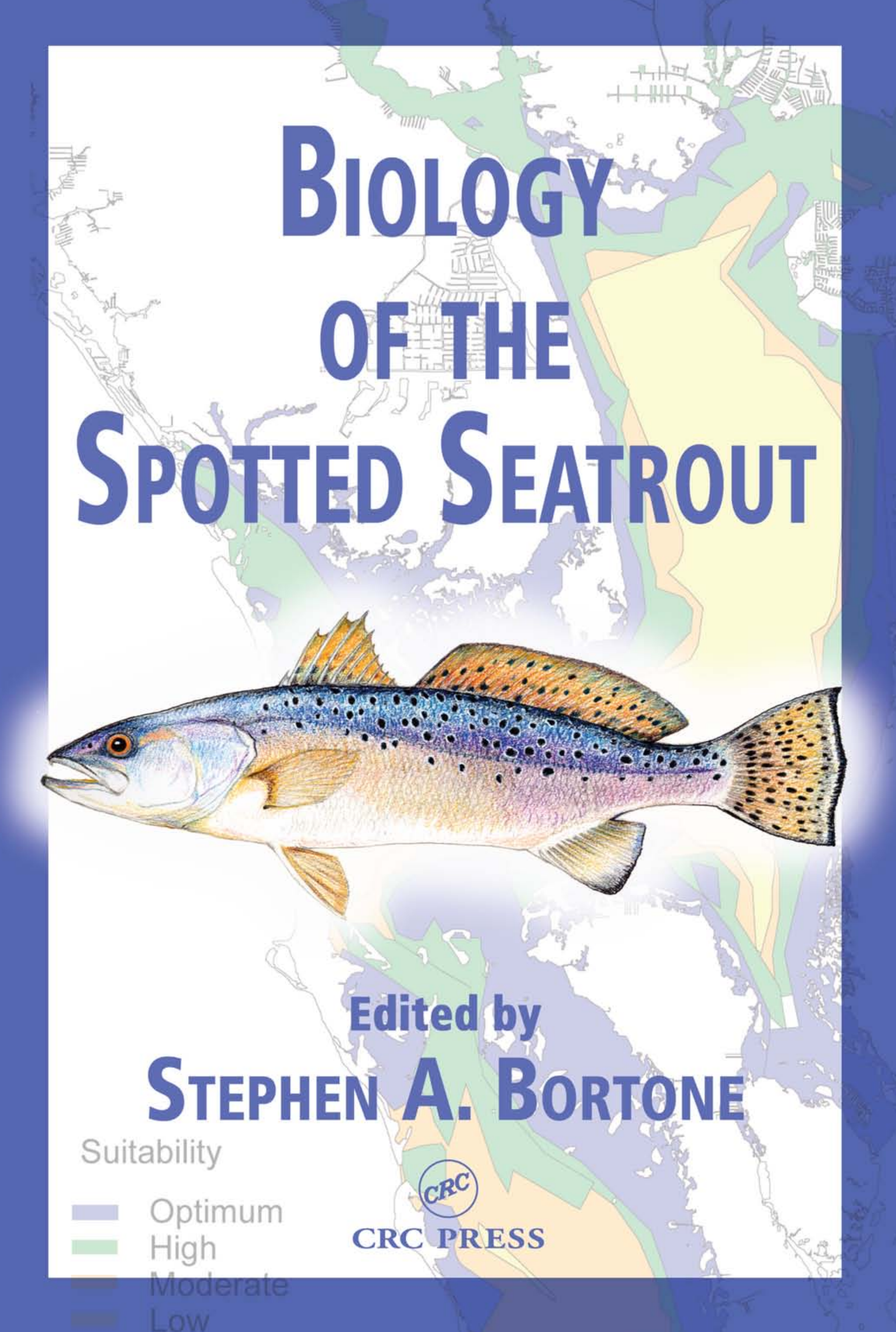
BIOLOGY OF THE SPOTTED SEATROUT

Edited by

STEPHEN A. BORTONE



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Preface

Many estuaries around the world are becoming environmentally stressed due to a trend toward increased human habitation along their shores. This stress can be manifested by changes in water quality or biotic measures of relative condition such as the abundance of seagrasses. Often it reflects the biotic integrity of the entire ecosystem or is manifested in modifications to the life history attributes of its living components. Thus, there is growing interest in being able to carefully assess the conditions and health of these coastal aquatic biotopes, with the hope of determining the specific factors that might be altered to correct a perceived overall downward trend in biotic conditions.

The spotted seatrout is often the target of commercial and recreational fishers throughout its range (i.e., throughout coastal estuaries of the temperate and warm-temperate Atlantic coast of North America). Although widely distributed among various biotopes in coastal areas, it is most often associated with grass beds. It is a noted sound-producing fish and an important trophic link within the estuary between filter feeders, such as fish and shrimp, and the higher-level predators, notably bottlenose dolphins. One of the most intriguing aspects of its life history, however, is that most of the individuals apparently remain within a single estuary their entire lives. Thus, the spotted seatrout is unlike many estuarine fishes that usually have some aspect of their life history met by waters outside the estuary proper. Depending upon the species, most other estuarine-associated fish species migrate offshore (like most other croakers or drums) or upstream (such as striped bass) to spawn or move between estuaries on feeding forays.

Because it is widely distributed and highly regarded as a food and sport fish, and especially because it has been well studied and found to be nearly restricted to its “home” estuary throughout its life, the spotted seatrout has the potential to serve as an important estuarine biological sentinel and monitor. This idea is based on the premise that the life history condition of this and other fishes is largely dependent upon the quality of the aquatic environment in which they live. Thus, it is likely that many biological attributes of aquatic species can reflect changes in aquatic conditions over time or between places. Special here is the totally estuarine dependent and restricted nature of the spotted seatrout.

This book represents compilation and summary chapters on the biological knowledge of spotted seatrout by noted authorities in their respective fields. The primary objective is to make the latest and most up-to-date life history information available on this species for the express purpose of beginning the task of assessing differences in estuarine-restricted subpopulations of spotted seatrout. A second objective is to indicate areas in which life history aspects of spotted seatrout can be used to show their potential as indicators of estuarine conditions. A third objective is to begin to integrate estuarine-specific life history features into the overall management of estuaries and of an estuarine-dependent fishery.

Above all, this publication demonstrates a directed effort toward a goal of improving our ability to monitor estuaries and fisheries simultaneously and gives purposeful direction to future research efforts regarding the biology of estuarine fishes. Clearly, this is an initial and untried effort for any species in any habitat, but, if the principles presented here hold true, the “spotted seatrout biology–estuarine condition” sentinel should serve as a guide to develop information sources in other estuaries, using a broad suite of life history characters from other estuarine-dependent species as indicators of environmental conditions.

Stephen A. Bortone, Ph.D.

Acknowledgment

Thanks to many individuals who helped with various stages of this volume's development. Discussions with laboratory personnel from the U.S. Environmental Protection Agency in Gulf Breeze, Florida, and especially Michael Lewis initiated the search for fish life history data that could be used to evaluate estuaries. On a grant funded by the Florida Department of Environmental Protection (now the Florida Fish and Wildlife Conservation Commission), co-investigators Chad Bedee, Doug DeVries, Churchill Grimes, and Chris Palmer helped gather some of the initial data that formed the basis of discussions on the need for such a book. Later, Ken Cummins, then of the South Florida Water Management District, developed the concept more fully and suggested spotted seatrout as a potential candidate for a fish species to evaluate estuaries. The quality of chapters was greatly enhanced by the expert editorial and referee advice selflessly offered by Robert Chapman, Richard Cody, John Couch, James Cowan, Douglas DeVries, R. Grant Gilmore, John Gold, and, especially, Charles Wenner. Thanks also to John Sulzycki, Pat Roberson, Judith Kamin, and the staff at CRC Press for their thoughtful guidance and patience in the production of this volume. Lastly, but most importantly, the authors are acknowledged for their professionalism and diligence in preparing their respective manuscripts for timely inclusion.

Stephen A. Bortone

Editor

Stephen A. Bortone is director of the Marine Biology Laboratory at the Sanibel-Captiva Conservation Foundation in Sanibel, Florida. He holds administrative appointment to the graduate faculty at the University of South Alabama, courtesy faculty appointment at the Florida Gulf Coast University, and is research professor at Florida Atlantic University and its Florida Center for Environmental Studies. Previously he was professor at the University of West Florida, where he also served as director for the Institute for Coastal and Estuarine Research. He also was the director of environmental science at the Conservancy of Southwest Florida. Dr. Bortone received a B.S. degree from Albright College in Reading, Pennsylvania, an M.S. degree from Florida State University, Tallahassee, and a Ph.D. from the University of North Carolina, Chapel Hill.

For the past 35 years, Dr. Bortone has conducted research on the life history of estuarine organisms, especially fishes and seagrasses, chiefly in the southeastern U.S. and the Gulf of Mexico. He has published more than 130 scientific articles on the broadest aspects of biology, including such diverse fields as anatomy, behavior, biogeography, ecology, endocrinology, evolution, histology, oceanography, physiology, reproductive biology, sociobiology, systematics, and taxonomy.

Conducting his research and teaching activities, Dr. Bortone has traveled widely. He has served as visiting scientist at The Johannes Gutenberg University (Mainz, Germany) and conducted extensive field surveys with colleagues from La Laguna University in the Canary Islands. He was Mary Ball Washington Scholar at University College, Dublin, Ireland. He has received several other teaching and research awards, including the title “Fellow” from the American Institute of Fishery Research Biologists.

Dr. Bortone has served as scientific editor and reviewer for numerous organizations, such as the National Science Foundation, the Environmental Protection Agency, the National Marine Fisheries Service, and the U.S. Fish and Wildlife Service, and several journals, including *Bulletin of Marine Science, Copeia, Estuaries,* and *Transactions of the American Fisheries Society.*

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Introduction

Stephen A. Bortone

The spotted seatrout, *Cynoscion nebulosus*, is a fish species of the croaker and drum family (i.e., Sciaenidae) that has special interest among a wide audience of individuals. Broadly distributed in coastal areas along the eastern Atlantic and Gulf of Mexico coasts of the U.S., it is known officially as the spotted seatrout (Robins et al., 1990) but colloquially and locally as speck, seatrout, gray trout, trout, spotted weakfish, spotted seateague, winter trout, and speckled trout (Johnson and Seaman, 1986). In the southern portion of its range along the Gulf Coast of Mexico it is known as trucha del mar, corvina, and corvina pinta. In both countries it is the target of recreational and commercial fishers as well as of the seafood-eating public because of its size and taste.

Scientists have their own interests in the species. Biologically, it is a sound-producing species that serves as an important trophic link in estuaries, between invertebrates and small fishes and the larger, fish-eating predators such as groupers, snappers, sharks, and bottle-nosed dolphins. Ecologically, it is found nearly exclusively within estuaries where it seems to have a strong habitat affinity for seagrasses. Interest in this species can also be found among those who help manage and protect natural coastal resources as the influx of coastal dwellers increases in virtually every part of the world.

Estuarine coasts have become prime settlement areas for new inhabitants. Increasing human settlement results in stress to the coastal waters through increases in storm-water runoff that reduce water quality, destruction of natural shoreline habitat, and elimination of submerged aquatic vegetation (Kennish, 1992). Unfortunately, estuaries often reflect the negative effects of coastal development; this reality means that environmental managers should be vigilant in making sure that declining conditions of coastal waters are kept to a minimum. Subsequent to the immediate problem of reducing the amount of deterioration of water quality is the objective of restoring estuaries and coastal habitats to a state that emulates a minimally disturbed ecosystem, thus assuring the sustainability of our near-shore natural resources.

The task at hand, then, is to monitor the condition of estuarine waters to assure minimal deterioration of environmental conditions and then to objectively evaluate efforts to restore and maintain the ecosystem to a level supporting an acceptable level of biotic integrity. Recently, several colleagues and I produced a book (Bortone, 2000) aimed at establishing a source of biological information and assessment methodology on seagrasses that could be used to assess estuarine conditions. While meeting the overall objective is becoming a reality, more than one biotic component of estuaries should be established as a biological sentinel. Since seagrasses are primary producers and are able to reflect biological impacts of long-term environmental conditions at a point (because they are rooted), a measure of more general biotic conditions within an estuarine ecosystem could be monitored by examining a motile species that is broadly distributed but restricted to a particular estuary.

After considerable discussion with colleagues with the broadest range of biological expertise, it became apparent that few animal candidates had the potential to provide a platform to study biological impacts on estuarine conditions. For example, oysters, mussels, and clams, while sedentary and long-lived, have larvae that are widely dispersed and have no specific estuarine affinity. Most estuarine fishes (including other croakers and drums) and crustaceans (such as shrimps and crabs) tend to migrate offshore to spawn; they have eggs or larvae that are discharged to the ocean and,

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thus, also have no affinity to a "home" estuary. Some estuarine fishes such as striped bass move upstream to spawn and are subjected to non-estuarine conditions for a considerable amount of their lives. Nearly every species considered had characteristics that readily disqualified them for the purpose of estuarine monitoring.

The life history of the spotted seatrout, however, had fewer features to merit disqualification. It is broadly distributed along coasts that encompass a considerable number of estuaries. It is long-lived and thus able to be subjected to estuarine conditions for a period of time sufficient to serve as a time-series monitor. A species that serves as a trophic link between low-level secondary producers and top-level predators, it is common to abundant within the estuaries it inhabits. Importantly, it is entirely estuarine dependent, only rarely moving out of its home estuary. Lastly, because the species has attracted considerable attention from recreational and commercial fisheries, a reasonably detailed historical and current database on its life history and biology exists (e.g., Johnson and Seaman, 1986; Bortone et al., 1997).

There is, of course, a rather large number of potential candidates for a species whose life history attributes could serve as a biological monitor for estuarine conditions. However, when considered in total, the attributes of the spotted seatrout demand further examination into its utility to serve as an indicator of estuarine condition.

Our purpose here is to present summaries as well as new information on the current state of knowledge of spotted seatrout biology. The book begins with an introduction to the current taxonomic understanding of the species in the genus *Cynoscion* in order to establish its phylogenetic associates and to set the stage for future comparative biological studies with other species in the genus (see Roff, 1992; Stearns, 1992). An examination of the importance of genetic structure and population limits of the spotted seatrout follows, with interpretations of genetic data on its population structure from the Gulf of Mexico and southeastern Atlantic Ocean.

Long-term effects of environmental conditions have been most often inferred from data on age and growth attributes of populations. The potential importance of these life history attributes is evident and included as two separate but complementary examinations of the age and growth aspects of spotted seatrout. Numerous researchers have conducted reproductive studies for extended periods; the comprehensive summary presented here examines those studies from the broadest geographic perspective and fully explores this life history feature. Once fertilization takes place within its home estuary, the spotted seatrout is subjected to the vagaries of the environment as a fully independent organism. Early life history features are summarized, with special reference to the relationship larvae and juveniles have with a predominant environmental variable — salinity. Habitat affinities dominate many of the constraints of the species' life history attributes and are examined, with special reference to habitat features associated with inshore estuarine areas in the northern Gulf of Mexico.

Sound is a peculiar and significant aspect of the life history of the spotted seatrout. Sound production and its relationship to habitat are given special treatment as a life history attribute. Concomitantly, diseases and parasites play a role in constraining the life history response of any species to the environment. Since the spotted seatrout is a prime target of both recreational and commercial fishers, it is important to have a clear understanding of the depth of the fisheries' impact on the populations. Two chapters are presented that offer a perspective of mathematical modeling to gain an understanding of spotted seatrout. These two, very different approaches underline the fact that the spatial and temporal scales within which the spotted seatrout exists are considerable and will require the special skills that modelers can provide to facilitate understanding. Lastly, the relevancy of these data and perspectives to the overall objective to establish the life history attributes of the spotted seatrout as potential indicators of estuarine condition is examined.

The goal is ambitious and fraught with complications, but the end result gives large-scale perspective to a plethora of studies, independent examinations, and bits of information on a species that could serve as a significant indicator of the future of estuarine ecosystems to a major part of the world. If successful, it is hoped that other species that qualify with similar features will become established in other coastal areas as potential indicators of estuarine conditions. A vigilant assessment of appropriate life history information should allow us to repair some estuarine ecosystems and return them to fully functional systems. Moreover, through the integration of several levels of inspection, we will be able to maintain our estuaries at a level appropriate for sustaining their natural resources while retaining their biological integrity.

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2 Taxonomy of the Seatrout, Genus *Cynoscion* (Pisces, Sciaenidae), with Artificial Keys to the Species

Ning Labbish Chao

CONTENTS

INTRODUCTION

Sciaenid fishes are an important fishery resource in the shallow warm seas and estuaries of the world. The family Sciaenidae is the seventh largest among the 150 families of Perciformes and includes about 80 genera and 300 species. Four recognized genera with 20 plus species have adapted to living in the freshwater rivers and lakes of the Americas. Many marine species use the estuarine environment as a nursery and feeding ground for the young. Sciaenid body forms and mouth positions are among the most diverse of the percoids and appear to be the result of adaptations related to different feeding modes and life history patterns (Chao and Musick, 1977).

The family is characterized by an elongated soft dorsal fin separated from the spinous dorsal fin by a deep notch (rarely well spaced) and two anal spines (rarely one, never three); the lateral line extends to the tip of caudal fin. Sciaenid fishes have large otoliths and often complex gas bladders that are usually associated with well-developed drumming muscles in males or in both sexes. Many species have cavernous skulls and enlarged slits and pores on the snout and underside of the lower jaw. The lower jaw may also bear one or more mental barbels (also see Sasaki, 1989, for synapomorphies).

Species of the genus *Cynoscion* are commonly known as seatrout or weakfishes due to their tender flesh. Along the West Coast of the U.S., they are also known as corbina or corvina. Most species

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of *Cynoscion* are popular food and sport fishes usually found along inshore waters, lower reaches of estuaries, salt marshes, and mangrove swamps. Two eastern Pacific *Cynoscion* species may also be found in deeper coastal waters of 100 to 200 m in depth (e.g., *C. nannus* and *C. nortoni*).

Studies on phylogenetic relationships among species of *Cynoscion* are still incomplete (Aguirre-Maldonado, 2000; Moshin, 1973; Paschall, 1986; Schwarzhans, 1993; Weinstein and Yerger, 1976). Phylogenetic relationships of *Cynoscion* and other genera of Sciaenidae reported by Sasaki (1989) and Casatti (2000) are in accord with the observations of Trewavas (1962) and Chao (1978, 1986). That is, the genera *Atractoscion, Cynoscion, Isopisthus,* and *Macrodon* form a monophyletic tribe, the Cynoscionini. It is endemic to the tropical and warm temperate regions of the Americas, with the exception of *Atractoscion aequidens* (Cuvier), which is distributed along the eastern Atlantic coast of southern Africa and off southern and eastern Australia. All four genera have an elongated body form and a pair of variably developed large horn-like appendages at the front of the gas chamber (Figure 2.1; also see the diagnosis below). *Atractoscion* can be further distinguished from other genera of Cynoscionini by lack of enlarged canine-like teeth at the tip of the upper jaw and a much thicker sagittal otolith (Chao, 1986; Schwarzhans, 1993).

The Indo–Pacific genus *Otolithes* Oken 1817 (written *Otolithus* by Cuvier 1829 and later authors) has a pair of canine-like teeth on upper and lower jaws; this is probably why several authors included American seatrouts in this genus. The genus *Otolithes* (tribe Otolithini) is not closely related to *Cynoscion.*

Genus *Cynoscion* consists of 24 species: 12 species in the eastern Pacific and 12 in the western Atlantic. Distribution records of *Cynoscion* for the eastern Pacific extend from southern California (*C. parvipinnis*) to northern Chile (*C. analis*) and in the western Atlantic from the Bay of Fundy (*C. regalis*) to northern Patagonia (*C. guatacupa*). Most species are found in the tropical and subtropical regions of Central and South America.

This review presents an updated taxonomy of *Cynoscion* species and provides artificial keys for species identification. Primary synonyms, references to original authors, type localities, and sizes of examined type specimens are listed. Complete references to the original species descriptions are readily available in Eschmeyer (1998). Museum collection acronyms follow Leviton et al. (1985).

GENUS *CYNOSCION* GILL 1861

DIAGNOSIS

The body is elongate, moderately compressed, and the predorsal profile nearly straight, ventral evenly arched. The head is conical, snout pointed. The mouth is large and oblique, with the lower jaw projecting; teeth are sharp and set in narrow ridges — the tip of the upper jaw usually with a pair

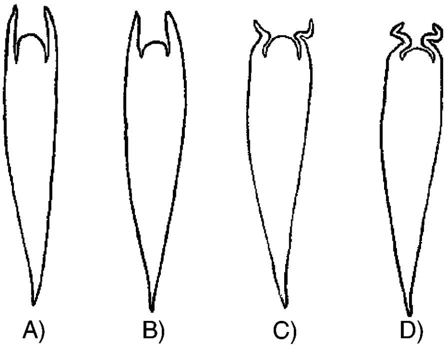

FIGURE 2.1 Gas bladder of *Cynoscion* has a pair of stout horn-like appendages. A: *C. microlepidotus*; B: *C. nothus*; C: *C. virenscense*; D: *C. leiarchus.*

of large canines at least twice the size of other teeth, tapering from base to tip (no obviously enlarged teeth in *C. steindachneri)*. The preopercular margin is membranous or ciliate, never with spines. Gill rakers are moderately long and slender. Vertebrae are usually 13(12) + 12(13) = 25, except 15 +12 = 27 in *C. nothus* and 12 +10 = 22 in *C. microlepidotus.* The gas bladder has a pair of stout, horn-like appendages arising anteriorly from the gas chamber; the horns are mostly directing straight forward, but a few are curved medially (Figure 2.1). Sagitta (saccular otolith) are usually oval and elongate (Figure 2.2) with a tadpole-shaped sulcus mark. The head portion (ostium) is broad, not reaching the anterior margin of the sagitta in most species; the tail portion (cauda), not deeply grooved, is usually long and often expanded toward the tip in adults.

SYNONYMS

Cestreus Gronow in Gray 1854:49 (type-species: *Cestreus carolinensis* Gronow in Gray 1854, by monotypy, preoccupied by *Cestreus* McClelland 1842)

Cynoscion Gill 1861: 81 (type-species: *Johnius regalis* Bloch and Schneider 1801, by original designation)

Apseudobranchus Gill 1862:18 (type-species: *Otolithus toeroe* Cuvier in Cuvier and Valenciennes 1830 = *Cynoscion acoupa* (Lacepède 1801), by original designation and monotypy)

Archoscion Gill 1862:18 (type-species: *Otolithus analis* Jenyns 1842, by original designation and monotypy)

Cynoscion (Buccone) Jordan and Evermann 1896:394 (type-species: *Cestreus praedatorius* Jordan and Gilbert in Jordan and Eigenmann 1889, by original designation and monotypy)

Symphysoglyphus A. Miranda Ribeiro 1915, Sciaenidae: 43 (type-species*: Otolithus bairdi* Steindachner 1879 = *Cynoscion microlepidotus* (Cuvier), by monotypy)

Paralarimus Fowler and Bean 1923:18 (type-species: *Paralarimus patagonicus* Folwer and Bean 1923 = *Cynoscion acoupa* (Lacepède 1801), by original designation and monotypy)

Cynoscion (Eriscion) Jordan and Evermann 1927:506 (type-species: *Cynoscion nebulosus* Cuvier *in* Cuvier and Valenciennes 1830, by original designation, also monotypy)

Remarks — Based on the sagitta morphology of recent and fossil *Cynoscion*, Schwarzhans (1993) used the available names of the genus and divided *Cynoscion* into four subgenera: *Cynoscion, Apsuedobranchus, Buccone,* and *Archoscion.* He also defined the subgenus *Archoscion* (including *C. analis* and *C. orthonopterus*) as intermediate between the genera *Cynoscion* and *Isopisthus.* This relationship was consistent with the phylogenetic relationship of *C. analis* and *Isopisthus remifer* inferred from mitochondrial DNA sequence data by Aguirre-Maldonado (2000). Since the related genera *Atractoscion* and *Macrodon* were not included in either analysis as out groups, the subgeneric divisions within the *Cynoscion* probably need further scrutiny.

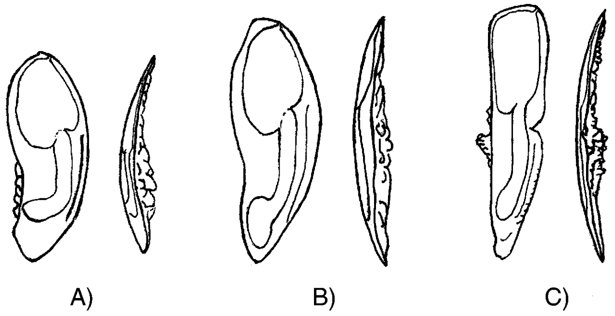

FIGURE 2.2 Sagitta otoliths of *Cynoscion* are mostly oval elongated, with few exceptions. A: *C. nebulosus*; B: *C. regalis*; C: *C. virenscense.*

VALID SPECIES

A total of 24 species of *Cynoscion* are recognized here. The 12 western Atlantic and Caribbean species are *C. acoupa, C. guatucupa, C. arenarius, C. jamaicensis, C. leiarchus, C. microlepidotus, C. nebulosus, C. nothus*, *C. regalis, C. similis, C. steindachner,* and *C. virescens*. The 12 eastern Pacific species are *C. albus, C. analis, C. nannus, C. nortoni, C. parvipinnis, C. orthonopterus, C. phoxocephalus, C. praedatorius, C. reticulatus, C. squamipinnis, C. stolzmanni*, and *C. xanthulus*.

Remarks — Two large sciaenids, *Atractoscion nobilis* (Ayres, 1860) and *Totoaba macdonaldi* (Gilbert, 1890), were commonly included in the *Cynoscion* until a new genus, *Totoaba,* was recently described (Villamar, 1980). Both species lack large canine-like teeth on their jaws. Furthermore*, T. macdonaldi* has a distinct gas bladder with a pair of thick, long, tubular appendages running along the sides of the main gas chamber (Villamar, 1980). Trewavas (1962) included Indo–Pacific monotypic *Atractosion aequidens* in the tribe Cynosionini for its gas bladder, which is the same type as that of *C. regalis* and more abdominal than caudal vertebrae (14 + 11 = 25), which is not diagnostic for the tribe. Trewavas (1977) also included the eastern Pacific *Cynoscion nobilis* in the genus *Atractoscion* for lack of large canine-like teeth. *C. nobilis* and *C. aequidens* have distinctly thicker sagittal otoliths than all other *Cynoscion* species; including them in a separate genus *Atractoscion* is valid. The adults of Brazilian *C. steindachneri* (Jordan) also lack enlarged canine-like teeth on the upper jaw. *Cynoscion fusiformes* Borodin (1933) from the Florida Keys (holotype: VMM1267, 215 mm TL, now at AMNH) is not a sciaenid. A photo of the holotype resembles the *Stizostedion* species (Percidae).

WESTERN ATLANTIC SPECIES

Cynoscion acoupa (Lacepède)

Cheilodipterus acoupa Lacepède 1801, Cayenne, French Guiana (holotype: MNHN 5502, 262 mm SL, Cayenne, other syntypes from Surinam and Brazil; also see Bauchot and Desoutter, 1987)

Lutjanus cayenensis Lacepède 1802, Cayenne, French Guiana (holotype: MNHN 5502, 262 mm SL)

Otolithus rhomboidalis Cuvier 1829, Cayenne, French Guiana (based on "Lutjan de Cayenne," Lacepède)

Otolithus toeroe Cuvier *in* Cuvier and Valenciennes 1830, Cayenne, French Guiana (syntypes: MNHN 4616, 347mm SL, Cayenne; MNHN 5500, 175 mm SL, Brazil; MNHN A.4518, two specimens, 493 and 485 mm SL, Cayenne; also see Bauchot and Desoutter, 1987)

Paralarimus patagonicus Fowler and Bean 1924, Patagonia, Argentina (holotype: USNM 83222, 136 mm SL)

Remarks — The specimen was collected during the Wilkes expedition and catalogued on 1 March 1919. I suspect the stated locality of the holotype was incorrectly registered.

Cynoscion maracaiboensis Schultz 1949, Rio Agua Caliente, 2 to 3 km above Lake Maracaibo, Venezuela (holotype: USNM 12742, 251 mm SL, paratypes: see Eschmeyer, 1998).

Cynoscion arenarius Ginsburg

Cynoscion arenarius Ginsburg 1929, Texas (holotype: USNM 89385, 245 mm SL)

Remarks — Two independent electrophoresis studies of four western North Atlantic *Cynoscion* (Weintein and Yerger, 1976; Paschall, 1986) have suggested that *C. arenarius* and *C. regalis* formed one phyletic line. These authors questioned the species status of *C. arenarius* and have suggested that *C. arenarius* may be a subspecies of *C. regalis*.

Cynoscion guatucupa (Cuvier)

"Guatucupa" Marcgrave 1648, Brazil (non-binominal)

Otolithus striatus Cuvier 1829 (after Marcgrave)

Otolithus guatucupa Cuvier *in* Cuvier and Valenciennes 1830, Montevideo (syntypes: MNHN 7517, two specimens, 358 and 366 mm SL; also see Bauchot and Desoutter, 1987)

Remarks — Figueiredo (1992) correctly regarded *Cynoscion striatus* (Cuvier, 1829) as a *nomen dubium* that is valid as *Cynoscion guatucupa* (1830).

Cynoscion jamaicensis (Vaillant and Bocourt)

Otolithus jamaicensis Vaillant and Bocourt 1883, Jamaica (holotype: MNHN A.557, 205 mm SL)

Archoscion petranus A. Miranda Ribeiro 1913, Campo Grande, Brazil (no type known)

Cynoscion leiarchus (Cuvier)

Otolithus leiarchus Cuvier *in* Cuvier and Valenciennes 1830, Brazil (syntypes: MNHN 5503, two specimens, 152 and 234 mm SL; MNHN A.2690, 187 mm SL; MNHN A.5422, a dried stuffed specimen, 112 mm SL, Brazil; also see Bauchot and Desoutter, 1987).

Cynoscion microlepidotus (Cuvier)

Otolithus microlepidotus Cuvier *in* Cuvier and Valenciennes 1830:79, Surinam (holotype: ZMB; see Bauchot and Desoutter, 1987)

Otolithus bairdii Steindachner 1879, Santos, Brazil (syntypes: one of several examined NMW 51130, 152 mm SL, label states - donated by Steindachner)

Cynoscion nebulosus (Cuvier)

Labrus squetaegue var. *maculatus* Mitchill 1815, New York (not *Labrus maculatus* Bloch 1793; no type known)

Otolithus nebulosus Cuvier *in* Cuvier and Valenciennes 1830, locality unknown (holotype: MNHN 7527, 233 mm SL)

Otolithus carolinensis Valenciennes *in* Cuvier and Valenciennes 1833, Charleston, South Carolina (holotype: MNHN 7507, 335 mm SL)

Otolithus drummondii Richardson 1836, New Orleans, Louisiana (holotype: whereabouts unknown)

Cynoscion nothus (Holbrook)

Otolithus nothus Holbrook 1855, South Carolina (no type known)

*Cynoscion regalis (*Bloch and Schneider)

Johnius regalis Bloch and Schneider 1801, New York (holotype: ZMB 8700, not examined)

Roccus comes Mitchill 1814, New York (no type known)

Labrus squeteague Mitchill 1815, New York (no type known)

Cestreus carolinensis Gronow *in* Gray 1854, off the Carolinas, U.S. (holotype: BMNH 1853.11.12.42, a dried skin, 344 mmTL not of *Otolithus carolinensis* Valenciennes)

Otolithus thalassinus Holbrook 1855, Charleston, South Carolina (no type known)

Otolithus obliquatus Valenciennes *in* Sauvage 1879, Martinique Island, West Indies (lectotype: MNHN 7632, 209 mm SL; paralectotypes: MNHN1987-151 [ex MNHN 7632], 182 mm SL; also see Bauchot and Desoutter, 1987).

Remarks — The identity of *Otolithus obliquatus* (Valenciennes) was discussed by Jordan and Evermann (1898), Randall and Cervigón (1968), and Chao (1978). The types were collected by M. Plée from Martinique and are the only records of *C. regalis* from the West Indies. They have higher soft dorsal and anal ray counts (30 dorsal rays, 12 anal rays in MNHN 7632 and 28 dorsal rays, 11 anal rays in MNHN 1987-151), whereas the *C. jaimaicensis* has 23 to 25 dorsal rays and 8 to 10 anal rays.

Cynoscion similis (Randall and Cervigón)

Cynoscion similis Randall and Cervigón 1968:170, Isla de Margarita, Venezuela (holotype: USNM 201382, 284 mm SL)

Cynoscion steindachneri (Jordan)

Cestreus steindachneri Jordan in Jordan and Eigenmann 1889: 372, Brazil (MCZ 10922, 318 mm SL)

Cynoscion virescens (Cuvier)

Otolithus virescens Cuvier *in* Cuvier and Valenciennes 1830, Surinam (holotype: ZMB, not examined)

Remarks — Chao's (1978) inclusion of *Otolithus microps* Steindachner 1879 as a synonym of *C. virenscens* is doubtful. The locality, Porto Alegre, Rio Grande do Sul, is in southern Brazil and is not a coastal city; I have not examined the holotype (NMW 31111) to verify its identity.

KEY TO ATLANTIC SPECIES OF *CYNOSCION*

1a. Scales on body cycloid, much smaller than pored lateral line scales; more than 100 transverse rows above lateral line... 2

1b. Scales on body ctenoid, about same size or larger than pored lateral line scales; fewer than 70 transverse rows of scales above lateral line 4

2a. Caudal fin truncate in adults; inner row of lower jaw teeth slightly enlarged, uniform in size and closely set: anal fin with 10 to 12 soft rays; about 110 transverse scale rows above lateral line ....***C. leiarchus***
(*Caribbean coast to southern Brazil)*

2b. Caudal fin rhomboidal in adults; inner row of lower jaw teeth distinctly larger, gradual increase in size posteriorly and widely spaced; anal fin with 7 to 10 soft rays; about 140 transverse scale rows above lateral line 3

3a. Soft dorsal fin almost entirely covered with small scales; 22 to 25 dorsal fin soft rays; gas bladder with a pair of long, straight, horn-like appendages; 22 vertebrae ....***C. microlepidotus***
(*Caribbean coast of South America to northeastern Brazil*)

3b. Soft dorsal fin unscaled, except 1 to 2 rows of small scales at base; 27 to 31 dorsal fin soft rays; gas bladder with a pair of curved horn-like appendages; 25 vertebrae ....***C. virescens***
(*Caribbean coast to southeastern Brazil*)

4a. Body with spots or stripes on back, dorsal, or caudal fins; caudal fin truncate or emarginated in adults 5

4b. Body uniformly silver, may have some faint streaks on back, but never with spots or stripes; caudal fin rhomboidal or double emarginated in adults.....................................9

5a. Back with distinct spots scattered randomly on dorsal and caudal fins; soft dorsal fin unscaled; pectoral fin shorter than pelvic fin .... ***C. nebulosus***
(*Atlantic coast from Nova Scotia to Florida and Gulf of Mexico coast from Florida to Texas*)

5b. Back with numerous small spots forming oblique and undulating lines, usually not extending to dorsal or caudal fins; pectoral fin slightly longer than pelvic fin 6

6a. Dotted stripes on trunk irregular or reticulated; anal fin with 11–13 soft rays.. ***C. regalis***
(*Atlantic coast from Virginia to Florida and Gulf of Mexico coast of Florida*)

6b. Dotted stripes on trunk follow oblique scale rows; anal fin with 8 to 10 soft rays 7

7a. Soft dorsal fin with 18 to 21 rays; 21 to 26 gill rakers, longer than gill filaments on first gill arch ....***C. guatucupa***
(*Southeast Brazil to Patagonia, Argentina*)

7b. Soft dorsal fin with more than 23 rays; fewer than 13 gill rakers, shorter than gill filaments on first arch 8

8a. Lower jaw teeth closely set, similar in size; unscaled soft dorsal fin membranes, except two to three rows of small scales along its base..........***C. similis***
(*Caribbean coast of South America to northeastern Brazil*)

8b. Lower jaw teeth widely spaced, gradually increasing in size posteriorly; soft dorsal fin covered with small scales $^{3}/_{4}$ of fin height..........***C. jamaicensis***
(*West Indies and from Caribbean coast of South America to Mar del Plata, Argentina*)

9a. Pectoral fin shorter than pelvic fin, two times or more in head length. 10

9b. Pectoral fin about equal to or longer than pelvic fin, less than two times in head length 11

10a. Large canine-like teeth often absent from tip of upper jaw; soft dorsal fin with 21 to 24 rays and almost entirely covered with small scales; 25 vertebrae.......... ***C. steindachneri***
(*Caribbean coast of South America to northeastern Brazil*)

10b. A pair of large canine-like teeth always present; dorsal fin with 26 to 31 soft rays, covered with small scales to half of fin height; 27 vertebrae..........***C. nothus***
(Atlantic coast of U.S. from Virginia to Florida and Gulf of Mexico coast to Texas)

11a. Dorsal fin with 17 to 22 soft rays; anal fin with 7 to 9 soft rays ....***C. acoupa***
(*Caribbean coast of South America to northeastern Brazil*)

11b. Dorsal fin with 25 to 29 soft rays; anal fin with 10 to 12 soft rays. ....***C. arenarius***
(*Gulf of Mexico coast from Florida to Texas*)

EASTERN PACIFIC SPECIES

Cynoscion albus (Günther)

Otolithus albus Günther 1864, Chiapam, Guatemala (holotype: BMNH 1864.1.26.240, 305 mm SL)

Cynoscion analis (Jenyns)

Otolithus analis Jenyns 1842, Callao, Peru (holotype: BMNH 1917.7.14.44, 242 mm SL)
Otolithus peruanus Tschudi 1845, coast of Peru (syntypes: ZMB 864, not examined)

Cynoscion nannus (Castro-Aguirre and Arvizu-Matinez)

Cynoscion nannus Castro-Aguirre and Arvizu-Matinez 1976, off Rio Baluuarte, Sinaloa, Mexico (holotype: L.E.M. (Lab. Ecol. Mar. Cole) 4109, 137 mm SL; paratypes: L.E.M. 4108, 10, 86 to 123 mm SL, not examined)

Cynoscion nortoni (Béarez)

Cynoscion nortoni Béarez 2001, Puerto López fish market at Manabí, Ecuador (holotype; MNHN 99–0961, 260 mm SL; paratypes: CAS 208889,1, 272 mm SL; MCZ 156126, 1, 280 mm SL; MNHN 99–0962, 7, 250–293 mm SL; USNM 357280, 1, 303 mm SL; and SIO 83–75,1, 380 mm SL Paita, Peru)

Cynoscion orthonopterus (Jordan and Gilbert)

Cynoscion orthonopterum Jordan and Gilbert 1881, Punta San Felipe, Gulf of California, Mexico (holotype: USNM 29385, 56 cm SL)

Cynoscion parvipinnis (Ayres)

Cynoscion parvipinnis Ayres 1861, coast of Baja, California, 27°N (no types known)

Otolithus magdalenae (Steindachner)

Otolithus magdalenae Steindachner 1876, Magdalena Bay, Baja, California, Mexico (syntypes: MCZ 10880, 3, 265 to 308 mm SL; NMW 32256, 1, 408 mm SL and others, not examined)

Cynoscion phoxocephalus (Jordan and Gilbert 1881)

Cynoscion phoxocephalum Jordan and Gilbert 1881, Panama Bay, Panama (syntypes: USNM 29339, 1, 230 mm SL; not examined USNM 29296, 1; USNM 29724,1; USNM 29389,1, missing?)

Cynoscion praedatorius (Jordan and Gilbert)

Cestreus praedatorius Jordan and Gilbert *in* Jordan and Eigenmman 1889, Panama (syntypes: MCZ 10901, 2, 315 and 402 mm SL); MCZ 10902, 1, 332 mm SL, labeled as *Otolithus panamensis* Steindachner

Cynoscion reticulatus (Günther)

Otolithus reticulatus Günther 1864, San José, Guatemala (holotype; BMNH 1864.1.26.324, 316 mm SL)

Cynoscion squamipinnis (Günther)

Otolithus squamipinnis Günther 1867, Panama (syntypes: BMNH 1865.7.20.20–21, 2, 223 to 266 mm SL)

Cynoscion stolzmanni (Stendachner)

Otolithus stolzmanni Stendachner 1879 Tumbes, Peru (several syntypes: MW3113, 1, 315 mm SL examined)

Cynoscion xanthulus (Jordan and Gilbert)

Cynoscion xanthulum Jordan and Gilbert 1881, Mazatlán, Mexico (holotype: USNM 28109: not located)

KEY TO PACIFIC SPECIES OF *CYNOSCION*

1a. Second dorsal fin with small scales covering at least to the basal half of the membranes between rays 2
1b. Second dorsal fins without scales extending on membranes, some with one to three rows of small scales forming a low sheath along the base 6
2a. Scales all cycloid. 3
2b. Scales ctenoid on at least posterior $^3/_4$ of body, cycloid on head or breast 4

3a. Anal fin long, with 13 to 15 soft rays, 22 to 24 dorsal rays; head 2.8 to 3.5 times in standard length; caudal fin emarginated .... ***C. analis***
(*Ecuador to Chile*)

3b. Anal fin with 8 to 10 soft rays; 18 to 21dorsal rays; head 3.5 to 3.9 in standard length; caudal fin double truncate...***C. predatorius***
(*Costa Rica to Panama*)

4a. Roof of mouth black; head large, 2.6 to 2.8 in. standard length; eye 4.4 to 5.3 times in head .... ***C. nanus***
(*Southern Gulf of California to Guatemala*)

4b. Roof of mouth pale; head 3.1 or more in standard length; eye more than six times in head 5

5a. Posterior end of maxilla reaching beyond the hind margin of eye; dorsal fin with VII-VIII + I spines, 21 to 23 soft rays; gill rakers 12 to 16; caudal fin double truncate. .... ***C. squamipinnis***
(*Gulf of California to northern Peru*)

5b. Posterior end of maxilla short of the hind margin of eye; dorsal fin with IX–X + I spines, 23 to 27 soft rays; gill rakers 24 to 27; caudal fin emarginated ....***C. othonopterus***
(*Gulf of California, Mexico*)

6a. Scales small, cycloid on body and head; tip of mouth pointing upward, above the mid level of the eye; gill rakers much shorter than gill filaments at the angle of gill arch ....***C. phoxocephalus***
(*Southern Mexico to northern Peru*)

6b. Scales ctenoid on at least posterior $^{3}/_{4}$ of body, tip of mouth below the mid level of eye; gill rakers about equal to or longer than filaments at the angle of first gill arch.............7

7a. Back with prominent stripes and reticulation; pectoral fin tip extends beyond that of pelvic fins; second dorsal fin long, with 25 to 29 rays ....***C. reticulatus***
(*Gulf of California to northern Peru*)

7b. Back uniformly bluish-gray, some backs with faint stripes never reticulated; pectoral fin length about equal to or much shorter than the pelvic fins; second dorsal with 24 or fewer rays 8

8a. Scales mostly ctenoid on body and head; pectoral fin short, 2.0 or more times in head length, its tip falling short of tip of pelvic fins; a dark lunate band median to lower 9

8b. Scales ctenoid on body, cycloid below pectoral fins and on head; pectoral fin 1.8 times or less in head length; its tip reaching to or beyond that of pelvic fins. 11

9a. Lining of gill cover and pectoral axils dark but never black; dorsal fin with VIII–IX + I spines, and 21 to 23 soft rays; caudal fin emarginated ....***C. parvipinnis***
(*Southern California, Gulf of California to Mazatlán, Mexico*)

9b. Inside mouth and gill chamber black; dorsal fin with X – XI + I spines 10

10a. Soft dorsal fin with 23 to 26 rays; caudal fin truncate ....***C. nortoni***
(*Ecuador and Peru*)

10b. Soft dorsal fin with 20 to 21 rays; caudal fin nearly rhomboidal................***C. stolzmanni***
(*Southern Mexico to Peru*)

11a. Pectoral fin tip reaching as far back as pelvic fin tip; first dorsal fin with usually 10 spines, few ctenoid scales on opercle; 54 to 58 pored lateral line scales, 64 to 69 parallel scale rows above lateral line; inside mouth pale to yellowish ....***C. albus***
(*Gulf of California to Ecuador*)

11b. Pectoral fin tip reaching much short of pelvic fin tip; first dorsal fin usually with nine spines; scales cycloid on opercle; 58 to 68 pored lateral pored scales, 74 to 86 parallel scale rows above lateral line; inside mouth bright orange .... ***C. xanthulus***
(*Gulf of California to Guerrero, Mexico*)

FUTURE STUDIES AND CONSERVATION OF SEATROUT

Phylogenetic and life history studies of the *Cynoscion* species and populations are still lacking over most of their geographic range, except for those of the Atlantic and Gulf of Mexico coasts of the U.S. Because seatrout are also a group of important sport fish, seatrout studies are well funded in the U.S., but the knowledge of impacts of recreational fishing on seatrouts and their management is lacking in Central and South America. For example, studies of possible population structuring of the broader ranged and highly exploited South American species such as *C. acoupa, C. jaimaicensis,* and *C. virescens* are urgently needed for local fishery management.

One of the largest seatrout species, *Cynoscion acoupa*, is still abundant along the northeastern Atlantic coast of South America from Venezuela to northern Brazil, or roughly between the Orinoco and south of the Amazon delta (Figure 2.3). The inshore habitats of *C. acoupa* are often associated with mangrove swamps and the historically small artisan fisheries of the region, which may have helped preserve it. However, local fishery managers should be aware that this large seatrout could be rapidly overfished to critical levels if more efficient fishing and processing techniques are implemented. The first endangered seatrout-like species, the Totoaba (*Totoaba macdonaldi*), is an example *not* to follow (Villamar, 1980).

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This article was "thrust" upon me by Steve Bortone and has been prepared practically in the middle of the Amazon (Manaus), where I have had extremely limited access to recent literature. I have used the fish collections at the USNM and MCZ to update the keys provided here and in the species identification sheets that I prepared for the FAO (Chao 1977, 1995). Bruce B. Collette (Systematics Laboratory, NMFS at USNM) has let me use the same bench space in the NMFS fish preparation room, where I started my studies of the Sciaenidae in the early 1970s. I also wish to thank colleagues in the basement of the Fish Division (USNM) for keeping things almost the same for 30 years for the return of this still "young" VIMS student. I also thank W. E. Aguirre-Maldonado (SUNY, Sony Brook) and Karsten Hartel (MCZ) for reviewing drafts of this article; Karsten also remeasured types and searched references for me. Scott Schaefer and Damaris Rodriguez (AMNH) sent me the digital images and x-ray film of the holotype *C. fusiformes.*

FIGURE 2.3 "Snapper," *Cynoscion acoupa*, is apparently abundant in Georgetown, Guyana (5 December 2000, at Georgetown Fishermen's Co-op landing area).

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3

Population Structure of Spotted Seatrout (*Cynoscion nebulosus*) along the Texas Gulf Coast, as Revealed by Genetic Analysis

John R. Gold, Leah B. Stewart, and Rocky Ward

CONTENTS

ABSTRACT

Allelic variation at (presumed) nuclear-encoded microsatellites was assayed among spotted seatrout sampled from localities along the Gulf Coast of Texas. Tests of Hardy-Weinberg equilibrium at each microsatellite within each sample and tests of genotypic equilibrium among pairs of microsatellites within and among samples were nonsignificant. Homogeneity (exact) tests of allele distributions at each microsatellite and estimates (the θ estimator of Wright's F_{ST}) of population structure were nonsignificant following correction for multiple tests executed simultaneously. The absence of a geographic pattern to microsatellite variation among spotted seatrout sampled from the Texas coast differs from that reported previously for the nuclear-encoded gene aspartate aminotransferase (*sAAT-2*) and for mitochondrial (mt)DNA: genetic divergence at *sAAT-2* and mtDNA was significant and related in part to increasing geographic distance between sample localities (isolation by distance).

Several possibilities to account for the difference in patterns of geographic variation among these three types of genetic markers are discussed. We suggest that population structure of spotted seatrout along the Texas coast is best modeled as a series of overlapping subpopulations or stocks distributed linearly along the coastline: individual subpopulations are centered in individual (natal) estuaries, but gene flow between geographically proximate estuaries is sufficient to prevent significant genetic divergence. This type of model also has been hypothesized for red drum (*Sciaenops ocellatus*), a related sciaenid, in the northern Gulf of Mexico. Microsatellite variation also was assayed in a sample of spotted seatrout from the Atlantic coast of Florida. Significant differences in allele frequencies between the sample from the east coast of Florida and four samples from the Texas Gulf coast were detected at all five microsatellites assayed. These findings parallel results from several studies on marine fishes (including other sciaenids) where regionally distinct populations reside in the northern Gulf of Mexico and along the southeast (U.S.) Atlantic coast.

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INTRODUCTION

Spotted seatrout, *Cynoscion nebulosus*, is an estuarine-dependent sciaenid fish distributed from coastal waters in Massachusetts to the Bay of Campeche on the Yucatan Peninsula in Mexico (Patillo et al., 1997), extending perhaps into the Mexican Caribbean (Aguilar-Salazar et al., 1993). The species is most abundant in the northern Gulf of Mexico (hereafter called Gulf) from Florida to Texas (Lassuy, 1983; Mercer, 1984) and at one time supported both recreational and commercial fisheries (Patillo et al., 1997). A small (~48,500 kg in 2000) commercial fishery industry still exists in western Florida, Mississippi, and Louisiana (http://www.st.nmfs.gov/st1/commercial/landings/annual_landings.html) but is dwarfed by the recreational fishery in the Gulf where more than 4 million kg were landed in 1998 and (exclusive of Texas waters) over 6,350,000 kg were landed in 2000 (http://www.st.nmfs.gov/st1/recreational/queries/catch/time_series.html; L. Green, Coastal Fisheries Division, Texas Parks and Wildlife, personal communication). Perceived declines in spotted seatrout abundance across the Gulf have led to decreases in or prohibition of commercial catches and increasing restrictions on recreational catches (references in Bortone et al., 1997). Both overfishing and loss of habitat are hypothesized (Shipp, 1986; Patillo et al., 1997) as instrumental in spotted seatrout declines.

Assessment and allocation of spotted seatrout recreational resources in the Gulf are the responsibility of individual states and vary from state to state (GSMFC, 1993). With the exception of Florida — where management of spotted seatrout is regionally based (Muller et al., 1997) — regulations in most Gulf Coast states are predicated on a single-stock model; i.e., allocation is the same across bays and estuaries within a state. Past studies asking whether a single-stock model is appropriate are equivocal. Nongenetic studies include those of Colura and King (1989), who found that shapes of scales and otoliths varied among spotted seatrout collected from several bays along the Texas coast, and Iverson and Tabb (1962), who reported different growth rates for spotted seatrout obtained from the Gulf Coast of Florida. The differences reported by Iverson and Tabb (1962), however, were hypothesized by Murphy and Taylor (1994) to stem from environmental or harvest factors, not from existence of discrete stocks. Tagging studies (Overstreet, 1983; Baker and Matlock, 1993), generally have indicated little "coastwise" movement of juveniles or adults, with most returns occurring less than 50 km from the release site. Movement of spotted seatrout from bays and estuaries does occur but appears to be primarily associated with spawning or in response to changes in salinity or temperature (Lorio and Perret, 1978; Helser et al., 1993).

Genetic studies have been less equivocal, as differences in general protein banding patterns (Weinstein and Yerger, 1976), allozymes (Ramsey and Wakeman, 1987; King and Pate, 1992), and mitochondrial (mt)DNA (Gold et al., 1999) have been reported among spotted seatrout sampled from various bays and estuaries of the Gulf. In three of these studies, i.e., Ramsey and Wakeman (1987), King and Pate (1992), and Gold et al. (1999), genetic divergence, although comparatively small, appeared to be, in part, a function of geographic distance between pairs of sample localities. In their study of 44 allozyme loci among 12 samples along the Gulf Coast of Texas and northern Mexico, King and Pate (1992) attributed this "isolation-by-distance" effect to westerly directed transport of eggs and larvae in nearshore waters. King and Zimmerman (1993) hypothesized that the difference in frequencies of alleles at the aspartate aminotransferase locus reported by King and Pate (1992) may reflect adaptation to temperature or salinity differences but that a nearshore dispersal mechanism might limit genetic divergence. Gold et al. (1999) assayed mtDNA variation across a broader geographic range, from the Lower Laguna Madre in southern Texas to Tampa Bay on the west coast of Florida, and hypothesized that the isolation-by-distance effect stemmed from factors (e.g., behavioral, physiological) that limited female dispersal from natal bays and estuaries.

In this chapter, we report results from ongoing, independent studies in our laboratories on variation in (presumed) nuclear-encoded microsatellites among geographic samples of spotted seatrout from the Gulf Coast of Texas. Briefly, microsatellites are abundant, short stretches of DNA composed of di-, tri-, or tetranucleotide arrays that are embedded in unique DNA, inherited in a Mendelian fashion, highly polymorphic, found in all eukaryotic species, and distributed evenly throughout euchromatic regions of chromosomes (Weber, 1990; Wright, 1993; Weber and May, 1989). Microsatellites are considered superior to all other known genetic markers for population-genetic studies because of high levels of polymorphism and allele frequencies that are generally consistent with HW equilibrium expectations of diploid, Mendelian loci. In addition, because identification of each microsatellite is via amplification using specific polymerase-chain-reaction (PCR) primers, few problems are associated with homology of alleles (Weber, 1990; Wright and Bentzen, 1994). While our long-term interest is assessing population structure of spotted seatrout in the northern Gulf, our initial work (reported here) is restricted to spotted seatrout from the Texas Gulf Coast. Understanding the genetic structure of spotted seatrout in Texas waters has important management implications, especially for an ongoing stock enhancement program (King et al., 1995) conducted by Texas Parks and Wildlife.

MATERIALS AND METHODS

Our study was conducted in two different laboratories: one at Texas A&M University (TAMU) in College Station, Texas, and one at the Perry R. Bass Marine Fisheries Research Station of Texas Parks and Wildlife (TPW) in Palacios, Texas. Work at TAMU involved 162 spotted seatrout collected by angling and gill netting from three localities in Texas (Lower Laguna Madre, Tres Palacios Bay, and Sabine Pass) and one locality from the Atlantic coast of Florida (Mosquito Lagoon). Work at TPW involved 186 spotted seatrout sampled by gill netting from nine localities along the Texas coast (Lower Laguna Madre, Upper Laguna Madre, Corpus Christi Bay, Aransas Bay, San Antonio Bay, West Matagorda Bay, East Matagorda Bay, Galveston Bay, and Sabine Lake). Collection localities are shown in Figure 3.1; the number of individuals sampled at each locality is given in Tables 3.1A and 3.1B. For TAMU samples, heart and spleen tissues were removed, frozen in liquid nitrogen, and stored at –80°C until processed. For TPW samples, clippings of soft dorsal-fin tissue were removed, placed in 100% ethanol, and stored at room temperature. Genomic DNA was extracted for TAMU samples following Gold and Richardson (1991) and for TPW samples by the PureGene DNA isolation kit and protocols (Gentra Systems, Inc., Minneapolis, MN).

Polymerase-chain-reaction (PCR) primers for five microsatellites developed initially by Turner et al. (1998) for red drum were used for TAMU samples. The five microsatellite repeat motifs in red drum are *Soc*12 — $[GT]_7$, *Soc*50 — $[GT]_7$, *Soc*133 — $[TGC]_8$, *Soc*201 — $[CCT]_6$, and *Soc*243 — $[CCT]_9$. Details regarding primer sequences, length of the cloned allele, and annealing temperature may be found in Turner et al. (1998). The primers for *Soc*12 and *Soc*243 were used for TPW samples, along with primers for two additional microsatellites (*Cne*133 and *Cne*133′). Primers for the latter were amplified from primers designed by sequencing the product from amplifications of *Soc*133 and then identifying internal primers that gave more consistent results than did the original *Soc*133 primers. Primers (forward/reverse) for *Cne*133 and *Cne*133′ were 5′-CCGAGCTGAAA-CACATTCTTGC- 3′/5′-CTTGGCATTTCCAGACATCACTG-3′ and 5′-CATTTGGACCATCGC-TACTGCTG-3′/5′-TGTGTTTCAGCTCGGCTCG-3′, respectively.

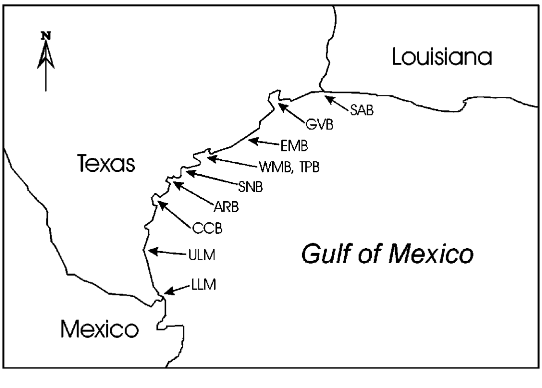

FIGURE 3.1 Sampling localities for spotted seatrout (*Cynoscion nebulosus*) examined from the Texas Gulf Coast. LLM – Lower Laguna Madre; ULM – Upper Laguna Madre; CCB – Corpus Christi Bay; ARB – Aransas Bay; SNB – San Antonio Bay; WMB – West Matagorda Bay; TPB – Tres Palacios Bay; EMB – East Matagorda Bay; GVB – Galveston Bay; and SAB – Sabine Pass and Sabine Lake.

TABLE 3.1A
Summary Statistics for Spotted Seatrout (*Cynoscion nebulosus*) Assayed in College Station

Microsatellite	Sample LLM	TPB	SAB	EFL
*Soc*12				
N	55	35	31	41
n_a	6	3	4	2
P_{HW}	0.504	0.230	0.470	1.000
*Soc*50				
N	55	35	31	39
n_a	4	4	4	3
P_{HW}	0.503	0.781	0.116	0.664
*Soc*133				
N	55	35	31	41
n_a	4	4	4	3
P_{HW}	0.320	1.000	0.290	0.073
*Soc*201				
N	55	35	31	40
n_a	4	4	4	4
P_{HW}	0.425	0.378	1.000	0.010[a]
*Soc*243				
N	55	33	39	39
n_a	3	3	4	4
P_{HW}	0.793	0.870	1.000	1.000

Notes: Sample acronyms are as in Figure 3.1. N = number of individuals assayed; n_a = number of alleles; and P_{HW} = probability of conforming to Hardy-Weinberg (expected) proportions.

[a] Nonsignificant ($P > 0.05$) when corrected for multiple tests.

DNA amplifications (TAMU) were conducted in 10-µl reactions following conditions described in Turner et al. (1998). The forward primer of each pair was end-labeled with [γ^{32}P]-dATP and amplification reactions consisted of 25 cycles of denaturation (94°C, 30 sec), annealing (56°C, 30 sec), and extension (72°C, 30 sec), with an initial denaturation of 94°C for 2 min. Amplifications in Palacios were conducted in 25-µl reactions, utilizing a modified "touchdown" protocol where samples were denatured (95°C, 30 sec), annealed (55°C, 30 sec — decreasing 1°C per cycle), and extended (72°C, 1 min) for 10 cycles, followed by 20 additional cycles of denaturation (95°C, 30 sec), annealing (50°C, 30 sec), and extension (72°C, 1 min, increasing 3 sec per cycle). Amplifications concluded with a 7-min "hold" at 72°C. PCR products (TAMU) were separated on 6% polyacrylamide gels and visualized by autoradiography, whereas PCR products (TPW) were separated on 10% polyacrylamide gels and visualized by ethidium bromide (0.5 µg/ml in 1X TBE buffer for 20 min). Alleles in both laboratories were scored via comparisons with internal standards.

Genotype frequencies at each microsatellite for both TAMU and TPW samples were tested for deviation from Hardy-Weinberg (HW) equilibrium frequencies by using exact tests performed with Markov-chain randomization (Guo and Thompson, 1992). Probability (P) values for HW tests at each microsatellite within each sample were estimated via permutation with 1000 resamplings (Manly,

TABLE 3.1B
Summary Statistics for Spotted Seatrout (*Cynoscion nebulosus*) Assayed in Palacios

				Sample					
Microsatellite	**LLM**	**ULM**	**CCB**	**ARB**	**SNB**	**WMB**	**EMB**	**GVB**	**SAB**
*Soc*12									
N	40	40	41	40	40	40	40	39	30
n_a	3	4	4	3	2	3	2	3	3
P_{HW}	0.322	0.376	0.230	0.581	1.000	0.564	0.216	0.381	0.346
*Soc*243									
N	40	40	41	40	40	40	40	39	30
n_a	3	3	3	3	4	3	3	3	3
P_{HW}	0.844	0.306	0.186	0.007^a	0.035^a	0.347	0.102	0.105	1.000
*Cne*133									
N	40	40	41	40	40	40	40	39	30
n_a	3	4	3	4	3	4	4	3	3
P_{HW}	0.748	1.000	1.000	0.201	1.000	0.310	0.315	0.358	1.000
*Cne*133′									
N	40	40	41	40	40	40	40	39	30
n_a	2	3	3	3	2	2	2	4	2
P_{HW}	0.398	1.000	0.172	1.000	1.000	1.000	0.247	0.016	1.000

Notes: Sample acronyms are as in Figure 3.1. N, n_a, and P_{HW} are as in Table 3.1A.

[a] Non-significant ($P > 0.05$) when corrected for multiple tests.

1991); significance levels for simultaneous tests were adjusted using the sequential Bonferroni approach (Rice, 1989). Tests of genotypic equilibrium at pairs of microsatellites were used to assess whether any microsatellites might be linked. Significance of probability values obtained from exact tests of genotypic equilibrium was generated by 1000 resamplings. Tests of HW and genotypic equilibrium were executed using the statistical program GENEPOP (Raymond and Rousset, 1995).

Homogeneity of allele distributions at each microsatellite was assessed for both TAMU and TPW samples via exact tests as implemented in GENEPOP. Significance of tests of genetic homogeneity employed permutation with 1000 resamplings per individual comparison. Estimates of population subdivision among TAMU samples employed Weir and Cockerham's (1984) θ generated via GENEPOP. Statistical significance of θ was assessed using the analysis of molecular variance (AMOVA) of Excoffier et al. (1992), employing 1000 random permutations. For TPW samples, θ values and determination of whether individual θ values differed significantly from zero (1000 random permutations) were obtained using the statistical program ARLEQUIN (Schneider et al., 1999).

RESULTS

Summary statistics, including sample sizes, number of alleles detected at each microsatellite, and results of tests of genotype conformance to expectations of HW equilibrium for each microsatellite at each sample locality are given in Tables 3.1A and 3.1B. The distribution of alleles and allele frequencies at each microsatellite for each locality may be obtained from JRG (TAMU samples) or RW (TPW samples). The number of alleles over all samples ranged between two and four for most microsatellites at most localities; six alleles were detected at *Soc*12 in the TAMU sample from Lower Laguna Madre (LLM), and six alleles (total) at *Soc*201 were found among all TAMU samples. Following Bonferroni correction, genotype proportions for all microsatellites in all samples did not differ significantly from expected HW equilibrium proportions. Tests of genotypic equilibrium within sample localities also were nonsignificant following Bonferroni correction, as were tests carried out with all sample localities pooled (Table 3.2).

Exact tests of allele distribution homogeneity and the θ measure (after Weir and Cockerham, 1984) of population structure among TAMU and TPW samples were nonsignificant following Bonferroni correction (Table 3.3). A probability value of 0.035 before Bonferroni correction was obtained for allele distributions at *Soc*201 among TAMU samples. Frequency plots (Figure 3.2) of the four common alleles at *Soc*201 indicate an elevated frequency of *Soc*201–9 in the sample from Sabine Pass (SAB) and an elevated frequency of *Soc*201–10 in the sample from Lower Laguna Madre (LLM). It is also interesting that frequencies of three alleles (*Soc*201–9, *Soc*201–10, and *Soc*201–11) appear to display a pattern of east-to-west clinal variation. A probability value of 0.013 before Bonferroni correction was obtained for allele distributions at *Soc*12 among TPW samples; this value is near the Bonferroni adjusted alpha of 0.0125. Frequency plots (Figure 3.2) indicate that the heterogeneity likely is due to varying frequencies of alleles *Soc*12–82, *Soc*12–84, and *Soc*12–94, none of which appears to display a pattern of clinal variation. Estimates (θ) of population structure (Table 3.3) ranged from zero (including negative values) to 0.015 for TAMU samples; however, none of the θ values differed significantly from zero. For TPW samples (Table 3.3), θ estimates ranged from 0.004 to 0.013. The θ estimate of 0.013 (for *Soc*12) differed significantly from zero before but not after Bonferroni correction (adjusted alpha of 0.0125).

Exact tests for TAMU samples, including the sample from the Atlantic coast of Florida, were significant before and after Bonferroni correction: *Soc*12 ($P = 0.002$), *Soc*50 ($P = 0.011$), *Soc*133 ($P = 0.004$), *Soc*201 ($P = 0.017$), and *Soc*243 ($P = 0.000$). Except for *Soc*201 ($P = 0.128$), θ values in comparisons that included the sample from the Atlantic coast of Florida differed significantly from zero (data not shown). Genetic distances, estimated as the $(\delta\mu)^2$ metric of Goldstein et al. (1995), revealed that the average difference between the sample from the Florida east coast and the three TAMU samples from Texas waters was considerably greater than the average difference among the three Texas samples.

DISCUSSION AND CONCLUSIONS

The primary purpose of our independent studies was to assess population structure of spotted seatrout in coastal waters of Texas. Divergence (population structure) among spotted seatrout in coastal waters might be expected (Chapman et al., 1999) based on observed life history patterns and results from tag-and-release studies. Briefly, spotted seatrout are generally perceived to be resident to individual estuaries and to spend their entire life cycle in inshore waters (Patillo et al., 1997). Spawning locations tend to be inside estuaries, and larvae and juveniles are found primarily in grass beds, although they can be abundant in areas without seagrass (McMichael and Peters, 1989). Sexual maturity generally occurs after age one (Saucier and Baltz, 1993; Saucier et al., 1992). Tagging studies are consistent with the notion of estuarine residency, as movement of juveniles and adults between estuaries appears to be limited (Overstreet, 1983; Baker and Matlock, 1993). In one study (Moffett, 1961), a re-

TABLE 3.2
Probability of Genotypic Equilibrium (pairwise comparisons) at Microsatellites among Spotted Seatrout (*Cynoscion nebulosus*) Assayed in College Station (above diagonal) and Palacios (below diagonal)

Microsatellite	*Soc*12	*Soc*50	*Soc*133	*Soc*201	*Soc*243	*Cne*133	*Cne*133′
*Soc*12	— -	0.546	0.682	0.893	0.090	— -	— -
*Soc*50	— -	— -	0.445	0.197	0.181	— -	— -
*Soc*133	— -	— -	— -	0.201	0.516	— -	— -
Soc201	— -	— -	— -	— -	0.810	— -	— -
*Soc*243	0.362	— -	— -	— -	— -	— -	— -
*Cne*133	0.323	— -	— -	— -	0.026[a]	— -	— -
*Cne*133′	0.177	— -	— -	— -	0.802	0.469	— -

[a] Non-significant ($P > 0.05$) when corrected for multiple tests.

TABLE 3.3
Results of Tests for Homogeneity in Allele Distributions and Estimates of Population Structure among Geographic Samples of Spotted Seatrout (*Cynoscion nebulosus*) Sampled from Coastal Waters of Texas

	College Station Samples[a]			**Palacios Samples**		
Microsatellite	P_{EXACT}	θ	P	P_{EXACT}	θ	P
*Soc*12	0.305	0.015	0.103	0.013[b]	0.013	0.043[b]
*Soc*50	0.878	–0.011	0.981	—	—	
*Soc*133	0.362	0.000	0.331	—	—	
*Soc*201	0.035[b]	0.005	0.180	—	—	
*Soc*243	0.285	–0.012	0.936	0.211	0.004	0.233
*Cne*133	—	—		0.250	0.006	0.095
*Cne*133′	—	—		0.054	0.006	0.196

Notes: P_{EXACT}: Probability of allele distribution homogeneity based on exact test. θ: Estimate of population subdivision (after Weir and Cockerham, 1984). P: probability that $\theta = 0$.

[a] Results are for samples from the Texas coast (i.e., the sample from the east coast of Florida was excluded).

[b] Nonsignificant ($P > 0.05$) when corrected for multiple tests.

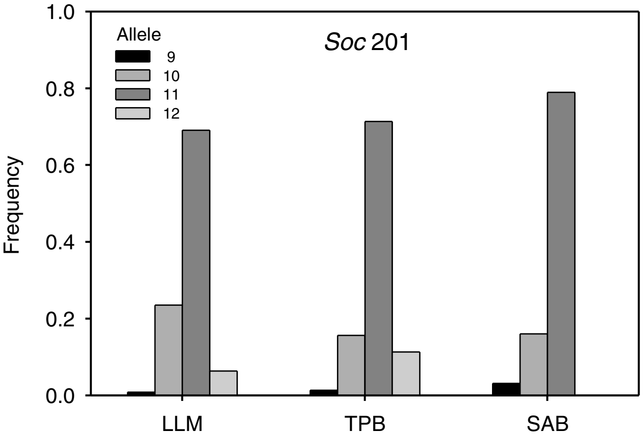

FIGURE 3.2 Allele-frequency histograms for microsatellite *Soc*201 among College Station samples of spotted seatrout (*Cynoscion nebulosus*). Abscissa: sample localities (LLM – Lower Laguna Madre, TPB – Tres Palacios Bay; and SAB – Sabine Pass); ordinate: frequencies of alleles *Soc*201-9, -10, -11, and -12.

turn of more than 450 km from a release site was reported, but in general, nonrandom movements of spotted seatrout are thought to be largely in response to changes in temperature or salinity (Lorio and Perret, 1978; Helser et al., 1993). Nongenetic studies based on growth rates (Iverson and Tabb, 1962, but see Murphy and Taylor, 1994) and shapes of scales and otoliths (Colura and King, 1989) also have been consistent with the notion of resident stocks within estuaries.

Prior genetic studies on spotted seatrout from the northern Gulf have documented varying degrees of divergence among samples from different estuaries. Weinstein and Yerger (1976) assayed general proteins and reported significant differences among spotted seatrout from various estuaries on the west (Gulf) coast of Florida. Ramsey and Wakeman (1987) found significant heterogeneity at three of 40 putative allozyme loci among spotted seatrout sampled from Texas to Florida. However, homogeneous subsets of samples were generated upon removal of specific alleles at one or a few loci in one or a few samples; overall, the only evident spatial patterning was a weak isolation-by-distance effect indicated by a significant Moran's I value at a locus for glucose-6-phosphate isomerase (*Gpi-B*). King and Pate

(1992), alternatively, surveyed 44 putative allozyme loci among spotted seatrout sampled from 11 localities along the Texas coast and one locality from northern Mexico. They found significant heterogeneity at a locus for aspartate aminotransferase (*sAAT-2*) and significant spatial autocorrelations (indicative of isolation by distance) for alleles at both *sAAT-2* and a locus for tripeptide aminopeptidase (*PEP-B*). Finally, Gold et al. (1999) examined mtDNA restriction-site variation among spotted seatrout sampled from eight localities in the northern Gulf (five from Texas) and found significant heterogeneity among all samples from the northern Gulf and among samples from the western Gulf. Heterogeneity among samples from the western Gulf appeared to stem primarily from mtDNA haplotype frequency differences in a sample from the Lower Laguna Madre. Spatial autocorrelation analysis of common mtDNA haplotypes revealed an isolation-by-distance effect, where significant, positive Moran's I values were found between proximal sample localities and significant, negative values were found between geographically distant ones. Collectively, the studies of Ramsey and Wakeman (1987), King and Pate (1992), and Gold et al. (1999) have not demonstrated significant genetic differences among spotted seatrout in individual estuaries but, rather, a pattern in which genetic divergence increases with geographic distance and significant differences arise ostensibly from comparisons between samples near the extremes of geographic sampling. Thus, while there may be different subpopulations or stocks of spotted seatrout in the northern Gulf, sufficient gene flow appears to occur between geographically proximate subpopulations such that significant genetic divergence is observed only between geographically distal bays and estuaries. King and Pate (1992) suggested that the intracoastal waterway linking most bays and estuaries of the northern Gulf may provide the mechanism whereby gene flow could occur in a species such as spotted seatrout that spends virtually all of its life cycle in nearshore waters.

Results from our independent studies of microsatellite variation among spotted seatrout from the Texas coast are not directly comparable with the studies of Weinstein and Yerger (1976) and Ramsey and Wakeman (1987), because their samples came from Florida and from across the northern Gulf, respectively. The study by Ramsey and Wakemen (1987) also included only a single sample from Texas waters. However, results from this study are comparable with those of King and Pate (1992) and Gold et al. (1999), as all three involved spotted seatrout sampled along the Texas Gulf Coast from Sabine Lake (or Sabine Pass) near the Louisiana border to the Lower Laguna Madre near the border with Mexico.

Patterns of geographic variation for different types of genetic markers used in the three studies differ. King and Pate (1992) and Gold et al. (1999) found significant divergence among samples in allele frequencies of allozymes and mtDNA, respectively, whereas in this study allele frequencies at microsatellites essentially were homogeneous across the same geographic sampling surface. King and Pate (1992) and Gold et al. (1999) also found that genetic divergence at *sAAT-2* and mtDNA, respectively, was related in part to increasing geographic distance between sample localities (isolation by distance), giving rise to an east-west clinal pattern along the Texas coast; little evidence of such an effect was detected for any of the microsatellites.

Differences in patterns of geographic variation between or among various genetic markers have been reported previously in other marine species, including yellowfin tuna, *Thunnus albacares* (Ward et al., 1994), Atlantic cod, *Gadus morhua* (Pogson et al., 1995), and American oyster, *Crassostrea virginica*. The last study is perhaps the best known. Buroker (1983) assayed 14 polymorphic allozyme loci among *C. virginica* sampled from Texas to Massachusetts and found little detectable geographic heterogeneity; however, Reeb and Avise (1990) found large differences in mtDNA restriction fragment length polymorphisms (RFLPs) between samples from the northern Gulf and the southeastern U.S. Atlantic coast. Subsequently, Karl and Avise (1992) identified restriction site polymorphisms at four anonymous nuclear-encoded sequences that also exhibited large differences in allele frequency between the northern Gulf and the southeastern U.S. Atlantic coast. In general, when different types of polymorphic genetic markers exhibit different patterns of geographic variation, the usual inference is that at least one type of polymorphism may be affected by natural selection in addition to genetic drift (McDonald, 1994).

Assuming that anonymous (and presumably noncoding) nuclear DNAs and mtDNA RFLPs are selectively neutral, Karl and Avise (1992) interpreted the different patterns in *C. virginica* as indicating that balancing selection was acting to maintain allele frequencies at the allozyme loci. Under this hypothesis, the geographic divergence in mtDNA and anonymous nuclear DNAs would be hypothesized to stem from small effective population size (mtDNA) and from a combination of reduced gene flow, effective population size, and genetic drift.

Pogson et al. (1995) employed similar logic in their study of genetic variation in Atlantic cod, where the average F_{ST} value of several anonymous nuclear DNA polymorphisms was significantly greater than the average of several allozyme polymorphisms. The findings in *C. virginica*, however, were questioned subsequently by the discovery that six additional anonymous nuclear DNA polymorphisms, sampled over essentially the same geographic surface, displayed geographic variation that was not significantly greater than that exhibited by the allozymes (McDonald et al., 1996).

The patterns of variation exhibited by the three types of genetic markers, i.e., allozymes, mtDNA, and nuclear DNA, in spotted seatrout from the Texas coast differ from the patterns in American oysters and Atlantic cod, in that significant divergence among samples of spotted seatrout was detected in mtDNA and allozymes but not in noncoding nuclear DNAs (microsatellites in this case). The differences in patterns of geographic variation in the three types of genetic markers among spotted seatrout may stem from one of several possibilities. The first and simplest possibility is that the pattern of variation in one or more of the genetic markers may not be representative of "true" geographic variation in the type of marker. In the study by King and Pate (1992), for example, only a single (putative) allozyme locus (*sAAT-2*) varied significantly among localities, representing effectively a sample size of one. However, a second allozyme locus (*PEP-B*) also varied clinally, supporting the inferred pattern of isolation by distance. The same is true for the mtDNA study by Gold et al. (1999), in that two mtDNA haplotypes differed significantly in frequency across localities and both showed strong east-west clines across the northern Gulf.

Relative to the microsatellites, the studies of anonymous nuclear DNA loci in American oyster have shown that different patterns may be obtained in different studies carried out in different laboratories (Karl and Avise, 1992; McDonald et al., 1996). Our studies of microsatellites in spotted seatrout, however, have revealed essentially the same pattern of geographic variation even though the studies were conducted in different laboratories and involved different samples. It may be that too few microsatellites have been assayed relative to a random sampling of variation at microsatellites in spotted seatrout. This can be tested easily in the future.

A second possibility is that observed patterns in the three types of markers are real and reflect different evolutionary, ecological, or genetic processes. King and Zimmerman (1993) hypothesized that the clinal variation in *sAAT-2* observed by King and Pate (1992) could reflect adaptation to temperature or salinity gradients and, moreover, that divergence along such gradients might be minimized by gene flow, given that the effective number of migrants (N_em) estimated by King and Pate (1992) ranged from 9.75 (at *sAAT-2)* to 49.75 (at *PEP-B*). The hypothesis that nonrandom patterns of allozyme variation can stem from natural selection is not without precedent (Christiansen and Frydenberg, 1974), and the observation of clinal variation is certainly consistent with expectations based on directional selection where one genotype is favored at one end of an environmental gradient and disfavored at the other end (Hartl, 1980).

Alternatively, clines theoretically can arise from migration (gene flow) coupled with founder effects at geographic extremes and hence are not necessarily *prima facie* evidence of selection (Hartl, 1980). The latter (i.e., gene flow coupled with founder effects) would seem the more likely explanation for the cline observed at *sAAT-2*, given that the same clinal pattern is observed for mtDNA haplotypes. That is, a directional selective force acting jointly on both *sAAT-2* and mtDNA and along the same geographic gradient would seem unlikely, in part because the two are inherited independently, and in part because variation in mtDNA RFLPs typically stems from synonymous base substitutions in third codon positions of protein-coding genes, which generally are assumed to be selectively neutral.

The absence of (spatial) heterogeneity or a marked cline in allele frequencies at any of the spotted seatrout microsatellites assayed, however, is puzzling because polymorphisms at microsatellites are typically assumed to be selectively neutral. This means that one would expect geographic patterns at spotted seatrout microsatellites to parallel patterns observed at *sAAT-2* and mtDNA if, in fact, observed clinal variation at *sAAT-2* and mtDNA is primarily a function of gene flow, effective population size, and genetic drift. One explanation might be that too few microsatellites were assayed relative to detecting clinal variation. King and Pate (1992), for example, assayed seven polymorphic loci, yet significant divergence was found only at *sAAT-2*. Another explanation might be allele-size homoplasy (Estoup et al., 1995), where co-migrating alleles at microsatellites are assumed to be homologous yet represent different sequence motifs and hence are not identical by descent. This phenomenon has been documented in a number of animals, including fishes (Angers and Bernatchez, 1997), and clearly could confound population diversity assessment (Culver et al., 2001).

A last possibility is that variation in *sAAT-2* is a consequence of directional selection, as suggested by King and Zimmerman (1993), and that variation in mtDNA and microsatellites reflects the interactions among gene flow, effective population size, and genetic drift expected of selectively neutral genetic markers. If so, the finding that divergence in spotted seatrout mtDNA is greater than that at any of the spotted seatrout microsatellites may suggest a sex-biased difference in gene flow. Because mtDNA provides information only on female gene flow, greater divergence in mtDNA relative to nuclear-encoded DNA has been inferred in other marine species (Ferguson et al., 1995; Rassmann et al., 1997; Buonaccorsi et al., 1999) to indicate male-mediated dispersal, female philopatry, or both. Interestingly, the opposite (i.e., female-mediated dispersal, male philopatry, or both) has been suggested as an explanation to account for patterns of mtDNA and microsatellite divergence in the red drum (Gold and Turner, 2001). Clearly, this issue bears further investigation in spotted seatrout.

Although we cannot distinguish satisfactorily between the latter two possibilities, both are consistent with the hypothesis that genetic divergence in spotted seatrout is in part a function of the interaction among gene flow, effective population size, and genetic drift, and that gene flow occurs primarily (but not exclusively) between adjacent or neighboring estuaries. Population structure of spotted seatrout along the Texas coast may thus be modeled as a series of overlapping subpopulations or stocks distributed linearly along the coastline, where individual subpopulations are centered in individual (natal) estuaries but where gene flow between geographically proximate estuaries is sufficient to prevent significant genetic divergence. This type of model also has been hypothesized (Gold et al., 2001) for red drum (*Sciaenops ocellatus*) in the northern Gulf. The genetic data in red drum, however, were far more extensive, both spatially and temporally, permitting an estimate of the geographic neighborhood size of individual populations. We suggest that future genetic studies of spotted seatrout should be directed along similar lines, as migration and its extent from individual estuaries may be an important component to recruitment in adjacent estuaries. This could mean that conservation and management planning for spotted seatrout should perhaps include a wider geographic context and that adults employed in hatchery-based supplementation programs should not necessarily be procured from the same bay or estuary.

Our finding that the sample of spotted seatrout from the Atlantic coast of Florida differed significantly in allele frequencies from the samples in the northern Gulf paralleled those findings of Ramsey and Wakeman (1987) and Gold et al. (1999), in which significant divergence at two allozyme loci and in mtDNA haplotype frequencies, respectively, were documented between spotted seatrout from the two regions. Wiley and Chapman (2001) also found significant differences in allele frequencies at two microsatellites between a sample from the northern Florida Gulf coast and several samples from the southeast (U.S.) Atlantic coast. These findings parallel results from several marine fishes (including other sciaenids) for which regionally distinct populations reside in the northern Gulf and along the southeast (U.S.) Atlantic coast (Avise, 1992; Gold and Richardson, 1998a, b). As noted by Gold et al. (1999) and Wiley and Chapman (Chapter 4, this volume), these shared patterns of regional population structure likely stem from similar vicariant histories possibly related to climatic changes occurring during glaciation, absence of suitable habitat at spatial junctures between populations, or oceanographic currents that minimize movement from the Atlantic into the Gulf.

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4 Population Structure of Spotted Seatrout, *Cynoscion nebulosus*, along the Atlantic Coast of the U. S.

Bradley A. Wiley and Robert W. Chapman

CONTENTS

ABSTRACT

Allelic variation was assessed at two microsatellite loci in 711 individuals of the spotted seatrout (*Cynoscion nebulosus*) sampled from six locations along the Atlantic coast of the U.S. and a single location in the Gulf of Mexico. Tests for conformity to Hardy-Weinberg (HW) equilibrium were not significant at both loci in any of the Atlantic samples but were significant at one locus or the other in some locations. Significant departure from HW were noted at both loci in the Gulf of Mexico sample. Tests for homogeneity in allele frequencies among populations found significant differences among populations separated by known zoogeographic barriers and general uniformity among populations within zoogeographic realms. These data suggest a combination of historical events and residential behavior as major factors contributing to genetic population structure in this species.

INTRODUCTION

The spotted seatrout, *Cynoscion nebulosu*s (Sciaenidae), is an important commercial and recreational fish throughout much of its range from New York to Mexico (Welsh and Breder, 1924; Guest and Gunter, 1958; Baker et al., 1986). The species grows to an average length of 35 cm and is common in areas of dense concentrations of seagrass or tidal creeks bordered by marsh grasses or mangrove (Tabb, 1966; Bryant et al., 1989; Chester and Thayer, 1990). Tagging studies indicate that they are residential and rarely leave their natal estuary, especially in the southern portion of their range

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(Music, 1981; Baker et al., 1986; Bryant et al., 1989; Baker and Matlock, 1993). Spotted seatrout aggregate for spawning in the lower portions of estuaries from May through September, although the spawning season may be shorter at higher latitudes (Baker et al., 1986; Peebles and Tolley, 1988; Baker and Matlock, 1993; Helser et al., 1993). Spotted seatrout mature after age one, and young from the previous year mature in time to spawn toward the end of the current year's spawning season. Older fish become reproductively active earlier in the season and may spawn multiple times in a spawning season (McMichael and Peters, 1989), except in the most northern latitudes of the range of the species (Brown-Peterson and Thomas, 1988). Larval *C. nebulosus* are capable of vertical migration in the water column and position themselves in the water column so that they are recruited into the shallow, upper portions of estuaries (Peebles and Tolley, 1988; McMichael and Peters, 1989).

Inshore spawning and limited inter-estuary migration in *C. nebulosus* suggest that genetic exchange over distance may be quite limited. Previous population studies (Iversen and Tabb, 1962; Weinstein and Yerger, 1976; Ramsey and Wakeman, 1987; King and Pate, 1992; Gold et al., 1999) suggest that there is some degree of population subdivision within *C. nebulosus* from the Gulf of Mexico; however, not all these reports are in total agreement as to the extent of the isolation. Analysis of growth rates and tagging data (Iversen and Tabb, 1962) indicated independent populations of spotted seatrout in five estuaries in Florida. Weinstein and Yerger (1976), utilizing protein electrophoresis, reported independent populations of *C. nebulosus* in seven estuaries in Florida and Texas. They also suggested that the Mississippi River plume forms a barrier that divides spotted seatrout in the northern Gulf of Mexico into major eastern and western populations. Ramsey and Wakeman (1987), in a survey of allozymic variation at 40 loci in 15 estuaries in eastern Florida and the northern Gulf of Mexico, concluded that *C. nebulosus* was only weakly differentiated by region and not by estuary. In contrast to Weinstein and Yerger (1976), they failed to find any evidence of a population barrier associated with the Mississippi Delta. King and Pate (1992) obtained similar results in a study of allozyme variation along the Texas coast and northern Mexico. The conclusions based on allozyme studies should be interpreted with caution because the levels of variation reported were quite low (Ramsey and Wakeman, 1987; King and Pate, 1992). In contrast, Gold et al. (1999) found significant heterogeneity in the distribution of mtDNA (mitrochondrial DNA) haplotypes, which supported the hypothesis that *C. nebulosus* was divided into subpopulations or stocks. In addition, Gold et al. (1999) suggested that the divergence between mtDNA profiles found in the Gulf of Mexico and the Atlantic was related to historical vicariance stemming from climactic changes during glacial periods.

The degree of spatial heterogeneity in spotted seatrout along the Gulf of Mexico and Atlantic coasts remains uncertain, as the mtDNA and allozyme data bases give qualitatively different results as to the degree of spatial subdivision. Many Atlantic states have research programs that have examined aspects of the life history of *C. nebulosus*, but the population structure there has not been as well studied as it has in the Gulf of Mexico. The tagging studies indicate that inter-estuarine migrations by adults are rare, but it is not known if this results in restrictions to gene flow.

In this chapter we examine the distribution of genetic variation in two microsatellite loci from *C. nebulosus*. We focus our attention on sampling sites along the Atlantic coast of the U.S. to add to the existing information on the species generated largely by studies in the Gulf of Mexico. We examine the differentiation among populations on local and regional scales.

MATERIALS AND METHODS

FIELD METHODS

Collections of spotted seatrout were made from May through September in 1994 and 1995. In 1994, collections of at least 30 adult spotted seatrout were taken from commercial fisheries in the Indian River Lagoon, Florida, and in three South Carolina estuarine systems: Charleston Harbor, Cape Romain, and the ACE Basin (Ashepoo, Combahee and Edisto rivers)/Saint Helena Sound (Table 4.1

TABLE 4.1
Summary of Allele Frequencies, Heterozygosity, Sample Size (N), and Significance (P) of Deviation from Hardy-Weinberg Equlibrium for *Cynoscion nebulosus* Populations

Locus	Allele:	Choctawhatchee Bay	Indian River	Brunswick	South Carolina	Ace Basin	Charleston Harbor	Cape Romain	Chesapeake Bay
Cne 4-2	113	0.2088	0.2864	0.1316	0.0887	0.0763	0.0955	0.0763	0.2324
	115	0.2198	0.2727	0.1316	0.0799	0.0763	0.1000	0.0647	0.0493
	119	0.4286	0.4091	0.7842	0.8081	0.8305	0.7818	0.8103	0.7183
	121	0.1429	0.0318	0.0000	0.0233	0.0169	0.0227	0.0302	0.0000
Expected H		0.704	0.6752	0.3606	0.3321	0.2983	0.3691	0.3293	0.4276
Observed H		0.5055	0.5000	0.3474	0.3372	0.3220	0.3455	0.3448	0.3662
N		91	110	95	344	118	110	116	71
P		0.0006	0.0000	0.7917	0.3609	0.7406	0.4843	0.5862	0.0823
Fis		0.2820	0.2595	0.0366	0.0154	–0.0795	0.0639	–0.0471	0.1436
Cne 6-11	110	0.0220	0.0091	0.0000	0.0233	0.0212	0.0045	0.0431	0.0000
	112	0.0385	0.0136	0.0301	0.0189	0.0127	0.0273	0.0172	0.0000
	114	0.5714	0.5364	0.5542	0.5189	0.5000	0.5091	0.5474	0.4437
	116	0.1429	0.0591	0.9542	0.0596	0.0720	0.0591	0.0474	0.0211
	118	0.2143	0.3773	0.3614	0.3750	0.3941	0.3864	0.3448	0.5000
	120	0.0110	0.0000	0.0000	0.0015	0.0000	0.0045	0.0000	0.0070
	122	0.0000	0.0045	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
	124	0.0000	0.0000	0.0000	0.0029	0.0000	0.0091	0.0000	0.0282
Expected H		0.6051	0.5662	0.5584	0.5857	0.5889	0.5972	0.5770	0.5519
Observed H		0.4286	0.5455	0.4819	0.5029	0.5424	0.4909	0.4741	0.3803
N		91	110	83	344	118	110	116	71
P		0.0068	0.2953	0.5963	0.0000	0.2172	0.0000	0.0508	0.0000
Fis		0.2917	0.0366	0.1370	0.1414	0.0790	0.1640	0.1783	0.3109

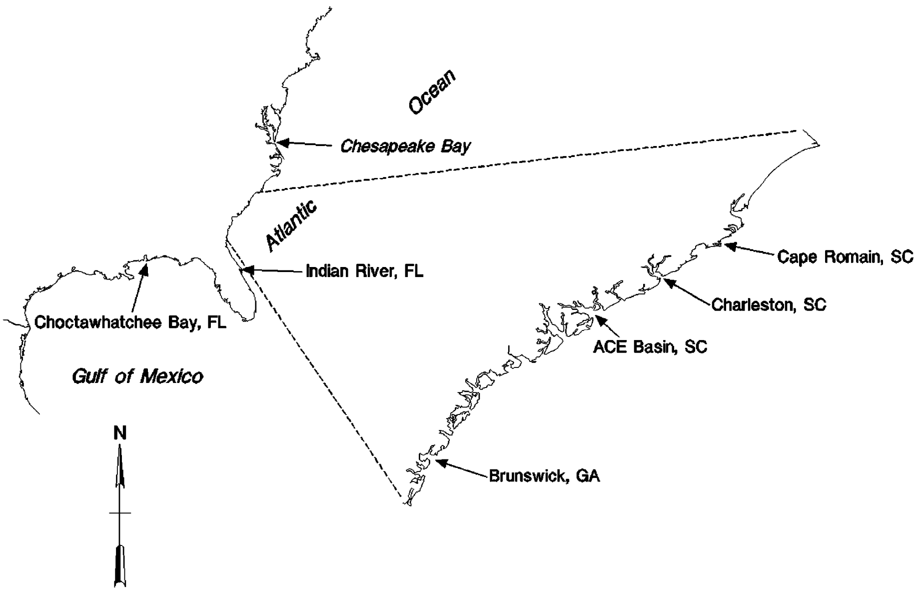

FIGURE 4.1 Map of the southeastern U. S. showing the collecting locations.

and Figure 4.1). Heart tissue from each individual (ca. 0.5 g) was placed in a 1.5-ml microfuge tube containing 1 ml of SDS/urea (1% urea, 8 M SDS, 180 mM NaPO4, and 4 mM EDTA) or SDS/NaOH (1% SDS, 200 mM NaOH) for isolation of total genomic DNA (Chapman et al., 1999a).

In 1995, seven collections of approximately 100 adult fish each were made. All four of the estuaries sampled in 1994 were resampled in this effort. Two additional collections were obtained from commercial fishers in Chesapeake Bay, Virginia, and Brunswick, Georgia. The remaining collection was made in Choctawhatchee Bay, Florida (Gulf of Mexico), by hook and line.

LABORATORY METHODS

The microfuge tubes containing the tissue samples in either SDS/urea or SDS/NaOH were incubated at 55°C for at least 24 hr to lyse the tissue. Isolation of total genomic DNA was performed, following the protocol described by Chapman et al., 1999b. Successful isolation of high-molecular-weight DNA was confirmed by running 5 μl of each sample on an 0.8% agarose gel containing ethidium bromide and a 1-Kb ladder (Gibco BRL, Inc.) used as a standard for DNA size reference. Methods for the development of microsatellite primers, the primer sequences, and PCR conditions may be found in Ball et al. (1998) and Chapman et al. (1999b). The amplified products were separated on 20 × 25 native polyacrylamide gels, stained with ethidium bromide and photographed. Estimates of molecular weights were obtained by regression using a *Hae* III digested pBS standard.

STATISTICAL ANALYSIS

Statistical analyses of the data were performed using the computer program TFPGA Version 1.3, available at http://www.public.asu.edu/~mmille8/tfpga.htm. Expected heterozygosities were computed using Levene's (1949) correction. Global estimates of F_{IS} were calculated following Weir and Cockerham (1984). Tests for conformity to Hardy-Weinberg equilibrium (Louis and Dempster, 1987; Rousset and Raymond, 1995) were conducted using the Markov chain method (Guo and Thompson, 1992). Tests for allele frequency differences between populations were conducted using Fisher's exact test described in Raymond and Rousset (1995) and Goudet et al. (1996). Pairwise comparisons of all samples at all loci were done and then combined across loci (c.f. Manly, 1985). The default conditions in TFPGA were used for the Markov chain parameters in the tests of Hardy-Weinberg equilibrium and tests for population differentiation. All results were adjusted for multiple simultaneous comparisons using a sequential Bonferroni correction (Rice, 1989).

Hierarchical *F*-statistics were calculated following Weir and Cockerham (1984). A weighted average over loci was calculated by averaging numerators and denominators separately before taking the ratio (Weir and Cockerham, 1984). The null hypotheses $F_{ST} = 0$ and $F_{IS} = 0$ were evaluated by chi-square tests (Workman and Niswander, 1970). Genetic distances were calculated using Nei (1978) and subjected to UPGMA analysis as implemented in TFPGA.

RESULTS

Amplification products for *Cne* 4–2 and *Cne* 6–11 ranged between 110 and 124 base pairs (bp) in length (Table 1). A total of five alleles was recognized at the *Cne* 4–2 locus, but a low frequency allele (117) had been combined with allele 115 for this analysis. Allele 119 represented 69.26% of the total, while the 4 remaining alleles had considerably lower frequencies (Table 4.1). Eight alleles were scored at the *Cne* 6–11. Two of these alleles, 114 and 120, were common, representing 52.97% and 35.66% of the total allele count (Table 4.1). A casual inspection of the allele frequencies at *Cne* 4–2 shows that allele 119 is much more common in populations north of Indian River Lagoon. The combined frequencies of alleles 115 and 113 decrease over this range. Allele 121 at *Cne* 4–2 and allele 116 at *Cne* 6–11 were common in the Choctawhatchee Bay sample but rare or absent from the Atlantic samples.

At the *Cne* 4–2 locus, all individual collections conformed to Hardy-Weinberg (HW) expectations except Indian River Lagoon and Choctawhatchee Bay (Table 4.1). Pooling the South Carolina collections (Charleston Harbor, Cape Romain, and the ACE Basin) did not generate a significant deviation from Hardy-Weinberg expectations. Analyses at the *Cne* 6–11 locus indicated significant deviation from Hardy-Weinberg expectations at Cape Romain, Choctawhatchee Bay, Chesapeake Bay, and the combined South Carolina data (Table 4.1).

The *F*-statistics (Table 4.2) indicate that a substantial proportion of the overall variation is within each sampling location at both loci. However, substantial variation exists between sampling locations at *Cne* 4–2 among the South Carolina locations and among Atlantic coast populations.

Pairwise comparisons of gene frequencies (Table 4. 3) showed highly significant differences between Choctawhatchee Bay, Indian River, and Chesapeake Bay and all other locations. Comparisons involving Georgia and South Carolina locations were not significant when corrected for multiple simultaneous tests. These relationships were reinforced by UPGMA analyses of Nei distances calculated over both loci (Figure 4.2). Genetic distances among the locations in South Carolina and Georgia were near zero, and this group was joined by Chesapeake Bay. The Indian River and Laguna Madre formed a separate group.

TABLE 4.2
Statistics for Hierarchical Comparisons of Spotted Seatrout Populations

Locus	Fit	Atlantic vs. Gulf	Among Atlantic	Among South Carolina	Fis
Cne 4–2	0.2510	0.0566	0.1372	0.1350	0.1341
Cne 6–11	0.1918	0.0295	0.0331	0.0315	0.1656
Both Loci	0.2192	0.0420	0.0813	0.0794	0.1519

TABLE 4.3
Results of Pairwise Comparisons for Gene Frequency Differences among Sampling Locations

	Choctawhatchee Bay	Indian River	Brunswick	ACE Basin	Charleston Harbor	Cape Romain
Indian River	0.0000					
Brunswick	0.0000	0.0004				
ACE Basin	0.0000	0.0004	0.0743 ns			
Charleston	0.0000	0.0004	0.3308 ns	0.5177 ns		
Cape Romain	0.0000	0.0002	0.0178 ns	0.5478 ns	0.1076 ns	
Chesapeake Bay	0.0000	0.0000	0.0001	0.0000	0.0001	0.0000

Note: The values are the probabilities that the populations are identical, and values denoted with ns are not significant when adjusted for multiple comparisons.

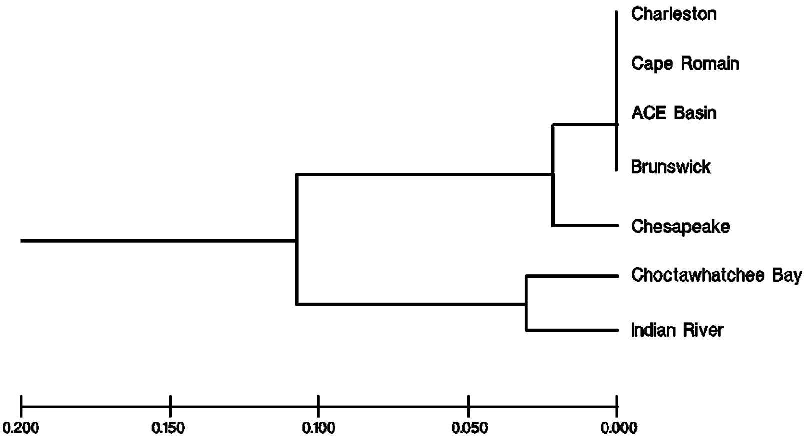

FIGURE 4.2 UPGMA phenogram of sampling locations based on Nei distances.

DISCUSSION

The significant differences found between Gulf and Atlantic populations of *C. nebulosus* are compatible with those found by Gold et al. (1999) and reminiscent of those found in other marine fishes (e.g., Avise, 1992; Gold and Richardson, 1999). It has been suggested that the divergences between Gulf and Atlantic populations are the result of climactic changes associated with glacial cycles (Avise, 1992) and therefore indicative of vicariant biogeography. The bulk of these studies is based on mtDNA data, and the present study indicates that nuclear DNA in *C. nebulosus* reflects this same history. Perhaps more provocative in this context are the significant gene frequency differences between Indian River Lagoon and the Georgia/South Carolina collections. These differences are equivalent, or nearly equivalent, to those between Choctawhatchee Bay and Indian River and were supported by the UPGMA, which clusters these locations apart from the other Atlantic samples. Similarly, fish from the Chesapeake Bay data were significantly different from all other Atlantic locations. These comparisons transcend the well known zoogeographic barriers at Cape Canaveral and Cape Hatteras (Briggs, 1974, 1995) and could reflect historical vicariant events, climactic transitions associated with these regions, and the sedentary nature of the species. This interpretation should be viewed with caution, as many more locations and more loci need to be examined. The notion is supported by the patterns of mtDNA divergence between Gulf of Mexico and Atlantic populations. In addition, the divergence between Mosquito Lagoon and Bulls Bay was nearly as great as that between Atlantic and Gulf of Mexico populations (Gold et al., 1999).

Overall, the data presented here support the conclusions of Gold et al. (1999) of extensive subdivision in *C. nebulosus* populations and are contrary to the allozyme data that suggest only weak differentiation (Ramsey and Wakeman, 1987; King and Pate, 1992). Such a disparity between allozyme data and mtDNA and anonymous nuclear markers was reported in the oyster, *Crassostrea virginica*, by Karl and Avise (1992). In this study, it was suggested that allozyme loci may be subject to balancing selection and may not be indicative of the homogenizing effects of gene flow. However, the situation in *C. nebulosus* may be somewhat different, as most of the allozyme loci exhibit limited polymorphism and suggest the operation of directional, rather than balancing, selection. While it is premature to suggest that the limited allozyme variation in *C. nebulosus* is the result of selection, the available data are consistent with this hypothesis. Gold et al. (1999) offered some additional reasons for the disparity between allozyme and mtDNA assessments of population structure in *C. nebulosus*. These included sexually asymmetric migration and the more rapid response of mtDNA to restrictions on gene exchange. Sexually asymmetric migration patterns could certainly lead to highly structured mtDNA profiles and nuclear gene homogeneity. This was not given much credence by Gold et al. (1999), and the present data support this view. The more rapid response of mtDNA to restrictions on genetic exchange would imply that, at some time in the past, the populations experienced greater levels of gene flow or recently occupied much of their current distribution. In other words, *C. nebulosus* populations have not yet reached an equilibrium between gene flow and drift due to the relatively recent isolation. Again, our data are contrary to this interpretation at least on a regional scale.

The genetic studies of *C. nebulosus* have unilaterally found some evidence of an isolation-by-distance effect (Gold et al., 1999). In the main, the difference is a matter of magnitude. The difference between the populations studied here supports an isolation-by-distance effect on a regional scale. However, the lack of a significant difference between the Georgia and Cape Romain sampling locations gives us some pause. The geographic distance between these locations is as great as the distance between Georgia and Indian River, where highly significant differences were found. Similarly, the geographic distance between Cape Romain and Chesapeake Bay is much greater than the distance between Brunswick, Georgia, and Indian River. Nonetheless, the South Carolina and Georgia populations clustered with Chesapeake Bay in the UPGMA analysis. These data would tend to suggest that geographic distance *per se* is not the sole determinant of relationships among populations.

The lack of highly polarized differences among locations within zoogegraphic provinces could be due to at least two processes. First, the observed homogeneity could be the result of contemporary gene flow among estuaries. While studies of movement patterns indicate limited dispersal between estuaries, a small amount of exchange could produce the patterns of differentiation noted here and in other studies (Ramsey and Wakeman, 1987; King and Pate, 1992; Gold et al., 1999). Alternatively, the homogeneity could be the result of recent colonization or isolation within zoogeographic provinces.

The management implications of the present data and those of Gold et al. (1999) are rather clear, at least on a regional scale. Distinct management units should be recognized according to known zoogeographic provinces in the southeastern U. S. (Briggs, 1974, 1995). Finer scale division within these regions may be warranted based on migration patterns (Music, 1981; Baker et al., 1986; Bryant et al., 1989; Baker and Matlock, 1993), but there does not appear to be a compelling genetic reason to support further division. Additional surveys of more nuclear loci and populations are needed before this conclusion can be strongly supported.

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5 Age Determination and Growth of Spotted Seatrout, *Cynoscion nebulosus* (Pisces: Sciaenidae)

Michael D. Murphy and Robert H. McMichael, Jr.

CONTENTS

ABSTRACT

Spotted seatrout exhibit differences in growth rates between sexes and among locations; however, different sampling designs, collection gears, and analytical techniques employed during growth studies have introduced different biases to the findings on spotted seatrout growth. Despite these biases, our compilation of the literature reveals that broad regional differences are apparent in spotted seatrout growth. Both sexes appear to be larger at age in the northern regions of the Gulf of Mexico and along the Atlantic coast than in the southern sections of the U.S. Gulf of Mexico. Because spotted seatrout are lifetime, estuary residents and show a high degree of plasticity in growth, their growth rates may be a good indicator of subtle changes in the biotic and abiotic conditions within individual estuaries.

INTRODUCTION

Studies on spotted seatrout growth have been conducted in many estuaries throughout the species' range. In the Gulf of Mexico, studies have been conducted in several bays in Texas (Pearson, 1929; Colura et al., 1984; Baker et al., 1986; Colura et al., 1994; Maceina et al., 1987) and Louisiana (Wakeman and Ramsey, 1985; Wieting, 1989); in coastal Mississippi (Sutter and McIllwain, 1983; Warren, 1995) and Alabama (Tatum, 1980; Wade, 1981); and in numerous estuaries in Florida (Welsh and Breder, 1923; Moody, 1950; Klima and Tabb, 1959; Moffett, 1961; Stewart, 1961; Rutherford et al., 1982; Murphy and Taylor, 1994; DeVries et al., 1997). Along the U.S. Atlantic coast, age and growth studies have been conducted in the Indian River Lagoon, Florida (Tabb, 1961; Cottrell, 1990; Murphy and Taylor, 1994); in several bays and tidal rivers in Georgia (Music and Pafford, 1984; Woodward et al., 1990) and South Carolina (Wenner et al., 1990); in Pamlico Sound, North Carolina (Brown, 1981); and in Chesapeake Bay, Virginia (Brown, 1981; Ihde, 2000).

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TABLE 5.1
Spotted Seatrout Growth Studies and Their Sampling Design and Area, Age-Determination Structure, Back-Calculation Technique, Growth Model Fit, Data Used, and Article Publication Type

Reference	Sampling design and area	Aging structure[a]	Back-calculation method[b]	Growth model fit[c]	Growth model input data[d]	Publication type
Klima and Tabb (1959)	Fishery landings/northwest Florida	S	DP	N	MBL	Final report
Moffett (1961)	Fishery landings/west Florida	S	DP	G	MBL	Final report
Stewart (1961)	Fishery landings, trawling/south Florida	S	DP	G	MBL	M.S. thesis
Tabb (1961)	Fishery landings/east-central Florida	S	DP	G	MBL	Final report
Brown (1981)	Fishery landings/Virginia and North Carolina	S	DP	VB	MBL	M.S. thesis
Rutherford et al. (1982)	Fishery landings/south Florida	SI	MDP	VB	MBL	Final report
Colura et al. (1984)	TPWD finfish sampling	SI	DP	VB	MBL	Final report
Music and Pafford (1984)	Gill nets with different-sized mesh, trammel net, trawls, cast nets, and seines/Glynn County, Georgia	SI	DP	EXP	MBL	Final report
Maceina et al. (1987)	Experimental gill nets/southeast Texas	OS	MDP	VB	MBL	Peer-review journal article
Wieting (1989)	Fishery landings and finfish survey/Louisiana	OS	R	VB	MBL	M.S. thesis
Cottrell (1990)	Hook and line, gill net, trammel net, bag seine, and fishery landings/east Florida	OS	MDP	VB	MBL	M.S. thesis
Wenner et al. (1990)	Gill net, stop net, rotenone, hook and line, trawl, cast net/South Carolina	OS	MDP	VB	MBL	Final report
Colura et al. (1994)	finfish sampling and some fishery landings/ Texas	OS	MDP	Q, VB	OL	Final report
Murphy and Taylor (1994)	Fishery landings/Florida	OS	MDP	GO, L	OL	Peer-review journal article
Warren (1995)	Gill nets with different-sized mesh/Mississipi	OS	MDP	VB	LBL	Final report
DeVries et al. (1997)	Fishery landings and finfish sampling/north-west Florida	OS	N	GO, VB, L	OL	Final report
Ihde (2000)	Fishery landings/Chesapeake Bay	OS	N	VB	OL	M.S. thesis

[a] S is scale, SI is scale impression, and OS is otolith section.

[b] DP is direct proportionality, MDP is modified direct proportionality, R is regression, and N is none.

[c] VB is von Bertalanffy, GO is Gompertz, EXP is exponential, L is linear, Q is quadratic, G is graphic, and N is none.

[d] MBL is mean of all back-calculated lengths at each age, LBL is back-calculated length at oldest age only, and OL is observed length at fractional age.

Area-specific studies have been conducted because of the perceived plasticity of spotted seatrout growth, either in response to different environmental conditions or as a result of genetic differences. The results from growth studies have been used to determine how different management regimes affect spotted seatrout yields (Condrey et al., 1985; Schirripa and Goodyear, 1994). However, a close examination of these studies reveals a large array of sampling strategies, age-determination techniques, and growth analyses that contribute to the observed differences in growth (Table 5.1). Most of these studies are also found only in gray-literature reports and theses rather than in the peer-reviewed literature, so the quality of the analyses is uncertain. This review is an attempt to compile the results of studies on the growth of larval, juvenile, and adult spotted seatrout, with notes on the various differences between studies.

SAMPLING TECHNIQUES

Several types of gear have been used to collect spotted seatrout for age and growth analyses. Using different types of gear or different sampling techniques may lead to different estimates of spotted seatrout growth because of collection biases inherent in each gear type or technique used. When a study's sampling gear and locations were predetermined, researchers often chose to use a less selective gear or a wide variety of gear with different selectivities and to deploy these gears at fixed or randomly chosen sampling sites (Table 5.1). Doing this assures that a wide size range of spotted seatrout is vulnerable to capture and that samples can be assumed to be representative of the area fished. Colura et al. (1984, 1994) used a variety of fishing gear — such as hook and line, gill nets, and trammel nets — and deployed them at randomly chosen stations in Texas bays. Warren (1995) used a variable-mesh 5- to 10-cm stretched mesh gill net to obtain spotted seatrout at fixed sampling stations in coastal Mississippi. Cottrell (1990) obtained specimens in Florida by using a variety of sampling gears, including hook and line, gill nets (5-to-12-cm mesh), seines, and trammel nets. Woodward et al. (1990) used a monofilament trammel net (inner mesh: 7 cm; outer mesh: 15, 23, and 30.5 cm) to catch spotted seatrout in coastal Georgia estuaries. Woodward et al. (1990) recognized the selectivity of their trammel net: it was most efficient at catching spotted seatrout larger than 30.5 cm in fork length (FL). In perhaps the least selective of the studies examined, Wenner et al. (1990) blocked tidal creeks in South Carolina with a 1-mm-bar-mesh net and captured spotted seatrout of all sizes after applying rotenone to the area. However, this gear was deployed in the preferred habitat for young-of-the-year (age 0) spotted seatrout.

Opportunistic sampling of the catches of recreational and commercial fisheries has also been used to obtain samples of spotted seatrout for growth studies. In this sampling strategy, gear selectivities and deployment locations were often unknown, and the fishery operated under management restrictions (e.g., size limits) that affected the sizes of fish available for sampling. Rutherford et al. (1982) sampled spotted seatrout captured by sportfishers (subject to a 12-in. [305-mm] minimum size limit) who landed fish at a boat ramp in Everglades National Park. Murphy and Taylor (1994) sampled fish collected by commercial fishers and recreational anglers in the Indian River Lagoon, Charlotte Harbor, and Apalachicola Bay, Florida. Although the researchers sampled all available undersized fish in Indian River Lagoon and Charlotte Harbor, the fishermen there were regulated by a 12-in. minimum size limit. Wieting (1989) collected spotted seatrout in Louisiana through both fishery-dependent and fishery-independent means. Tabb (1960, 1961) used sampling gear that included hook and line and commercial gill nets in the Indian River Lagoon, Florida. Klima and Tabb (1959) sampled spotted seatrout from a commercial hook-and-line and gill nets fishery in Apalachicola Bay. To study spotted seatrout growth in Alabama, Tatum (1980) and Wade (1981) sampled seatrout captured during fishing tournaments. Cottrell (1990) noted that the largest spotted seatrout he sampled in Florida were generally from recreational fish-camp catches. Ihde (2000) sampled spotted seatrout caught by commercial haul seines operating in six areas of Chesapeake Bay. Often data for growth studies have been collected by combining samples from researcher-deployed gear and samples from fishery landings (Wieting, 1989; Cottrell, 1990; DeVries et al., 1997).

The effects of different sampling strategies can be difficult to determine; however, one effect is that often only the largest members of the youngest age groups are included in the study. In general, if fish are obtained from a size-selective fishery (e.g., a fishery regulated by size limits or affected by market demand) or with size-selective gear, an analysis of growth will provide biased results (Goodyear, 1995). Ricker (1975) noted that size-selective sampling can produce what is known as "Lee's phenomenon," in which the faster growing fish are more vulnerable to capture than are the slower growing members of the same age group. The frequency with which large, old spotted seatrout are collected also depends upon the sampling gear and the number of fish sampled.

In summary, growth estimates for the youngest ages vulnerable to the sampling gear or the youngest ages legal to land are probably overestimated in most studies. Studies that employ a variety of gear and have no restrictions on the size of fish landed are probably less biased in their estimation of growth than are studies that use a single type of gear or are subject to landing restrictions.

AGE DETERMINATION AND VALIDATION

The study of fish growth requires determination of an absolute or relative age of individual fish or of a group of fish from the same cohort. The appropriate time scale for these ages is dependent on the length of the life stage studied. Larval studies often rely on the absolute age in days, which can be determined if the date of hatching or the number of growth-increments on the otoliths is known. McMichael and Peters (1989) validated the daily periodicity of growth increment formation on larval spotted seatrout sagittal otoliths by immersing larvae in a tetracycline hydrochloride solution. They determined that the maximum age of spotted seatrout larvae was about 15 days. Powell et al. (2000) determined that larval spotted seatrout first formed growth-increments in sagittal otoliths 2 to 3 days after hatching. In Naples and Fakahatchee Bays, Florida, Peebles and Tolley (1988) sampled larval spotted seatrout and determined their ages by counting the growth increments on sagittae; they found spotted seatrout larvae up to 14 days old. Fable et al. (1978) found that spotted seatrout reared in captivity hatched at 1.5-mm standard length (SL) and reached 4.5 mm in 15 days.

Ages of early juvenile spotted seatrout have been determined by examining hatchery-reared fish, whole otoliths, and otolith sections. McMichael and Peters (1989) validated the use of sections of sagittae in determining the daily ages of juvenile spotted seatrout (50 to 156 mm SL) by injecting the fish intraperitoneally with 0.1 mg tetracycline per gram of body weight and counting the growth increments. Their largest and oldest juveniles were about 200 days old. Daniel (1988) determined the ages of 8- to 50-mm-SL juvenile spotted seatrout by counting the daily growth increments on whole lapilli. The largest juvenile aged was about 80 days old. Results were mixed in Daniel's (1988) age-validation experiments in which fish were immersed in tetracycline; only 25% of the marked fish showed true daily growth-increment counts.

Annual ages of adult spotted seatrout have been determined mostly from recognizable markings on scales or on sectioned otoliths. Scales or scale impressions have been used to determine the ages of spotted seatrout in Texas (Pearson, 1929; Miles, 1950), Louisiana (Arnoldi, 1985; Wakeman and Ramsey, 1985), Florida (Moody, 1950; Klima and Tabb, 1959; Moffett, 1961; Stewart, 1961; Tabb, 1961; Rutherford al., 1982; Cottrell, 1990), Georgia (Music and Pafford, 1984; Woodward et al., 1990), South Carolina (Wenner et al., 1990), North Carolina (Brown, 1981), and Virginia (Brown, 1981; Ihde, 2000). Otolith sections have been used to determine the ages of adult spotted seatrout in Texas (Maceina et al., 1987; Colura et al., 1994), Louisiana (Wieting, 1989), Mississippi (Warren, 1995), Florida (Cottrell, 1990; Murphy and Taylor, 1994; DeVries et al., 1997), South Carolina (Daniel, 1988; Wenner et al., 1990), and Virginia (Ihde, 2000).

Although scales have often been used to determine the ages of adult spotted seatrout, marks seen on otolith sections are the most reliable indicators of age. Age determination using scales seems to be accurate for many adult fishes, but readers using scales to age older fish seem to increasingly underestimate age as the true age of the fish increases (Carlander, 1987). Wenner et al. (1990) found that the mean number of annuli on thin sections of spotted seatrout otoliths was significantly greater than the mean number counted on scale impressions from the same fish, with the number of discrepancies increasing dramatically after age 2. These results were supported by a study comparing techniques for determining ages of spotted seatrout collected from Chesapeake Bay, where scales overaged age-1 fish and underaged fish older than age 2 (Ihde, 2000). However, Cottrell (1990) found that using scales to age spotted seatrout collected from the Indian River Lagoon, Florida, often overestimated ages by one year — and occasionally by two — when compared to ages determined using otolith sections. In all studies that used both scales and otolith sections, the results support Ihde's (2000) findings that using scales to determine the ages of adult spotted seatrout is less precise than using otolith sections. Finally, the comparison of scales, otolith sections, whole otoliths, dorsal-fin spine sections, and pectoral-fin ray sections clearly showed that sectioned otoliths were the preferred structure to use in aging adult spotted seatrout in Chesapeake Bay (Ihde, 2000) and probably throughout their range.

The maximum reported ages for adult spotted seatrout in a given area generally range from 4 to 12 years for males and females (Welsh and Breder, 1923; Moody, 1950; Klima and Tabb, 1959; Moffett, 1961; Stewart, 1961; Tabb, 1961; Brown, 1981; Rutherford et al., 1982; Arnoldi, 1985; Maceina et al., 1987; Cottrell, 1990; Wenner et al., 1990; Woodward et al., 1990; Murphy and Taylor, 1994). Although females always appear to be more abundant than males at older ages, the oldest individual spotted seatrout observed in many studies is a male (Tables 5.2 and 5.3; Moffett, 1961; Maceina et al., 1987; Colura et al., 1994; Murphy and Taylor, 1994; DeVries et al., 1997). Bourgeois et al. (1996) concluded that spotted seatrout in the northern parts of their range, either within the Gulf of Mexico or along the Atlantic coast, live longer than do those in southern populations. In fact, in Chesapeake Bay, Virginia (Brown, 1981), and Galveston Bay, Texas (Maceina et al., 1987), observed maximum ages were higher than seen elsewhere — 12 years.

However, other maximum ages reported from the northern Gulf of Mexico were much lower (4 to 5 years in coastal Mississippi and Louisiana [Colura et al., 1984; Wieting, 1989; Warren, 1995]) than the maximum ages reported for spotted seatrout in the southern U.S. Gulf of Mexico (8 to 9 years [Colura et al., 1994; Murphy and Taylor, 1994]). Because the observed maximum age in a sample of fish is directly related to the number of fish examined, it may be that there is actually little real difference in the maximum age of spotted seatrout over the species' geographic range (Ihde, 2000).

The ages of spotted seatrout determined from sagittae otolith sections have been indirectly validated throughout the species' range. An annual pattern of marginal-increment width has been established for spotted seatrout: minimum widths occur once each year during spring (March to May) (Murphy and Taylor, 1994; Maceina et al., 1987; Cottrell, 1990; Wenner et al., 1990; Ihde, 2000).

Using thin sections of sagatae otoliths to age adult spotted seatrout and other members of Sciaenidae has been determined to be highly precise. Precision in fish-age determination is generally reported as the percent agreement between independent readings of aging structures. The percentage of agreement between readers or between readings is quite high for spotted seatrout aged by using thin-sectioned otoliths (99%, Maceina et al., 1987; 95%, Wenner et al., 1990; 88%, Murphy and Taylor, 1994; 100%, Ihde, 2000).

GROWTH ANALYSIS

Larval spotted seatrout growth has been studied in the laboratory and in the field. Larvae held in aquaria at 24 to 26°C grew from 1.5 mm at the time of hatching to 4.5 mm SL in 15 days (Fable et al., 1978). McMichael and Peters (1989) found that 15-day-old larvae sampled from the wild were about 7 mm SL. Peebles and Tolley (1988) found that larvae grew about 0.4 mm per day in southwest Florida estuaries, reaching about 5 mm SL in 12 days.

The analysis of length frequencies can be used to determine the average growth of fish within a modal length group if that group can be followed over time through a series of samples. This analysis has been used in the study of juvenile spotted seatrout, but it has been done with difficulty because spotted seatrout's long spawning season and recruitment period make following separate groups of fish over time difficult. Moody (1950) could not easily follow the progression of monthly length frequencies of spotted seatrout in samples collected near Cedar Key, Florida. Juvenile spotted seatrout appeared to recruit to his sampling gear in June at 32 to 74 mm SL and grew to 100 to 130 mm by November, but the continuous recruitment of juvenile fish into his sampling gear made age determination difficult. McMichael and Peters (1989) tracked modal groups of small spotted seatrout from August through November in Tampa Bay, Florida. They estimated average growth rates of 13 to 18 mm per month and noted that these fish had an average increase in size of from 15 mm SL in August to about 40 mm SL in November. Using a large 0.25-inch (0.6 cm) mesh seine in the Aransas-San Antonio Bay systems in Texas, Miles (1950) found modal standard lengths of juvenile spotted seatrout that were 31 to 35 mm in September and about 100 mm throughout the winter. Pearson (1929) found the modal total length (TL) of spotted seatrout along the central Texas coast was 130 mm by their first winter; growth was very slow during November through March, but increased in early spring. Daniel (1988) also found that little growth of spotted seatrout juveniles could be detected by using length frequencies because of continuous recruitment from July through September in South Carolina. However, the presence of fish as large as 77 mm SL in June and 130 mm SL in July suggested that early-spawned fish (April) grew quite rapidly. Colura et al. (1996) found that spotted seatrout eggs or larvae accidentally introduced into culture ponds in South Texas could potentially grow to 200 to 300 mm TL in 7 months; however, they speculated that this was not common in the wild. Hildebrand and Cable (1934) found that juveniles in North Carolina grew to 170 mm TL within 7 to 8 months of hatching. Juveniles in Lake Calcasieu, Louisiana, grew to 120 to 200 mm TL by November (Arnoldi, 1982). In general, length-frequency analyses are not suited for the study of spotted seatrout growth because of this species' long spawning season, the difficulty in sampling all sizes of juveniles without gear selectivity bias, and the natural variability in their growth.

In contrast to the difficulties described earlier, Tatum (1980) was able to determine the sizes of age 1+ to 6+ spotted seatrout from lengths of tournament-landed fish captured during 1964 to 1977 in Alabama. Wakeman and Ramsey (1985) recognized four modal groups in the overall length frequencies of spotted seatrout in Louisiana but commented on the difficulty of delineating the modal groups into annual ages.

The analysis of the growth of larval and juvenile spotted seatrout can be summarized by a model fit to the observed length-at-age data. A linear model of age on length was determined for small juvenile spotted seatrout (8 to 50 mm SL) in Charleston Harbor, South Carolina:

$$A = 1.319\,L + 16.245,\ n = 30,\ r^2 = 0.86,$$

where A is daily age and L is standard length in millimeters (Daniel, 1988). McMichael and Peters (1989) found that growth was described well for spotted seatrout in the early larval to juvenile stages (up to 50 mm SL) in Tampa Bay, Florida, by the linear model of length on age:

$$L = 0.509\,A,\ n = 50,\ r^2 = 0.96$$

or by the quadratic model of age on length:

$$A = 2.476L - 0.012\,L^2\ n = 50,\ r^2 = 0.96.$$

The daily ages of larger juveniles in Tampa Bay, Florida, were fit almost as well by the two equations:

$$L = 0.448\,A + 0.0002\,A^2,\ n = 98,\ r^2 = 0.86,\ \text{and}$$

$$A = 12.472 + 1.836\,L - 0.005\,L^2,\ n = 98,\ r^2 = 0.88.$$

Growth of adult spotted seatrout has most often been determined using the predicted sizes of fish at annulus formation, i.e., by back calculating lengths-at-age. Back calculation involves estimating the size of each fish at the time each annulus was formed. However, estimations of these sizes have been made using different methods, which would account for some of the observed differences in growth. In older studies, a direct proportionality formulation was used to estimate fish size from scale measurements (Table 5.1; Klima and Tabb, 1959; Moffett, 1961; Stewart, 1961; Iverson and Tabb, 1962; Sutter and McIllwain, 1983). More recent studies also directly relate scale or otolith section radius to body length but use a correction for a nonzero *y*-intercept (Rutherford et al., 1982; Maceina et al., 1987; Cottrell, 1990; Wenner et al., 1990; Murphy and Taylor, 1994; Ihde, 2000).

These differences may partly explain why early studies found smaller sizes at age, especially for young fish, than the most recent studies have. If direct proportionality is used when a correction factor is appropriate, then the calculated sizes at younger ages are always too small ("artificial" Lee's phenomenon; Ricker, 1975). Even if the correct back-calculation method is used, Vaughan and Burton (1994) suggested that there was less bias only if the back-calculated length for the most recently formed annulus was used in the growth analysis.

In addition to these potential sources of bias, the use of back-calculated length-at-age data has led to the development of growth models that predict smaller sizes at age than are likely to occur in nature. This may be because of the temporal offset between the time of annulus formation and the protracted spawning season (Maceina et al., 1987; Murphy and Taylor, 1994). For any individual spotted seatrout, an annulus can be formed any time up to about 7 months prior to the anniversary of its hatching; only early-spawned fish (April) would be likely to form an annulus on the anniversary of their hatching date (Maceina et al., 1987). Most specimens will be younger because they were spawned later in the spawning season. Adjusting the ages associated with these back-calculated lengths to correct for the time between the median hatching date and the period of annulus formation yields more realistic sizes at age.

Differences in growth rates between sexes have been reported for adult spotted seatrout. When differences between sexes were observed, females were generally found to grow more quickly than males (Mercer, 1984). Spotted seatrout of both sexes generally grow at the fastest rate during their first year. Fish reach about 200 to 250 mm TL by the end of their first winter, grow less than 100 mm in the second year, and then grow less than 75 mm per year thereafter.

In studies that used sagittal otolith thin sections to determine age for spotted seatrout, back-calculated sizes-at-age found in the northern regions of the Gulf of Mexico and along the Atlantic coast were generally larger than those found in southern sections of the U.S. Gulf of Mexico. Size-at-age for males was largest in Galveston Bay; coastal Mississippi; Perdido Bay, St. Joseph Bay, and Apalachicola Bay in the Gulf; and in the Chesapeake Bay on the Atlantic coast (Table 5.2). Colura et al. (1994) estimated sizes-at-age for males in Galveston Bay that were not as large as those of Maceina et al. (1987) for the same system.

Slower-growing young males were found along the peninsular Florida Gulf coast, although after age 5, males there reached sizes similar to those seen in some from northern Gulf and U.S. South Atlantic studies. Male spotted seatrout from the central and southern Texas coast generally grew more slowly than did those in other areas. The average back-calculated sizes across all studies in which otolith sections from samples of at least 50 fish were used show that male spotted seatrout were largest on the Atlantic coast, followed by males in the northern Gulf of Mexico, eastern Gulf of Mexico, and then western Gulf of Mexico (Figure 5.1).

As with males, females were larger at age in the northern areas of the Gulf of Mexico — Galveston Bay, Texas, coastal Mississippi; and Pensacola Bay, St. Joseph Bay, and Apalachicola Bay in Florida — than off southern Texas or along the peninsular Gulf coast of Florida (Table 5.3). Female spotted seatrout along the Atlantic coast reached larger sizes-at-age than did females in all other areas except the Indian River Lagoon, Florida (Cottrell, 1990). The results of Cottrell's (1990) study comparing the precision of determining fish ages by using scales and by using otolith sections were quite different from the results of others who compared these modes of aging (see above), so we have excluded his findings from further discussion of spotted seatrout growth. The

TABLE 5.2

Back-Calculated Lengths-at-Age of Male Spotted Seatrout in the Northern, Western, and Eastern U.S. Gulf of Mexico and the Southern U.S. Atlantic from Studies That Presented Sex-Specific Information

Northern Gulf of Mexico — Galveston, Texas, east to Apalachicola Bay, Florida

Study and sample size	Colura et al. (1994) N = 124	Maceina et al. (1987) N = 95	Wieting (1989) N = 446	Warren (1995) N = 123	DeVries et al. (1997) N = 96	DeVries et al. (1997) N = 235	DeVries et al. (1997) N = 163	DeVries et al. (1997) N = 493	DeVries et al. (1997) N = 292	DeVries et al. (1997) N = 157	Klima and Tabb (1959) N = 353	Murphy and Taylor (1994) N = 452
Annulus/ Area	Galveston	Galveston	Louisiana	Mississippi	Perdido	Pensacola	Chocta whatchee	St. Andrews	St. Joseph	Apalachi-cola	Apalachi-cola	Apalachi-cola
1	171	227	213	230	288	272	286	267	308	303	141	225
2	258	372	302	381	341	314	330	316	367	333	225	316
3	300	429	370	452	393	355	373	365	426	363	295	368
4	322	463	435	504	446	397	417	414	485	393	357	426
5	332	464	401		499	439	461	463	544	424	399	490
6		480			551	480		512			431	
7		491				522		561				
8		525						610				
9		570						659				
10		593										
11		610										
12		631										

Western Gulf of Mexico — Lower Laguna Madre, Texas, north to East Matagorda Bay, Texas

Study and sample size	Colura et al. (1994) N = 153	Colura et al. (1994) N = 73	Colura et al. (1994) N = 65	Colura et al. (1994) N = 33	Colura et al. (1994) N = 79	Colura et al. (1994) N = 48	Colura et al. (1994) N = 151	Colura et al. (1984) N = 151
Annulus/Area	Lower Laguna Madre	Upper Laguna Madre	Corpus Christi	Aransas	San Antonio	East Matagorda	Matagorda	Matagorda
1	201	175	168	161	163	170	204	182
2	226	271	243	231	246	243	275	250
3	245	328	290	277	304	284	314	302
4	259	361	319	309	345	308	335	344
5	268	380	338	330	375	321	347	392
6	277			344	395	328	354	431
7	282			354	409	332	357	
8	287					334		

TABLE 5.2 (continued)

Eastern Gulf of Mexico — Cedar Key, Florida, south to Everglades National Park, Florida

Study and sample size	Moffet (1961) N = 83	Murphy and Taylor (1994) N = 656	Moffett (1961) N = 258	Stewart (1961) N = 433	Rutherford et al. (1982) N = 215
Annulus/Area	Cedar Key	Charlotte Harbor	Fort Myers	Everglades National Park	Everglades National Park
1	157	237	156	156	255
2	245	305	245	250	307
3	310	345	302	315	343
4	378	384	364	367	383
5	443	417	414	407	440
6	505	480	508		470
7		500			
8		550			
9		585			

U.S. South Atlantic — Indian River Lagoon, Florida, north to Chesapeake Bay, Virginia

Study and sample size	Murphy and Taylor (1994) N = 624	Cottrell (1990) N = 28	Tabb (1961) N = 282	Music and Pafford (1984) N = 214	Wenner et al. (1990) N = 641	Brown (1981) N = 68	Ihde (2000) N = 300
Annulus/Area	Indian River	Indian River	Indian River	Georgia	South Carolina	Chesapeake Bay	Chesapeake Bay
1	238	129	145	175	256	156	229
2	331	206	200	268	339	245	381
3	386	276	259	328	398	378	476
4	434	340	322	378	438	432	536
5	471	384	380	424	464	500	573
6	518		410	449	497	500	596
7	565		437		523	552	611
8	593						

Notes: Lengths were converted from standard length to total length, if necessary, using relations presented in Murphy and Taylor (1994). When back-calculated length data were not available, the predicted length at age minus 0.5 years was used in the growth equation to estimate the back-calculated length. DeVries et al. (1997) data are in fork length, which is very similar to, though a bit shorter than, total length. Highlighted lengths were estimated using ages determined from otolith sections.

Table 5.3
Back-Calculated Lengths-at-Age of Female Spotted Seatrout in the Northern, Western, and Eastern U.S. Gulf of Mexico and the Southern U.S. Atlantic from Studies That Presented Sex-Specific Information

Northern Gulf of Mexico — Galveston Bay, Texas, east to Apalachicola Bay, Florida

Study and sample size	Colura et al. (1994) N = 86	Maceina et al. (1987) N = 286	Wieting (1989) N = 865	Warren (1995) N = 652	DeVries et al. (1997) N = 128	DeVries et al. (1997) N = 367	DeVries et al. (1997) N = 204	DeVries et al. (1997) N = 713	DeVries et al. (1997) N = 270	DeVries et al. (1997) N = 624	Klima and Tabb (1959) N = 568	Murphy and Taylor (1994) N = 754
Annulus/ Area	Galveston Bay	Galveston Bay	Louisiana	Mississippi	Perdido	Pensacola	Choctawhatchee	St. Andrew	St. Joseph	Apalachicola	Apalachicola	Apalachicola
1	193	209	220	192	272	251	261	250	281	291	144	234
2	308	421	360	389	371	378	353	332	390	359	228	376
3	375	520	469	504	453	480	435	410	479	419	304	478
4	415	588	509	605	514	551	504	480	545	470	369	564
5		612	515		558	598	558	540	590	513	434	631
6		635				626	600	590	621		492	631
7		657						630	641		508	
8		674						662	653			
9		705										

Western Gulf of Mexico — Lower Laguna Madre, Texas, north to East Matagorda Bay, Texas

Study and sample size	Colura et al. (1994) N = 283	Colura et al. (1994) N = 62	Colura et al. (1994) N = 48	Colura et al. (1994) N = 127	Colura et al. (1994) N = 64	Colura et al. (1994) N = 163	Colura et al. (1994) N = 634	Colura et al. (1984) N = 228
Annulus/Area	Lower Laguna Madre	Upper Laguna Madre	Corpus Christi	Aransas	San Antonio	East Matagorda	Matagorda	Matagorda
1	234	211	186	186	190	197	216	236
2	341	354	313	307	329	297	337	308
3	411	451	399	390	435	371	414	367
4	470	516	458	447	514	426	463	414
5	509	560	497	487	575	466	494	456
6	536			514		495	514	491
7	555						517	520
8	569							

Table 5.3 (continued)

Eastern Gulf of Mexico — Cedar Key, Florida, south to Everglades National Park, Florida

Study and sample size	Moffett (1961) N = 217	Murphy and Taylor (1994) N = 1088	Moffett (1961) N = 386	Stewart (1961) N = 562	Rutherford et al. (1982) N = 326
Annulus/Area	Cedar Key	Charlotte Harbor	Fort Myers	Everglades National Park	Everglades National Park
1	158	242	160	166	250
2	252	357	248	279	311
3	317	434	313	329	360
4	378	495	377	404	414
5	447	541	433	467	468
6		572	476	505	489
7		584	502	524	567
8		588	510		

U.S. South Atlantic — Indian River Lagoon, Florida, north to Chesapeake Bay, Virginia

Study and sample size	Murphy and Taylor (1994) N = 1142	Cottrell (1990) N = 96	Tabb (1961) N = 682	Music and Pafford (1984) N = 333	Wenner et al. (1990) N = 1401	Brown (1981) N = 92	Ihde (2000) N = 358
Annulus/Area	Indian River	Indian River	Indian River	Georgia	South Carolina	Chesapeake Bay	Chesapeake Bay
1	220	130	138	190	282	194	284
2	379	226	220	300	396	280	442
3	491	321	300	384	472	348	554
4	571	399	353	451	517	405	634
5	640	450	408	496	553	449	691
6	688	567	480	539	567	522	731
7	726		520	609	608	522	760
8	721		545	665		559	780
9						585	795
10						641	805

Notes: Lengths were converted from standard length to total lengths, if necessary, using relations presented in Murphy and Taylor (1994). When back-calculated length data were not available, the predicted length at age minus 0.5 years was used in the growth equation to estimate the back-calculated length. DeVries et al. (1997) data are in fork length, which is very similar to, though a bit shorter than, total length. Highlighted lengths were estimated using ages determined from otolith sections.

average back-calculated size across all studies in which otoliths from samples of at least 50 fish were used show that female spotted seatrout were also largest in Atlantic coast waters and smallest in the western Gulf of Mexico (Figure 5.1).

There has been little work on temporal changes in spotted seatrout growth within an area. Lassuy (1983) speculated that year-to-year differences may also be a source of the observed high degree of variation in growth seen between studies conducted in the same areas. Interestingly, Colura and Vickers (1998) examined the otoliths of spotted seatrout recovered from layers of sediment dating from 5000 to 800 years before the present. They found that growth rates of these fish appeared to be slower than the current growth rates for spotted seatrout in Texas, possibly because of selective fishing for smaller spotted seatrout. If these are valid differences, it could be argued that spotted seatrout growth may change in response to long-time scale changes in fish densities, intra- and interspecific competition, or even climate.

The reported growth of adult spotted seatrout is highly variable (Table 5.4); however, some differences may be explained by different sampling techniques and different analytical approaches to processing age and length data. When some of these variables are considered, we have shown that regional differences in average growth of spotted seatrout seem to be detectable. The apparent plasticity of spotted seatrout growth over a finer spatial scale may qualify them as a good indicator of the productivity of an estuary system. The spotted seatrout is an estuarine animal that spends its entire life in mesohaline and polyhaline habitats; its growth reflects the available energy and the associated physiological costs of living in an estuary. Lankford and Targett (1994) showed that the congener, *Cynoscion regalis*, was most abundant in salinities where optimal growth occurred. Using consistent methodology, it may be possible to utilize spotted seatrout growth increment data to monitor biotic and abiotic conditions in an estuary.

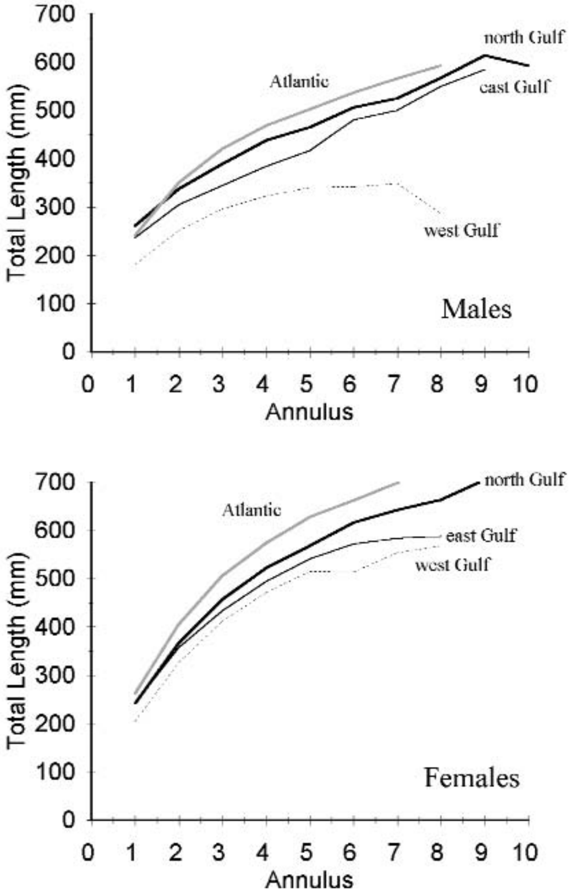

FIGURE 5.1 Total lengths of spotted seatrout at the time of annulus formation (generally formed during each spring). Shown are male and female average lengths from studies conducted in the northern Gulf of Mexico between Galveston Bay, Texas, and Apalachicola Bay, Florida (north Gulf), the lower Texas coast (west Gulf), the peninsular Gulf coast of Florida (east Gulf), and the southern U.S. Atlantic coast (Atlantic).

TABLE 5.4
Growth Models Available in the Literature and the Length Measurement Used in Each Model

Reference	Sampling Area	Length Unit	Model	
			Male	Female
Brown (1981)	Chesapeake Bay	Standard length	$l_t = 760(1\text{-}e^{-0.05(t+7.59)})$	$l_t = 854(1\text{-}e^{-0.05(t+7.93)})$
Rutherford (1982)	Everglades National Park, Florida	Standard length	$l_t = 591(1\text{-}e^{-0.12(t+2.95)})$	$l_t = 656(1\text{-}e^{-0.13(t+2.04)})$
Colura et al. (1984)	Matagorda Bay, Texas	Total length	$l_t = 487(1\text{-}e^{-0.33(t+0.08)})$	$l_t = 523(1\text{-}e^{-0.42(t+0.07)})$
Maceina et al. (1987)	Galveston Bay, Texas	Total length	$l_t = 664(1\text{-}e^{-0.18(t+1.94)})$	$l_t = 687(1\text{-}e^{-0.51(t-0.26)})$
Wieting (1989)	Louisiana	Total length	$l_t = 527(1\text{-}e^{-0.339(t+0.53)})$	$l_t = 605(1\text{-}e^{-0.465(t-0.03)})$
Cottrell (1990)	Indian River Lagoon, Florida	Standard length	$l_t = 333(1\text{-}e^{-0.54(t-0.24)})$	$l_t = 538(1\text{-}e^{-0.37(t+0.13)})$
Wenner et al. (1990)	South Carolina	Total length	$l_t = 580(1\text{-}e^{-0.27(t+1.16)})$	$l_t = 634(1\text{-}e\text{-}^{0.37(t+0.60)})$
Colura et al. (1994)	Galveston Bay, Texas	Total length	$l_t = 480(1\text{-}e^{-0.56(t+0.66)})$	$l_t = 716(1\text{-}e^{-0.25(t+1.50)})$
	East Matagorda Bay, Texas	Total length	$l_t = 571(1\text{-}e^{-0.28(t+2.34)})$	$l_t = 1054(1\text{-}e^{-0.11(t+2.64)})$
	Matagorda Bay, Texas	Total length	$l_t = 489(1\text{-}e^{-0.48(t+0.64)})$	$l_t = 713(1\text{-}e^{-0.34(t+0.56)})$
	San Antonio Bay, Texas	Total length	$l_t = 670(1\text{-}e^{-0.22(t+1.45)})$	$l_t = 1226(1\text{-}e^{-0.11(t+1.56)})$
	Corpus Christi Bay, Texas	Total length	$l_t = 507(1\text{-}e^{-0.63(t+0.13)})$	$l_t = 596(1\text{-}e^{-1.08(t-1.05)})$
	Upper Laguna Madre, Texas	Total length	$l_t = 588(1\text{-}e^{-0.43(t+0.53)})$	$l_t = 941(1\text{-}e^{-0.18(t+0.99)})$
	Lower Laguna Madre, Texas	Total length	$l_t = 543(1\text{-}e^{-0.17(t-0.44)})$	$l_t = 852(1\text{-}e^{-0.19(t+1.63)})$
Murphy and Taylor (1994)	Charlotte Harbor, Florida	Total length	$l_t = 267+33.96t$	$l_t = 698.3\exp(-\exp^{-0.363(t-0.39)})$
	Indian River Lagoon, Florida	Total length	$l_t = 287+42.52t$	$l_t = 839.2\exp(-\exp^{-0.361(t-0.74)})$
	Apalachicola Bay, Florida	Total length	$l_t = 250+51.260$	$l_t = 817.7\exp(-\exp^{-0.350(t-0.68)})$
Warren (1995)	Mississippi	Total length	$l_t = 450(1\text{-}e^{-0.53(t)})$	$l_t = 1357\exp(-\exp^{-0.15(t)})$
DeVries et al. (1997)	Perdido Bay, Florida	Fork length	$l_t = 236 + 52.6t$	$l_t = 643\exp(-\exp^{-0.45(t-0.17)})$
	Pensacola Bay, Florida	Fork length	$l_t = 231 + 41.6t$	$l_t = 669\exp(-\exp^{-0.54(t-0.46)})$
	Choctawhatchee Bay, Florida	Fork length	$l_t = 242 + 43.6t$	$l_t = 707\exp(-\exp^{-0.36(t-0.49)})$
	St. Andrews Bay, Florida	Fork length	$l_t = 219 + 48.9t$	$l_t = 767\exp(-\exp^{-0.29(t-0.89)})$
	St. Joseph Bay, Florida	Fork length	$l_t = 250 + 58.8t$	$l_t = 675\exp(-\exp^{-0.47(t-0.22)})$
	Apalachicola Bay, Florida	Fork length	$l_t = 273 + 30.2t$	$l_t = 664\exp(-\exp^{-0.29(t+0.17)})$
Ihde (2000)	Chesapeake Bay, Virginia	Total length	$l_t = 635(1\text{-}e^{-0.47(t+0.45)})$	$l_t = 831\exp(-\exp^{-0.34(t+0.73)})$

Notes: Each model is used to predict length in millimeters, l_t, from age of a fish in years, t. Additional information on sampling design, study area, age determination, and model inputs isgiven in Table 1. Only sex-specific models are shown here because female and male growth has been shown to be different.

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6 Estuary-Specific Age and Growth of Spotted Seatrout in the Northern Gulf of Mexico

Chad D. Bedee, Douglas A. DeVries, Stephen A. Bortone, and Christopher L. Palmer

CONTENTS

ABSTRACT

Age and growth of spotted seatrout collected from 1994 to 1996 were estimated from six bays along the panhandle of Florida: Perdido Bay, Pensacola Bay, Choctawhatchee Bay, St. Andrew Bay, St. Joseph Bay, and Apalachicola Bay. Age determinations were made using thin cross sections of sagittal otoliths. Annulus formation occurred during late winter to early spring; maximum observed ages for spotted seatrout were 5 to 9 for males and 5 to 8 for females. Female spotted seatrout generally grew larger and faster than males. Mean length at age 1 ranged from 296.3 to 340.8 mm FL for females and 264.7 to 310.5 mm FL for males. Mean length at age 3 ranged from 438.5 to 513.3 mm FL for females and 360.5 to 412 mm FL for males. Spotted seatrout data were fit to von Bertalanffy, Gompertz, and linear growth models. Sample sizes of older fish were small and did not fit well to nonlinear models. Differences in growth were determined by comparing slope and *y*-intercept of length-age linear regressions as well as comparing mean size-at-age. Male spotted seatrout length-age regressions were compared throughout the observed age range. Female regressions were compared through age 3.

Growth analyses showed that spotted seatrout displayed estuary-specific growth characteristics throughout the Florida Panhandle. There was no evidence of a geographic (east/west) trend in growth characteristics in the study area. Generally, spotted seatrout from St. Joseph Bay and Perdido

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Bay were larger and grew faster than those from other bays, while seatrout from Apalachicola and St. Andrew Bays generally grew slowest. The largest growth disparity was found between St. Joseph Bay and Apalachicola Bay, with discharges closer in proximity than other bays studied here.

INTRODUCTION

The euryhaline spotted seatrout, *Cynoscion nebulosus* (Cuvier), is associated with various estuarine habitats in bays, bayous, and lagoons from the Bay of Campeche, Mexico, north to Cape Cod (Tabb, 1966). Unlike most other sciaenids that reproduce offshore and utilize estuarine habitat primarily as a nursery, spotted seatrout tend to inhabit the estuary their entire lives. Moreover, individuals are generally nonmigratory, rarely traveling more than 50 km from their natal estuary (Moffet, 1961; Iversen and Tabb, 1962; Baker et al., 1986; Overstreet, 1983; Baker and Matlock, 1993).

The spotted seatrout has attracted much attention in the scientific community in recent years (Bortone et al., 1997) because it supports an important inshore recreational fishery along much of the U.S. South Atlantic and Gulf of Mexico coasts. Florida accounts for nearly 55% of all landings, with the majority of those from counties bordering the Gulf of Mexico (communication from the National Marine Fisheries Service, Fisheries Statistics and Economics Division). In 1955, commercial and recreational spotted seatrout fisheries began to decline in Florida (Tabb, 1961). Continuing with this trend, commercial harvest in Florida averaged 1.59 million kg from 1961 to 1970 and declined to 1.17 million kg from 1971 to 1980 and to 0.68 million kg during the 1980s (communication from the National Marine Fisheries Service, Fisheries Statistics and Economics Division). While catches were declining, widespread coastal development reduced habitat for spotted seatrout; in less developed areas of the state, lack of a minimum size limit allowed fish to be harvested before they reached maturity (Muller, 1997).

Regulation of spotted seatrout populations, each as a separate unit stock, was suggested in the 1960s (Moffet, 1961; Iversen and Tabb, 1962). Reports of genetically discrete populations of spotted seatrout, however, have been controversial. Some maintain that each estuary contains distinct populations of spotted seatrout (Weinstein and Yerger, 1976), while others argue that genetic isolation occurs only over long distances (Ramsey and Wakeman, 1987; King and Pate, 1992; Wiley, 1996). Gold et al. (1999) present evidence that both features are found among spotted seatrout populations. Importantly, however, regional differences in certain biological attributes of spotted seatrout, such as growth rate, age at maturity, and longevity, have repeatedly been reported (Pearson, 1929; Moody, 1950; Moffet, 1961; Tabb, 1961; Iversen and Tabb, 1962; Maceina et al., 1987; Cottrell, 1990; Murphy and Taylor, 1994).

Differences in age, growth, maturity, and mortality reported for various populations of spotted seatrout require that estuary-specific information regarding growth rates and age composition be obtained to manage the spotted seatrout fishery effectively. Our purpose here is to demonstrate the potential for separate stock recognition between proximate estuaries by providing estuary-specific information on age and growth of spotted seatrout populations in the northern Gulf of Mexico from the Panhandle region of Florida.

METHODS

Data for this study were collected from May 1994 through August 1996 in the six westernmost estuaries in Florida; from west to east, these are Perdido Bay, Pensacola Bay, Choctawhatchee Bay, St. Andrew Bay, St. Joseph Bay, and Apalachicola Bay (Figure 6.1). The sampling periods for each bay system were as follows:

Perdido Bay: May 1995 through July 1996
Pensacola Bay: May 1994 through April 1995
Choctawhatchee Bay: May 1995 through June 1996

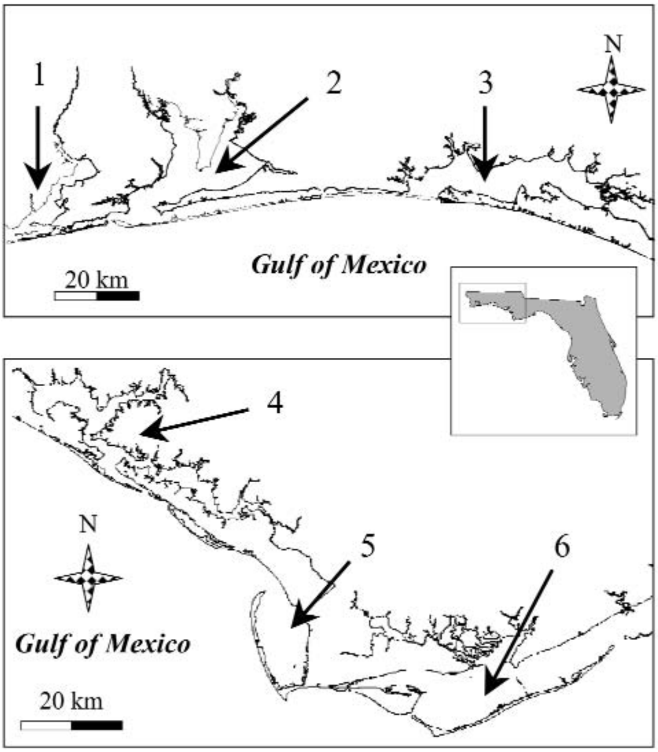

FIGURE 6.1 Study area. The top section displays the bay systems in the western half of the study area; from west to east, they are Perdido Bay (1), Pensacola Bay (2), and Choctawhatchee Bay (3). The bottom section indicates the eastern half of the study area; from west to east, the bay systems are St. Andrew Bay (4), St. Joseph Bay (5), and Apalachicola Bay (6).

St. Andrew Bay: May 1994 through November 1995
St. Joseph Bay: April 1995 through August 1996
Apalachicola Bay: April 1995 through August 1996

Spotted seatrout from Pensacola and St. Andrew bays were collected by hook and line, by a 79-mm stretch mesh gill net, and from monthly tournaments held by local hook and line clubs. A commercial fisher also provided fish harvested with a 91-mm stretch mesh gill net from Pensacola Bay. Spotted seatrout were collected from Perdido Bay and Choctawhatchee Bay using hook and line and a 79-mm stretch mesh gill net and from St. Joseph Bay and Apalachicola Bay using hook and line only. Many specimens collected from Apalachicola Bay were obtained from local fishing guides.

Upon capture, specimens were immediately put on ice. Fork length (FL) to the nearest millimeter and total body weight to the nearest gram were recorded within 24 hours of capture. Sex of small fish (< 250 mm FL) was determined via microscopic squash examination of gonadal tissue sections. Sex of all other individuals was determined macroscopically. Both otoliths (sagittae) were extracted and stored dry. Sections (approximately 0.5 mm thick) of otoliths were prepared using a Beuhler® Isomet, low-speed saw. Sections were mounted on glass slides using Baxter® S/P Pro-Texx mounting medium and later polished using 400- and then 600-grit sandpaper.

The otolith sections from Perdido, Pensacola, and Choctawhatchee specimens were read for age by Bedee three times. Readings were performed twice using a compound microscope at 40× magnification and once using the Optimas® image analysis system at 75×. Otoliths from which the age determination did not agree after the third analysis were discarded. The otolith sections from St. Andrew, St. Joseph, and Apalachicola specimens were read twice by Palmer with a compound microscope at 40×. All sections were read without knowledge of fish length, time of capture, or previous age determination. Age was determined by the number of complete annuli appearing on otolith sections. Annuli were identified as thin, opaque bands and were considered complete if distinct along the distal edge of the sacculus groove and at least faintly visible along the remainder of the distal edge (Figure 6.2).

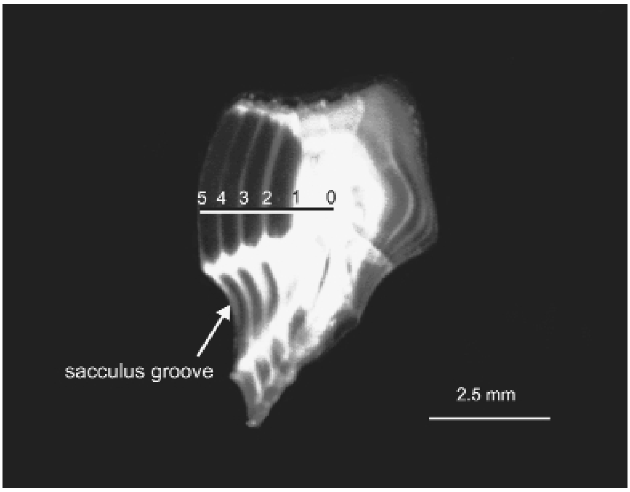

FIGURE 6.2 Sectioned view of a sagittal otolith extracted from an age 5 spotted seatrout.

Validation of annuli formation for spotted seatrout from Perdido Bay, Pensacola Bay, and Choctawhatchee Bay was accomplished indirectly by marginal increment analysis. Annulus measurements were recorded to the nearest micrometer (µm) from the center of the otolith (i.e., nucleus) to the distal edge of each annulus. The measurements were recorded consistently along a designated line from the nucleus center, distally to the lateral edge of the otolith section, and were aided using the Optimas® image analysis system. The mean marginal increment (i.e., the measured increase in otolith radius since the most recent annulus formation) for all fish was then plotted vs. month of capture. Time of annulus completion was determined by identifying the months with the lowest mean marginal increment.

Validation of annuli formation for spotted seatrout from St. Andrew, St. Joseph, and Apalachicola bays was accomplished indirectly by proportional estimates of marginal otolith growth. Marginal increment (MI) growth of each sagittal otolith section was given a value of 0.3, 0.6, and 0.9, based on whether the incremental growth since the most recent annulus was less than $^1/_3$, greater than $^1/_3$ and less than $^2/_3$, or greater than $^2/_3$ of the distance between the previous two annuli, respectively. Those values of MI were then plotted vs. month of capture. Annulus formation was determined by identifying months with lowest mean values of MI. This method was used to validate annuli because an image analysis system was unavailable.

January 1 was considered the birthdate for all fish. Fish collected after April 1 (April corresponds to the onset of spawning as well as annulus formation) but before January 1 of a given year were placed in an age class corresponding to the number of annuli. Fish collected between January 1 and April 1 were placed in an age class corresponding to the number of observed annuli plus 1, with the exception of the few fish that laid down new annuli between January 1 and April 1.

Age-class 0 fish were assigned an age value of 0.5 years when fitting data to growth models. This value was based on a conservative estimate of actual age in months of spotted seatrout hatched between May and September and harvested between October and February. More than one model (i.e., von Bertalanffy, Gompertz, and linear) have been used to describe spotted seatrout growth (Maceina et al., 1987; Cottrell, 1990; Murphy and Taylor, 1994). Spotted seatrout data from this study were fitted to each model previously used to describe spotted seatrout growth.

For the purpose of comparing growth of spotted seatrout among estuaries, we chose to define growth in two ways. The first method compared growth as an increase in length (FL) over time, using length–age linear regressions. Differences in length–age slopes were compared using students' *t*-tests of the linear regression slopes followed by *t*-tests for differences in elevation for those pairs with equal slopes (Zar, 1996). This method was used instead of comparing asymptotic growth curves because of the paucity of older fish collected, the wide asymptotic confidence intervals observed for L_∞ estimates, and an apparent lack of asymptote for male length–age relationships. Female age–length relationships were compared through age 3, while growth of male spotted seatrout was compared across the entire observed age range. The second method simply compares mean size at age (Francis, 1996). Mean lengths (FL) of spotted seatrout at ages 1, 2, and 3 were compared among estuaries using bootstrap, resampling analyses (Westfall et al., 1999). A significance level of $P \leq .05$ was used to evaluate statistical tests throughout.

RESULTS

A total of 3711 spotted seatrout were collected during the study period. Perdido Bay yielded 219 seatrout, 586 were collected from Pensacola Bay, 362 from Choctawhatchee Bay, 1204 from St. Andrew Bay, 561 from St. Joseph Bay, and 778 from Apalachicola Bay. The smallest spotted seatrout was a 171-mm FL female collected from St. Joseph Bay; the largest was a 790-mm FL female from Pensacola Bay. In general, female spotted seatrout were larger at age than males. Lengths (FL) of females had the following ranges (see Table 6.1):

202 to 624 mm (Perdido Bay)
235 to 790 mm (Pensacola Bay)
201 to 614 mm (Choctawhatchee Bay)
198 to 715 mm (St. Andrew Bay)
171 to 721 mm (St. Joseph Bay)
217 to 593 mm (Apalachicola Bay)

Lengths (FL) of male spotted seatrout (see Table 6.2):

220 to 472 mm (Perdido Bay)
203 to 543 mm (Pensacola Bay)
221 to 489 mm (Choctawhatchee Bay)
180 to 586 (St. Andrew Bay)
201 to 536 (St. Joseph Bay)
230 to 506 (Apalachicola Bay)

Agreement between the first two trials of age determination was 91% for Perdido Bay, Pensacola Bay, and Choctawhatchee Bay. Agreement in age determination from St. Andrew, St. Joseph, and Apalachicola bays was over 95%. This can be compared to other recent age-determination studies using spotted seatrout otoliths. Maceina et al. (1987) attained 99% agreement between first and second readings, and Murphy and Taylor (1994) had agreement of 88%. Disagreement in our study was attributable to a poorly prepared otolith section or, more commonly, to difficulty in distinguishing the presence of a new annulus.

Analysis of marginal increments indicated that spotted seatrout in the Florida Panhandle form a new opaque band on sagittal otoliths each year. Maximum marginal increment occurred in late fall and early winter months. Mean marginal increment was minimal for all bays in March and April, indicating that annuli form in late winter and are completed by spring (Figure 6.3). A new complete annulus was evident in 13 fish (seven from Perdido Bay, five from Pensacola Bay, and one from Choctawhatchee Bay) as early as January, and all fish showed marginal increment growth by May.

Female spotted seatrout were ages 0 to 8 and males were ages 0 to 9 Age 1 and 2 spotted seatrout dominated age composition for each bay (Figure 6.4). Generally, few spotted seatrout older than 3 years were collected from the study area. A high degree of variation in observed size at age was evident across all age classes in male and female spotted seatrout (Tables 6.1 and 6.2). Mean fork

TABLE 6.1
Mean Fork Length (FL) and Size Range of Female Spotted Seatrout Collected from Perdido, Pensacola, Choctawhatchee, St. Andrew, St. Joseph, and Apalachicola Bays

Age Class	Perdido Bay			Pensacola Bay			Choctawhatchee Bay		
	N	Mean FL	Range	N	Mean FL	Range	N	Mean FL	Range
0	1	202.0	•	•	•	•	26	254.6	201–315
1	56	324.7	242–490	96	296.3	235–426	72	311.8	209–420
2	63	413.4	324–499	135	409.0	327–526	64	390.3	277–469
3	2	500.0	376–624	73	485.5	350–605	28	468.7	289–562
4	2	512.5	511–514	47	536.9	410–740	7	555.7	502–583
5	1	605.0	•	7	601.3	545–790	4	557.5	542–565
6		•	•	1	617.0	•	1	614	•

Age Class	St. Andrew Bay			St. Joseph Bay			Apalachicola Bay		
	N	Mean FL	Range	N	Mean FL	Range	N	Mean FL	Range
0	31	253.3	198–311	73	277.4	171–334	13	278.4	231–321
1	252	297.6	189–431	125	340.8	268–460	226	325.6	217–420
2	263	377.8	286–495	46	433.9	292–511	277	391.6	325–498
3	57	447.4	357–560	6	513.3	485–541	92	438.5	380–524
4	55	514.9	376–620	9	581.2	551–610	12	501.5	381–587
5	30	578.3	504–651	8	591.9	535–660	3	561.7	541–593
6	19	624.5	553–715	1	609.0	•	•	•	•
7	3	573.3	497–633	•	•	•	•	•	•
8	1	644.0	•	1	721.0	•	•	•	•

length at age 1 ranged from 296 to 325 mm FL for females and 296 to 289 mm FL for males. By age 3, mean fork length ranged from 289 to 624 mm FL for females and 300 to 489 mm FL for males.

It was determined that, after age 1, growth of male spotted seatrout in the Panhandle region of Florida is best described as linear. Plots of raw length-at-age data for male spotted seatrout showed no apparent asymptote (Figure 6.5). Nonlinear procedures (i.e., NLIN; SAS Institute, Inc., 1988) to fit male spotted seatrout data to von Bertalanffy growth models failed to converge for Pensacola Bay, Choctawhatchee Bay, and St. Andrew Bay (Table 6.3). Male data from Pensacola Bay and Choctawhatchee Bay failed to converge in the Gompertz model (Table 6.4). In addition, asymptotic confidence intervals were extremely broad, with unrealistic upper limits for some fits.

The growth model best suited for female spotted seatrout in the Panhandle of Florida was less clear. The von Bertalanffy and Gompertz models converged for female spotted seatrout data from each bay system (Tables 6.5 and 6.6). However, sample sizes of older age classes were small. As a result, 95% confidence limits for the L_∞ parameter, an estimate of maximum size, were broad. Comparisons of nonlinear growth models or parameters were considered unreliable because the

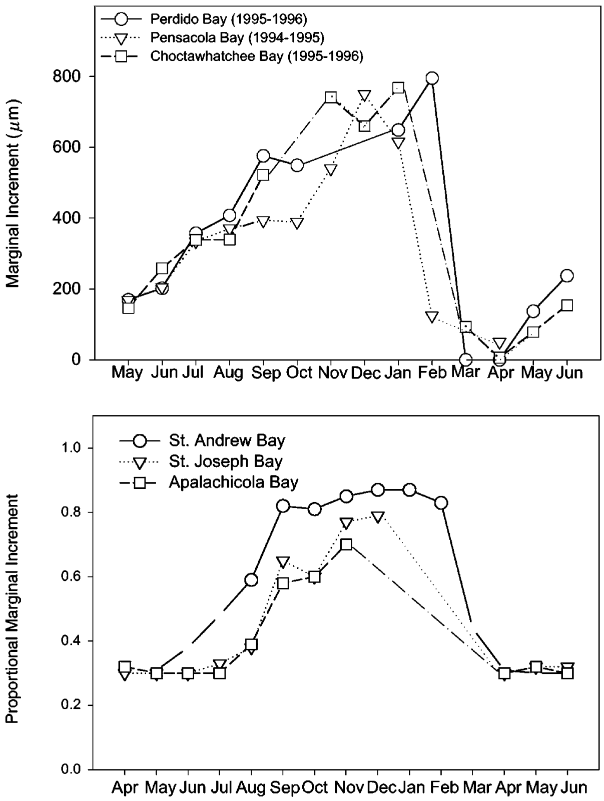

FIGURE 6.3 Marginal-increment growth of sagittal otoliths plotted by month for spotted seatrout collected from the Florida Panhandle. Note different scales of *y*-axes. Marginal increment growth of spotted seatrout otoliths from Perdido Bay, Pensacola Bay, and Choctawhatchee Bay were measured in micrometers (μm). Each sagittal otolith from spotted seatrout collected from St. Andrew Bay, St. Joseph Bay, and Apalachicola Bay was given a value of 0.3, 0.6, or 0.9, based on whether incremental growth from the most recent annulus was less than 1/3, greater than 1/3 and less than 2/3, or greater than 2/3 the distance between the previous two annuli, respectively.

model was heavily influenced by small sample sizes in the upper age range. Therefore, statistical comparisons were made on length–age linear regressions of female spotted seatrout through age 3 (Figure 6.6).

Nine of the fifteen slope comparisons among bays for female spotted seatrout length-age regressions were significantly different (Table 6.7). Male spotted seatrout from Apalachicola Bay had a significantly slower growth rate than spotted seatrout from all other bays. Male spotted seatrout from St. Joseph Bay displayed a significantly faster growth rate than spotted seatrout from all other bays except Perdido Bay. Males from St. Andrew Bay and Perdido Bay grew significantly faster than males from Pensacola Bay and Choctawhatchee Bay. The sample size of females from Perdido Bay warrants attention, however, and comparisons among Perdido Bay females and the other bay systems may not be appropriate.

Slope-elevation (*y*-intercept) comparisons of those length–age regressions with equivalent slopes showed that male spotted seatrout from St. Joseph Bay were significantly larger at age than males from Perdido Bay. Males from St. Andrew Bay were smaller at age than Perdido Bay and Choctawhatchee Bay males. There was no significant difference in length–age regressions for male spotted seatrout from Pensacola Bay and Choctawhatchee Bay.

Nine of the 15 slope comparisons were significantly different among bays for female spotted seatrout length–age regressions (Table 6.8). Female spotted seatrout from Apalachicola Bay grew significantly slower than spotted seatrout from all other bays. Females from St. Joseph Bay grew significantly faster than females from all bays except Perdido and Pensacola bays. Pensacola Bay females grew faster than females from all bays except St. Joseph Bay and Perdido Bay. Female spotted seatrout from Perdido Bay showed equivalent rates of growth with females from all other bays except Apalachicola Bay.

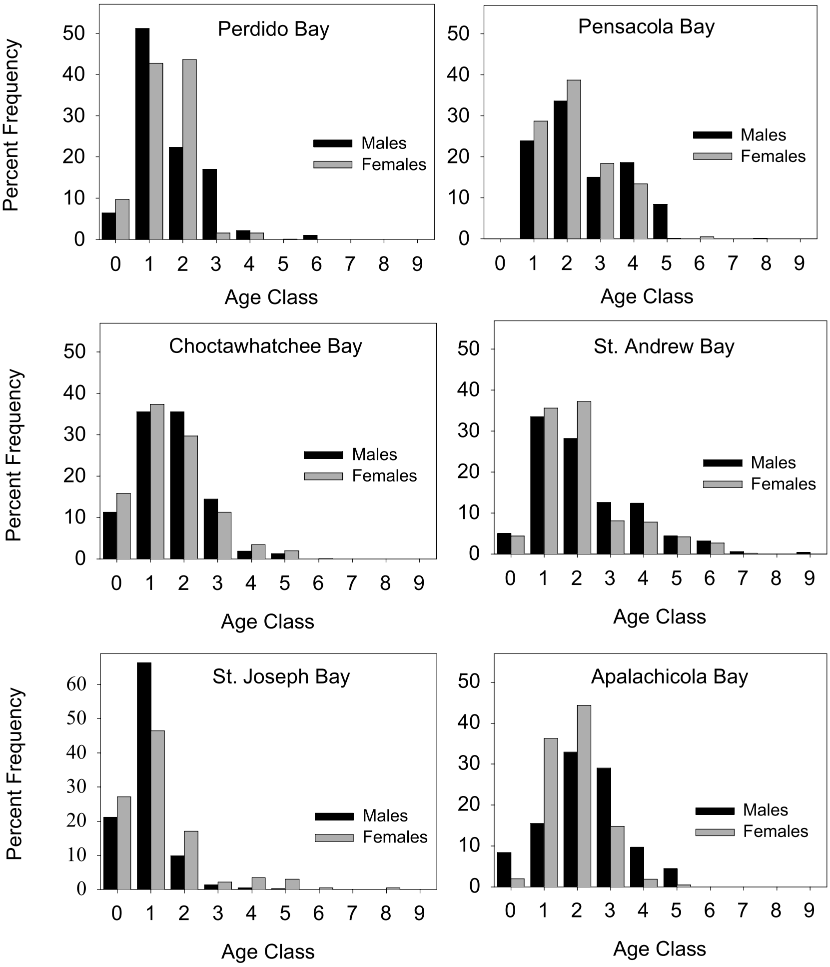

FIGURE 6.4 Age distribution of male and female spotted seatrout from Perdido Bay, Pensacola Bay, Choctawhatchee Bay, St. Andrew Bay, St. Joseph Bay, and Apalachicola Bay.

Slope elevation comparisons of those length-age regressions with equivalent slopes showed that females from Perdido Bay were larger at age than females from St. Andrew Bay, Choctawhatchee Bay, and Pensacola Bay, but smaller at age than females from St. Joseph Bay, which were also larger at age than females from Pensacola Bay. Finally, Choctawhatchee Bay females were larger at age than females from St. Andrew Bay.

Our second method of comparing growth compared mean sizes at individual age classes using bootstrap, resampling analyses. Most of the differences in mean size at age were found at ages 1 and 2 (Table 6.9). Male spotted seatrout from St. Joseph Bay were significantly larger at age 1 than males from all other bays except Apalachicola Bay. By age 2, St. Joseph Bay males were significantly larger than males from all other bays. Mean length of age 1 males from Perdido Bay was either less than or showed no significant difference from age 1 males of other bays; however, by age 2, Perdido Bay males were significantly larger than in all other bays, with the exception of St. Joseph Bay. Age 1 and age 2 males from Pensacola Bay and St. Andrew Bay showed no significant difference in length or were significantly smaller than males from all other bays.

TABLE 6.2
Mean Fork Length (FL) and Size Range of Male Spotted Seatrout Collected from Perdido, Pensacola, Choctawhatchee, St. Andrew, St. Joseph, and Apalachicola Bays

Age Class	Perdido Bay			Pensacola Bay			Choctawhatchee Bay		
	N	Mean FL	Range	N	Mean FL	Range	N	Mean FL	Range
0	•	•	•	•	•	•	10	262.6	236–308
1	37	280.9	220–382	54	272.7	202–331	55	289.3	221–376
2	36	349.0	288–461	76	316.5	237–403	62	325.9	218–402
3	18	397.1	351–441	33	345.5	301–451	28	378.3	320–489
4	2	440.5	436–445	43	394.7	311–503	3	392.0	360–436
5	1	•	•	18	447.7	386–526	2	473.0	471–475
6	1	472.0	•	2	477.0	411–543	•	•	•
7	•	•	•	1	534.0	•	•	•	•

Age Class	St. Andrew Bay			St. Joseph Bay			Apalachicola Bay		
	N	Mean FL	Range	N	Mean FL	Range	N	Mean FL	Range
0	25	250.9	180–307	62	274.7	201–332	13	265.8	230–291
1	170	264.7	197–368	194	310.5	242–407	24	310.3	237–371
2	134	314.0	239–474	29	374.4	261–437	51	338.3	305–385
3	62	376.3	300–485	4	412.0	378–445	45	360.5	315–417
4	62	394.7	312–523	1	485.0	•	15	392.3	335–436
5	22	477.1	373–615	2	516.5	497–536	7	419.4	355–506
6	15	519.0	433–578	•	•	•	•	•	•
7	2	529.0	520–538	•	•	•	•	•	•
8	•	•	•	•	•	•	•	•	•
9	1	586.0	•	•	•	•	•	•	•

St. Joseph Bay female spotted seatrout were significantly larger at ages 1 and 2 than all other females except those from Perdido Bay. Females from St. Andrew Bay were significantly smaller at age1 than females from Perdido Bay, St. Joseph Bay, and Apalachicola Bay and, by age 2, St. Andrew Bay females were significantly smaller than all females except those from Choctawhatchee Bay. Females from Choctawhatchee Bay were significantly smaller at ages 1 and 2 than females from St. Joseph Bay and significantly smaller at age 2 than Perdido Bay females.

DISCUSSION

GROWTH MODELS

The maximum observed ages of spotted seatrout reported in this study (5 to 9 for males, 5 to 8 for females) are similar to those in studies from other areas of Florida. Sample size was least in Perdido Bay and only slightly larger in Choctawhatchee Bay. For this reason, maximum age in these bays

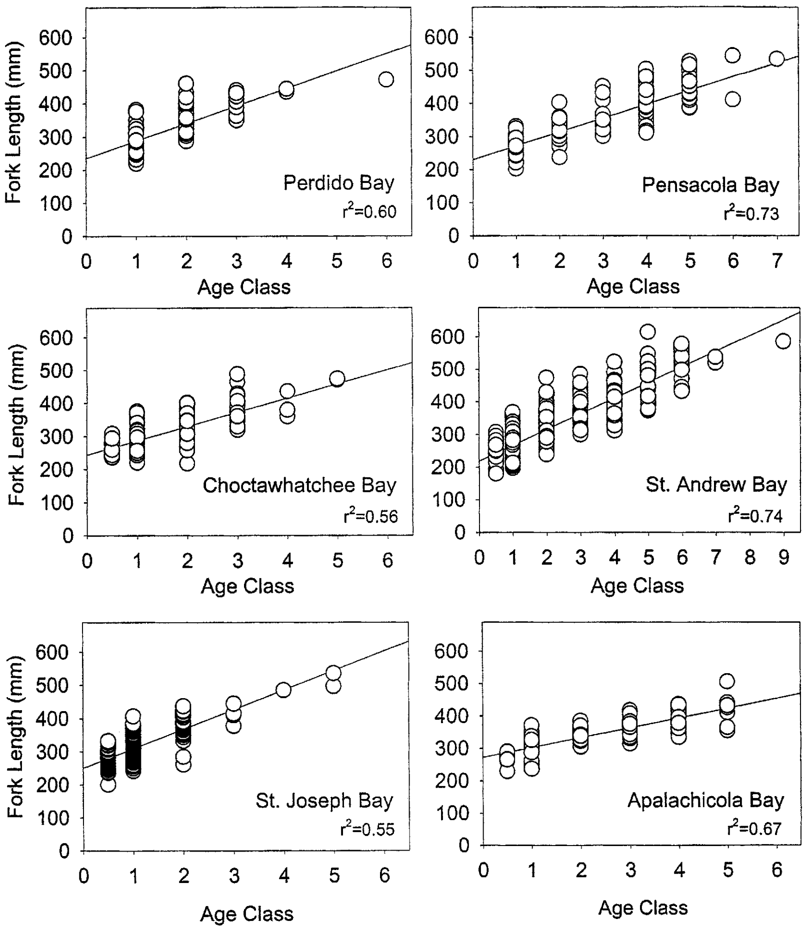

FIGURE 6.5 Plots of length-age regressions for male spotted seatrout from Perdido Bay, Pensacola Bay, Choctawhatchee Bay, St. Andrew Bay, St. Joseph Bay, and Apalachicola Bay.

may be older than reported. Apalachicola Bay is the only bay system in this study for which age and growth of spotted seatrout have previously been reported. Maximum age of 5 years for males and females from Apalachicola Bay in our study is consistent with maximum observed age of 5 and 6 years for males and females, respectively, reported by Murphy and Taylor (1994).

The linear growth after age 1 of male spotted seatrout as described by Murphy and Taylor (1994) is corroborated in this study. The Gompertz and von Bertalanffy equations were not reasonable models to estimate growth of male spotted seatrout in the Florida Panhandle. Plots of observed size at age did not suggest asymptotic growth, and procedures to fit the data to asymptotic models failed to converge in most cases.

Fishes typically do not demonstrate linear growth. Generally, growth is relatively rapid during early years, slows over succeeding years, and then becomes less apparent during senescence. The inability to fit male spotted seatrout data to asymptotic growth curves, coupled with the low number of observations of older spotted seatrout in the Florida Panhandle, suggests that attributes of growth and natural mortality of some populations may be such that asymptotic growth is difficult to detect. Another conclusion may be that, in addition to natural mortality, larger (i.e., older) fish may be selectively harvested from the population such that their numbers are too low for the population to demonstrate asymptotic growth.

TABLE 6.3

Parameter Estimates, Asymptotic Standard Error (ASE), and Upper and Lower (95%) Asymptotic Confidence Intervals (ACIs) of Male Spotted Seatrout Age–Length Data from Perdido, Pensacola, Choctawhatchee, St. Andrew, St. Joseph, and Apalachicola Bays, Fit to von Bertalanffy Growth Model

Bay System	von Bertalanffy				
	Parameter	Estimate	ASE	ACI	
				Lower	Upper
Perdido Bay	L_∞	696.89	128.47	442.62	951.22
	k	0.28	0.12	0.04	0.52
	t_o	-1.21	0.13	-0.23	0.57
Pensacola Bay	L_∞	628.93	24.32	581.13	676.79
	k	0.54	0.06	0.42	0.65
	t_o	0.46	0.06	0.35	0.58
Choctawhatchee Bay	L_∞	706.89	62.84	583.11	830.74
	k	0.35	0.06	0.24	0.47
	t_o	-1.21	0.22	0.05	0.93
St. Andrew Bay	L_∞	969.35	95.46	781.93	1156.78
	k	0.13	0.02	0.08	0.17
	t_o	-1.8	0.19	-2.17	-1.43
St. Joseph Bay	L_∞	732.29	35.55	662.29	802.29
	k	0.29	0.04	0.22	0.36
	t_o	0.13	0.13	-1.43	-0.91
Apalachicola Bay	L_∞	780.4	139.09	507.25	1053.55
	k	0.15	0.05	0.05	0.26
	t_o	-2.53	0.44	-3.40	-1.67

Several arguments given or cited by Zivkov et al. (1999) offer criticisms of asymptotic growth models. Some of their contentions regard the relationship of the L_∞ and k parameters, the dependency of L_∞ and k on the age of the population, and the fact that asymptotic growth models often overestimate the L_∞ parameter because the models are fitted mostly to young fish. While it is beyond the scope of this chapter to analyze or criticize various growth models, we felt our data were a good example of the arguments given by Zivkov et al. (1999).

The present study had very few older fish in the samples. This, coupled with the high degree of variation in size at age, resulted in broad confidence intervals as well as some unreasonable estimates of the L_∞ parameter for both male and female spotted seatrout. It is possible that growth could be more accurately described and compared in alternative contexts, including those presented by Francis (1996) and Wang and Milton (2000). Therefore, we described growth of spotted seatrout by using descriptive statistics and fitting data to standard asymptotic growth curves, but we chose to compare (and describe) spotted seatrout growth using other methods.

Our first method of comparing spotted seatrout growth uses adjusted mean squares to compare slope and elevation of length–age linear regressions (Zar, 1996). This method was used because a

TABLE 6.4
Parameter Estimates, Asymptotic Standard Error (ASE), and Upper and Lower (95%) Asymptotic Confidence Intervals (ACIs) of Male Spotted Seatrout Age–Length Data from Perdido, Pensacola, Choctawhatchee, St. Andrew, St. Joseph, and Apalachicola Bays, Fit to Gompertz Growth Model

Bay System	Gompertz				
	Parameter	Estimate	ASE	ACI	
				Lower	Upper
Perdido Bay	L_∞	696.88	128.52	442.58	951.24
	k	0.28	0.12	0.04	0.52
	t_o	-1.21	0.43	-2.06	-0.35
Pensacola Bay	L_∞	677.94	39.81	599.56	756.33
	k	0.34	0.05	0.23	0.45
	t_o	-0.68	0.17	-1.02	-0.35
Choctawhatchee Bay	L_∞	845.38	143.64	562.23	1128.361
	k	0.18	0.06	0.06	-0.29
	t_o	-1.57	0.31	-2.18	-0.96
St. Andrew Bay	L_∞	766.9	34.86	698.49	835.37
	k	0.29	0.02	0.24	0.33
	t_o	0.88	0.14	0.60	1.17
St. Joseph Bay	L_∞	674.46	21.95	631.24	717.69
	k	0.47	0.39	0.39	0.55
	t_o	0.22	0.06	0.10	0.33
Apalachicola Bay	L_∞	664.19	64.76	537.02	791.36
	k	0.29	0.05	0.18	0.40
	t_o	-0.17	0.26	-0.67	0.34

linear model was found to best describe male spotted seatrout growth. Length-age linear regressions of female spotted seatrout were compared through age 3 because so few older fish were observed. Ages 1 to 3 are of most concern because they are representative of the ages harvested from the population. It is also likely that ages 1 to 3 are a close representation of the k parameter, or rate of approach to $L_{\infty,}$ in a von Bertalanffy or Gompertz model of female spotted seatrout in the Panhandle region of Florida.

Our second method of comparing growth of spotted seatrout was simply to compare mean length at age (ages 1, 2, and 3) — one of six methods of age comparison given in Francis (1996). This method was chosen because of its simplicity and ability to complement our first method of comparison by indicating at which age a length–age regression slope might increase or decrease for a particular population.

ESTUARINE-SPECIFIC DIFFERENCES

Spotted seatrout populations in the estuaries of the Florida Panhandle were found to display differences in rate of growth as well as size at age. Interestingly, the bays with the largest growth disparity in this study are two of the closest in proximity. St. Joseph Bay was found to have the fastest growing (steepest regression slope) as well as the largest size at age in both sexes of spotted seatrout in the Florida Panhandle. Spotted seatrout in Apalachicola Bay, roughly 30 km east of St. Joseph

TABLE 6.5
Parameter Estimates, Asymptotic Standard Error (ASE), and Upper and Lower (95%) Asymptotic Confidence Intervals (ACIs) of Female Spotted Seatrout Age–Length Data from Perdido, Pensacola, Choctawhatchee, St. Andrew, St. Joseph, and Apalachicola Bays, Fit to von Bertalanffy Growth Model

Bay System	von Bertalanffy				
	Parameter	Estimate	ASE	ACI	
				Lower	Upper
Perdido Bay	L_∞	522.61	79.31	365.08	680.15
	k	0.33	0.15	0.02	0.64
	t_o	-1.33	0.61	-2.54	-0.12
Pensacola Bay	L_∞				
	k	failed to converge			
	t_o				
Choctawhatchee Bay	L_∞				
	k	failed to converge			
	t_o				
St. Andrew Bay	L_∞				
	k	failed to converge			
	t_o				
St. Joseph Bay	L_∞	748.19	190.53	373.17	1123.20
	k	0.15	0.08	0.01	0.30
	t_o	-2.46	0.55	-3.54	-1.38
Apalachicola Bay	L_∞	510.57	77.06	358.34	662.82
	k	0.19	0.09	0.01	0.36
	t_o	-3.74	1.11	-5.94	-1.54

Bay, were the slowest growing and attained the smallest size at age in most cases. Both sexes of spotted seatrout in Apalachicola Bay grew as large as or larger than seatrout from other bays by age 1. Growth slowed after age 1 so that rate of growth (over the entire age range for males and through age 3 for females) was significantly slower than in other bays in Florida.

Growth disparities among neighboring estuaries were found across the entire study area. Both sexes of spotted seatrout from Perdido Bay grew faster or were larger at age than those from neighboring Pensacola Bay. Spotted seatrout from St. Andrew Bay displayed different growth patterns than those from Choctawhatchee Bay and St. Joseph Bay. Only male spotted seatrout from Choctawhatchee Bay and Pensacola Bay showed no difference in growth rate, and very few differences were found in size at age for either sex between those bay systems.

HYPOTHESES FOR POSSIBLE CAUSATIVE FACTORS FOR DIFFERENCES IN GROWTH

Gene Exchange

Several researchers have reported varying degrees of genetic isolation among spotted seatrout populations and early genetic work provides an argument for individual "subpopulations." Weinstein and Yerger (1976) tested blood serum and eye lens proteins and determined that each estuary from

TABLE 6.6

Parameter Estimates, Asymptotic Standard Error (ASE), and Upper and Lower (95%) Asymptotic Confidence Intervals (ACIs) of Female Spotted Seatrout Age–Length Data from Perdido, Pensacola, Choctawhatchee, St. Andrew, St. Joseph, and Apalachicola Bays, Fit to Gompertz Growth Model

Bay System	Gompertz				
	Parameter	Estimate	ASE	ACI	
				Lower	Upper
Perdido Bay	L_∞	500.31	57.21	386.67	613.95
	k	0.46	0.15	0.16	0.77
	t_o	-0.18	0.17	-0.52	0.16
Pensacola Bay	L_∞				
	k	failed to converge			
	t_o				
Choctawhatchee Bay	L_∞				
	k	failed to converge			
	t_o				
St. Andrew Bay	L_∞	959.30	178.88	607.82	1310.77
	k	0.14	0.03	0.08	0.19
	t_o	2.85	1.41	0.07	5.63
St. Joseph Bay	L_∞	625.40	83.37	461.31	789.48
	k	0.31	0.08	0.16	0.46
	t_o	-0.14	0.35	-0.84	0.55
Apalachicola Bay	L_∞	486.48	54.73	378.35	594.61
	k	0.26	0.08	0.09	0.43
	t_o	-1.76	0.24	-2.23	-1.29

Florida to Texas contained a discrete population (subpopulation) of spotted seatrout. They noted that the most clearly established case of divergence occurred between populations west of the Mississippi and those on the east coast of Florida.

More recent genetic studies did not find conclusive evidence of isolated populations. Ramsey and Wakeman (1987) investigated enzymes and structural proteins of spotted seatrout from 15 bay systems in the Gulf of Mexico and Atlantic coast of Florida. The results of their study indicated that the population structure of spotted seatrout is best described by an "isolation-by-distance" population model. Similar levels of genetic variability, gene flow, and differentiation in spotted seatrout are reported from Texas and northern Mexico by King and Pate (1992): positive short-distance and negative long-distance correlation of allele frequencies are reported, along with a geographic cline in average individual heterozygosity with degree north latitude and west longitude. In addition, Wiley (1996) examined two polymorphic loci in spotted seatrout from Florida, Virginia, South Carolina, and Georgia and found no evidence of multiple populations in Georgia and South Carolina, although those populations deviated significantly from Florida and Virginia spotted seatrout.

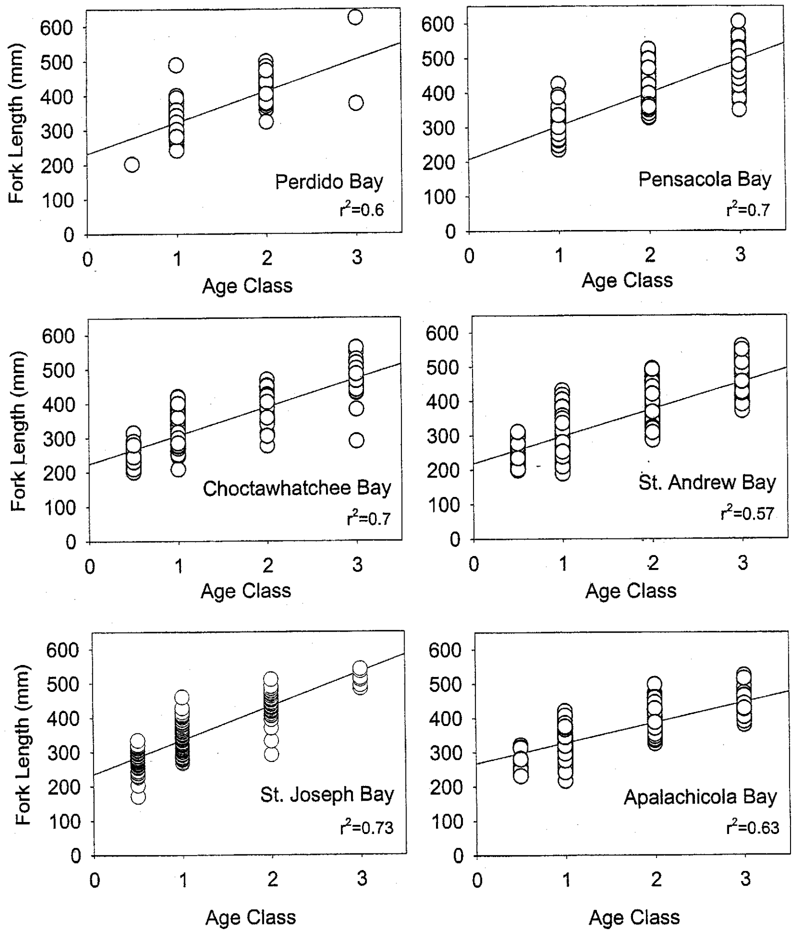

FIGURE 6.6 Plots of length-age regressions (through age 3) for female spotted seatrout from Perdido Bay, Pensacola Bay, Choctawhatchee Bay, St. Andrew Bay, St. Joseph Bay, and Apalachicola Bay.

Sustaining distinct fishery stocks requires a high degree of isolation between populations (Allendorf and Phelps, 1981; King and Pate, 1992). Apparently there is enough gene flow within the spotted seatrout distribution that differentiation into separate genetic stocks has been minor (Ramsey and Wakeman, 1987; King and Pate, 1992; Murphy and Taylor, 1994). Spotted seatrout have been known to make occasional long-distance migrations; a spotted seatrout tagged in Apalachicola, Florida, was recaptured near Grand Isle, Louisiana, more than 500 km (315 miles) from its release site (Moffet, 1961). Seventeen others were recaptured more than 100 km (60 miles) from their release sites (Moffet, 1961). While this behavior is uncommon, the high fecundity of spotted seatrout (Brown-Peterson et al., 1988), coupled with the low degree of genetic variability, allows for the maintenance of homogeneity, which deviates only with long distance separation (Ramsey and Wakeman, 1987; Murphy and Taylor, 1994).

The extensive area of suitable habitat between bay systems facilitates the possibility of movements and gene exchange of spotted seatrout in the Florida Panhandle. All these systems are relatively close together, and all six communicate by way of the Intracoastal Waterway. The portions of this waterway connecting Pensacola Bay communicate with Perdido Bay to the west via Big Lagoon and with Choctawhatchee Bay to the east via Santa Rosa Sound. Big Lagoon and Santa Rosa Sound are natural water bodies and have extensive areas of seagrass meadows.

TABLE 6.7

Results of Student's t-Test of Length–Age Regression Comparisons for Male Spotted Seatrout in the Panhandle Region of Florida

Comparison	Males					
	Slope			Elevation		
	DF	t_value	p_value	DF	t_value	p_value
PDO vs. PNS	318	2.51	$p < 0.01$	•	•	•
PDO vs. CHC	251	1.83	$p < 0.05$	•	•	•
PDO vs. SAB	584	0.92	$p > 0.10$	585	5.5	$p < 0.0005$
PDO vs. SJB	383	1.24	$p > 0.10$	384	5.3	$p < 0.0005$
PDO vs. APB	246	5.33	$p < 0.0005$	•	•	•
PNS vs. CHC	383	0.41	$p > 0.25$	384	1.17	$p > 0.10$
PNS vs. SAB	716	2.81	$p < 0.005$	•	•	•
PNS vs. SJB	515	4.78	$p < 0.0005$	•	•	•
PNS vs. APB	378	4.33	$p < 0.0005$	•	•	•
CHC vs. SAB	649	1.37	$p > 0.05$	650	4.27	$p < 0.0005$
CHC vs. SJB	448	3.66	$p < 0.0005$	•	•	•
CHC vs. APB	311	3.73	$p < 0.0005$	•	•	•
SAB vs. SJB	781	2.68	$p < 0.005$	•	•	•
SAB vs. APB	644	6.06	$p < 0.0005$	•	•	•
SJB vs. APB	443	7.98	$p < 0.0005$	•	•	•

Bay System	Length–Age Regression Equation
Perdido Bay (PDO)	FL = 235.67 + 52.57 (AGE)
Pensacola Bay (PNS)	FL = 230.58 + 41.57 (AGE)
Choctawhatchee Bay (CHC)	FL = 243.71 + 42.97 (AGE)
St. Andrew Bay (SAB)	FL = 218.68 + 48.10 (AGE)
St. Joseph Bay (SJB)	FL = 250.40 + 58.08 (AGE)
Apalachicola Bay (APB)	FL = 272.32 + 30.23 (AGE)

The Intracoastal Waterway connecting Choctawhatchee, St. Andrew, St. Joseph, and Apalachicola bays is a series of natural rivers and manmade canals. The habitat suitability between these systems is not as good as that in the western portion of the Intracoastal Waterway. However, movement between these systems remains possible, especially during winter when spotted seatrout move into rivers to avoid rapid temperature changes.

Gene exchange of spotted seatrout in the Florida Panhandle may also occur through larval transport between systems. Each bay contains deep, strong flowing channels running between barrier islands in which spotted seatrout frequently spawn (Saucier and Baltz, 1993). The close proximity of each bay system and the frequency of natural and manmade passes between them may allow currents to carry various stages of developing eggs and larvae into a new system.

TABLE 6.8
Results of Student's t-Test of Length–Age Regression Comparisons for Female Spotted Seatrout in the Panhandle Region of Florida

Comparison	Females					
	Slope			Elevation		
	DF	t_value	p_value	DF	t_value	p_value
PDO vs. PNS	422	0.54	$p > 0.10$	423	3.22	$p < 0.001$
PDO vs. CHC	308	1.09	$p > 0.10$	309	3.95	$p < 0.0005$
PDO vs. SAB	721	1.50	$p > 0.05$	722	6.85	$p < 0.0005$
PDO vs. SJB	368	1.14	$p > 0.10$	369	2.85	$p < 0.0025$
PDO vs. APB	726	5.28	$p < 0.0005$	•	•	•
PNS vs. CHC	490	2.42	$p < 0.01$	•	•	•
PNS vs. SAB	903	3.69	$p < 0.000$	•	•	•
PNS vs. SJB	550	0.69	$p > 0.25$	551	7.07	$p < 0.0005$
PNS vs. APB	908	9.89	$p < 0.0005$	•	•	•
CHC vs. SAB	789	0.47	$p > 0.25$	790	3.01	$p < 0.0025$
CHC vs. SJB	436	3.06	$p < 0.001$	•	•	•
CHC vs. APB	794	6.03	$p < 0.0005$	•	•	•
SAB vs. SJB	849	3.80	$p < 0.0005$	•	•	•
SAB vs. APB	1207	5.90	$p < 0.0005$	•	•	•
SJB vs. APB	854	9.75	$p < 0.0005$	•	•	•

Bay System	Length–Age Regression Equation
Perdido Bay (PDO)	FL = 231.42 + 91.29 (AGE)
Pensacola Bay (PNS)	FL = 207.58 + 95.72 (AGE)
Choctawhatchee Bay (CHC)	FL = 224.56 + 82.52 (AGE)
St. Andrew Bay (SAB)	FL = 218.65 + 79.09 (AGE)
St. Joseph Bay (SJB)	FL = 235.41 + 99.59 (AGE)
Apalachicola Bay (APB)	FL = 267.60 + 59.60 (AGE)

Fishing Pressure and Habitat

Murphy and Taylor (1994) concluded that differences in growth rate among Charlotte Harbor, Apalachicola, and Indian River spotted seatrout were independent responses to local fishing pressures, which probably affect growth of spotted seatrout in the Florida Panhandle, as well. In addition, habitat differences may interact with local fishing pressure. Some bays in our study, such as Perdido Bay and Apalachicola Bay, are very turbid. Locating suitable fishing areas without intimate local knowledge of these bays is difficult. Collection of spotted seatrout by our staff was hindered in those systems for this reason.

Other bays, such as St. Joseph and portions of Choctawhatchee and St. Andrew, are clear with extensive areas of seagrass meadows that facilitate location of suitable habitat by fishers. The interaction of habitat differences and types of fishing pressure may cause the effects of pressure to vary.

TABLE 6.9
P-Values for Mean Length-at-Age Bootstrapped Analyses, Mean, and Standard Deviations by Age Class of Male and Female Spotted Seatrout

Comparison	Males Age Class 1	Males Age Class 2	Males Age Class 3	Females Age Class 1	Females Age Class 2	Females Age Class 3
PDO vs. PNS	0.8667	0.0001	0.0001	0.0013	0.9717	0.9969
PDO vs. CHC	0.8554	0.0179	0.4146	0.5412	0.0090	0.9149
PDO vs. SAB	0.9940	0.0001	0.1848	0.0003	0.0001	0.5957
PDO vs. SJB	0.0001	0.0385	0.9618	0.1811	0.0643	0.9998
PDO vs. APB	0.0149	0.7058	0.0026	1.0000	0.0009	0.3535
PNS vs. CHC	0.1180	0.6000	0.0033	0.1844	0.1620	0.4944
PNS vs. SAB	0.6569	0.9962	0.0007	0.9998	0.0001	0.0007
PNS vs. SJB	0.0001	0.0001	0.0038	0.0001	0.0027	0.6461
PNS vs. APB	0.0003	0.0066	0.3578	0.0001	0.0002	0.0001
CHC vs. SAB	0.0002	0.2193	0.9998	0.1257	0.2605	0.4448
CHC vs. SJB	0.0010	0.0001	0.3997	0.0001	0.0001	0.2071
CHC vs. APB	0.1216	0.3922	0.2294	0.1656	0.9997	0.0243
SAB vs. SJB	0.0001	0.0001	0.2970	0.0001	0.0001	0.0172
SAB vs. APB	0.0001	0.0003	0.1512	0.0001	0.0023	0.5892
SJB vs. APB	1.0000	0.0002	0.0430	0.0197	0.0001	0.0002

Bay System	Males Age Class 1 Mean Std Dev	Males Age Class 2 Mean Std Dev	Males Age Class 3 Mean Std Dev	Females Age Class 1 Mean Std Dev	Females Age Class 2 Mean Std Dev	Females Age Class 3 Mean Std Dev
Perdido Bay (PDO)	280.92 39.74	348.97 42.20	397.11 28.97	324.71 42.37	413.40 32.43	500.00 175.36
Pensacola Bay (PNS)	272.72 24.51	316.51 23.97	345.48 31.93	296.30 33.61	408.98 51.11	485.53 50.75
Choctawhatchee Bay (CHC)	289.27 35.16	325.87 33.50	378.29 40.51	311.84 48.22	390.28 39.02	468.71 53.87
St. Andrew Bay (SAB)	264.73 38.64	313.99 41.90	376.32 40.15	297.60 52.77	378.84 40.18	450.35 51.45
St. Joseph Bay (SJB)	310.49 32.13	374.38 37.90	412.00 27.43	340.81 37.62	433.87 38.28	513.33 22.02
Apalachicola Bay (APB)	310.29 32.50	338.29 14.69	360.49 19.84	325.63 35.68	391.59 30.73	438.51 28.39

Systems such as Apalachicola Bay, a turbid system with a high concentration of fishing guides and low (human) population density, may show different impacts from pressure than systems such as St. Joseph Bay, where water clarity and habitat characteristics make it easier for less knowledgeable fishers to catch fish effectively, or Pensacola or St. Andrew Bay, which are more urban and have larger numbers of fishers living in the area.

Subtle differences in habitat types among the bay systems may also cause differences in growth rate by indirectly affecting interspecific and intraspecific food partitioning. In other words, community assemblages associated with each habitat type may differ and, as a result, interference competition from other species or size classes may influence growth rates of spotted seatrout. Lack of competition resulting from lower population densities in some bay systems may also influence growth rates.

INTERANNUAL VARIABILITY

Fish collections in this study were not all made in the same year. As a result, differences in spotted seatrout growth among bay systems may be attributable to annual variability. Environmental variables such as rainfall and river flows may affect larval growth and mortality, and variation in annual temperatures may affect the length of the growing season. Optimum salinity and temperatures have been reported for the survivability of larval spotted seatrout. Taniguchi (1981) and Banks et al. (1991) reported that age-linked changes in salinity tolerances occur in the larval stage. If larval fish are stressed by suboptimal temperature or salinity, slower growth may result and be reflected in smaller size at later age.

CONCLUSIONS

Variation in growth between estuarine systems as reported in this study is characteristic of spotted seatrout populations (Moody, 1950; Moffet, 1961; Iversen and Tabb, 1962; Murphy and Taylor, 1994). Many factors may explain differences in growth of spotted seatrout among bay systems, including but not limited to genetic isolation of populations, differences in habitat or water quality during one or more life history stages, and differences in fishing pressure. The causes for differences in growth may have significant relevance to measures of environmental differences between regions. Moreover, the actual differences in growth of spotted seatrout between bay systems should be pertinent to management applications. Immediately relevant to fisheries management is the integration of estuary-specific growth information, spawning potential ratios, and genetic characteristics with landings data.

Florida addressed this issue in 1995 when it implemented a regional management plan for the spotted seatrout fishery — an important step in spotted seatrout management. Since the implementation of the regional plan, regulations of the spotted seatrout fishery have been adjusted at least twice based on estuary-specific information. Much work is still needed, however; user-group conflicts exist among regions, with some claiming that there are no data from their region. Other problems with spotted seatrout management are the high cost of obtaining meaningful data, the time lag between data collection and stock assessment, and the need for better communication among user groups and managers.

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7 The Demographics and Reproductive Biology of Spotted Seatrout, *Cynoscion nebulosus,* in Six Northwest Florida Estuaries

Douglas A. DeVries, Chad D. Bedee, Christopher L. Palmer, and Stephen A. Bortone

CONTENTS

ABSTRACT

Spotted seatrout were collected from the six westernmost estuarine systems in northwest Florida — Perdido, Pensacola, Choctawhatchee, St. Andrew, St. Joseph, and Apalachicola bays — to determine if and how life history parameters and demographics differed among them. Most specimens were collected by hook and line, with gill nets providing the remainder. Length-frequency data on the recreational fishery were obtained from volunteer anglers and hook-and-line sampling was done by study personnel. Gonadosomatic indices (GSIs) were highest during late April to July; the spawning season varied slightly among the estuaries. Macroscopic maturity stage data indicated that spawning peaked during May and June. Size of females at 50% maturity was 230 mm FL, equating to an age of 1. Males appeared to mature at similar or even smaller sizes. Size distributions from the

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hook-and-line fishery were similar among estuaries. Recruitment occurred at 250 mm FL; modes were 275 to 375 mm FL; and virtually none were > 650 mm FL. St. Joseph and St. Andrew bays had the most truncated distributions. Fish ages 1 and 2 constituted 69 to 89% of the recreational fishery, with few over age 3. Age distributions varied considerably among bays and between years, seasons, and sexes within bays. Estimates of instantaneous total mortality rate (Z) were variable (0.49 to 2.05) and were highest in Perdido Bay and lowest in St. Andrew and Pensacola bays.

INTRODUCTION

Spotted seatrout, speckled trout, or specks (*Cynoscion nebulosus*) have long attracted the attention and interest of the commercial and recreational fishing sectors in Florida. They represent one of the most preferred recreational fish in the state, with many clubs dedicated to their pursuit. Spotted seatrout are often captured in larger numbers by the recreational sector than by the commercial (Mercer, 1984). Since the early 1970s, total Gulf landings have declined significantly, a trend attributed to habitat loss, winter cold kills, and overfishing (Mercer, 1984). Landings in the Florida Panhandle (Escambia to Franklin County) ranged from 69 to171 t (metric tons) during 1981 through 1989 and then dropped to 52 t in 1990 and 29 t in 1991 (Florida Department of Environmental Protection). These large drops can probably be attributed, in part, to the initiation of harvest limits by the Florida Marine Fisheries Commission (MFC) in late 1989, as well as to the previously mentioned causes. In July 1995, a constitutional amendment banning all entangling nets in Florida waters went into effect, virtually eliminating the commercial fisheries for the species.

The spotted seatrout is one of the few economically important species in Florida that is estuarine dependent throughout its life (Tabb, 1966). Several researchers have shown that the species is primarily nonmigratory; adults remain within the same estuary in which they were spawned, although they do show seasonal movements within the estuaries and to nearshore coastal waters (Guest and Gunter, 1958; Moffett, 1961; Iverson and Tabb, 1962; Tabb, 1966; Overstreet, 1983; Music and Pafford, 1984; Baker et al., 1986).

Findings of limited movements, differential growth among estuaries, and some genetic differences prompted some authors to suggest that estuaries may contain distinct subpopulations (Iverson and Tabb, 1962; Weinstein and Yerger, 1976; Baker et al., 1986); however, some electrophoretic studies have found no evidence to support that hypothesis (Paschall, 1986; Ramsey and Wakeman, 1987; King and Pate, 1992). Very recently, examination of restriction site variation in mtDNA yielded further evidence that spotted seatrout are spatially subdivided into discrete subpopulations or stocks (Gold et al., 1999).

Although the genetic evidence is conflicting, because of the well-documented nonmigratory nature of spotted seatrout, each estuary's population is subjected to different exploitation rates and environmental factors, which almost certainly impact demographics, reproduction, and recruitment. Sound management of this very important species requires current data on these parameters from as many estuaries as possible. To date, there is no published information on the life history parameters of spotted seatrout, and little or no detailed information on characteristics of the recreational fishery, from any of the five northwest Florida estuaries west of Apalachicola Bay. The species was studied in Apalachicola Bay from 1986 to 1988 (Murphy and Taylor, 1994) and from 1957 to 1958 (Klima and Tabb, 1959).

The overall goal of this study was to collect the life history and demographic information necessary to manage spotted seatrout in Northwest Florida rationally. Specific objectives were to develop estuary-specific information on age and growth, mortality rates, spawning seasonality, age and size at maturity, and age and size composition of the recreational fishery for Apalachicola, St. Joseph, St. Andrew, Choctawhatchee, Pensacola, and Perdido Bay systems, as well as to test the hypothesis that these life history parameters and demographics differed among each of these estuaries. Our findings on all but age and growth, which are presented in Chapter 6, are presented here.

METHODS AND MATERIALS

The study was conducted from May 1994 through August 1996 in the six westernmost estuaries in northwest Florida; from west to east, these are Perdido, Pensacola, Choctawhatchee, St. Andrew, St. Joseph, and Apalachicola bays (Figure 7.1). Perdido Bay was sampled from May 1995 to July 1996; Pensacola Bay from May 1994 to April 1995; Choctawhatchee Bay from May 1995 to June 1996; St. Andrew Bay from May 1994 to November 1995; St. Joseph Bay from April 1995 to August 1996; and Apalachicola Bay from April 1995 to August 1996.

Spotted seatrout were collected from St. Andrew and Pensacola bays using hook and line and gill nets (79-mm stretch mesh), although after June 1994, only the former gear was used in St. Andrew Bay. Biological data were also obtained from commercially harvested fish (91-mm stretch mesh) in Pensacola Bay and from fish entered in monthly fishing tournaments in St. Andrew Bay. These tournaments provided most of our larger, older specimens. Fish were collected using hook and line from St. Joseph and Apalachicola bays and hook and line and experimental gill nets from Choctawhatchee and Perdido bays. Many specimens from Apalachicola Bay were also obtained from a fishing camp, Bay City Lodge, where a number of guides specialize in fishing for spotted seatrout much of the year.

Upon capture, specimens were immediately put on ice. At the laboratory, and within 24 h of capture, the fish were measured to the nearest millimeter for fork length (FL), total length, and standard length, they were weighed to the nearest gram, their sexes were noted (except in very immature specimens), and their gonads were removed and weighed to the nearest 0.1 g. Maturity stage of gonads was determined visually, using criteria from Overstreet (1983) and Brown-Peterson et al. (1988). A squash preparation from the ovary of every fifth female processed was examined with a dissecting microscope at 6 to 50× as a quality control check for the visual staging. Gonadosomatic index (GSI) was calculated as gonad weight/total weight × 100. Otolith processing and aging methods are given in Chapter 6.

The official birth date for all fish was January 1. Fish collected after April 1 (April corresponds to the onset of spawning and annulus formation) but before January 1 of the next year were placed in an age class corresponding to the number of observed annuli. Fish caught between January 1 and April 1 were placed in an age class corresponding to the number of observed annuli plus one, with the exception of the few fish that laid a new annulus during that period; these were placed in an age class corresponding to the observed number of annuli.

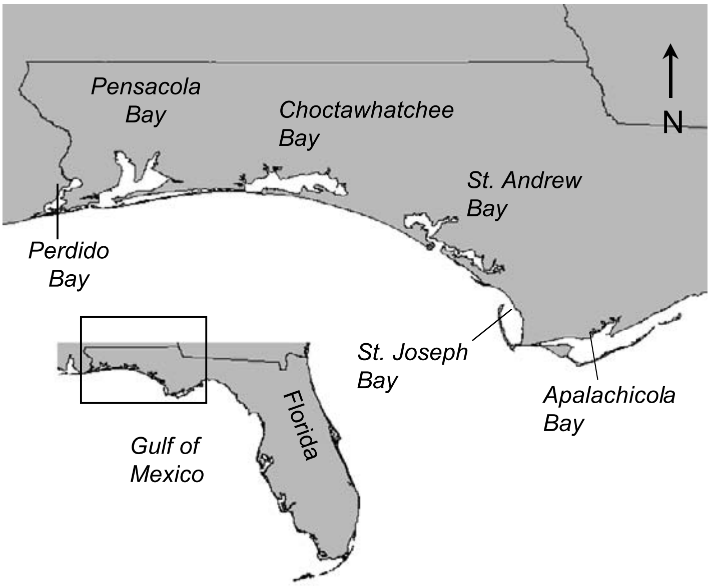

FIGURE 7.1 Northwest Florida estuarine systems where spotted seatrout were sampled.

Length frequency data on the recreational fishery were obtained from hook-and-line sampling by laboratory personnel and from volunteer recreational anglers. In most cases, lengths from hook-and-line-caught specimens collected for biological samples were included in the length frequency data sets. Length data from fishing tournaments were not included, as those catches were not representative of the fishery. Volunteers recorded the length of each spotted seatrout landed, including those released, using a measuring board with waterproof paper attached to it. The angler would lay the fish on the board and punch a hole in the paper at the middle margin of the caudal fin. When the sheet of paper was returned to project personnel, the data could be retrieved by measuring the distance to each hole. Anglers also recorded date, location, and number of fish caught on the waterproof paper. Each piece of paper had room for nine different trips.

Age composition of the recreational catch was estimated using a combination of two methods. For biological samples that were also valid length-frequency samples, we used the actual age. For the volunteer-caught fish that had not been aged, we converted length data to age data using age–length keys generated from aging data from the same bay, year, season (March to August and September to February), sex, and 50-mm size interval. For the few cases for which there were length data but no matching age data, we used the most appropriate age data available, such as those from the closest size interval or from the previous year or the nearest estuary. Sex was assigned to these unsexed length data using sex ratios generated from the biological samples collected in the same bay, year, season (March to August and September to February), sex, and 50-mm size interval. All references to length are in fork length.

Four different methods were used to estimate instantaneous total mortality rates (Z): standard least squares (LS) catch curve analysis (Ricker, 1975), the maximum likelihood (ML) method of Robson and Chapman (1961), and the methods of Hoenig (1983) and Royce (1972). For the least squares and maximum likelihood methods, we used the total, sexes-combined, age composition data (ln transformed for the least squares) from each estuary. For St. Andrew and Apalachicola bays, it was not obvious which was the first fully recruited age class, so two estimates were made, one with the youngest modal age class and one without it. Estimates were also made using data sets that excluded any of the older age classes with fewer than five fish for all but Apalachicola Bay, where the oldest age class had ten individuals. For the LS method, residuals were examined for homogeneity of variance (t test) and normality (Shapiro-Wilk statistic and normal probability plot). LS estimates of Z between estuaries were compared by examining the interaction terms in the analysis of variance (ANOVA).

Hoenig's (1983) method uses the predictive regression equation: $\ln(Z) = 1.44 - 0.982 \ln (t_{max})$, where t_{max} = maximum observed age. Hoenig developed this equation based on the relationship between maximum observed age and total mortality rate of 134 stocks and 79 species of fish, mollusks, and cetaceans. Royce's (1972) method was developed to estimate average annual instantaneous natural mortality (M) and was also based on its relationship to maximum observed age. Royce's equation basically equates to $M = 4.6/n$, where n = number of years from youngest age at full recruitment to maximum observed age. Royce's equation assumes an unfished population; because we were sampling exploited populations, these estimates were Z, not M.

RESULTS

Biological data were obtained from a total of 3742 spotted seatrout (2306 females and 1436 males) — 224 from Perdido Bay, 602 from Pensacola Bay, 367 from Choctawhatchee Bay, 1206 from St. Andrew Bay, 562 from St. Joseph Bay, and 781 from Apalachicola Bay. The overall size distributions by sex of the biological samples are shown in Figure 7.2.

REPRODUCTION

Plots of GSIs for both sexes by estuary showed elevated values, indicating spawning activity, from early April until mid-September across the region (Figures 7.3 and 7.4). Reproductive activity was

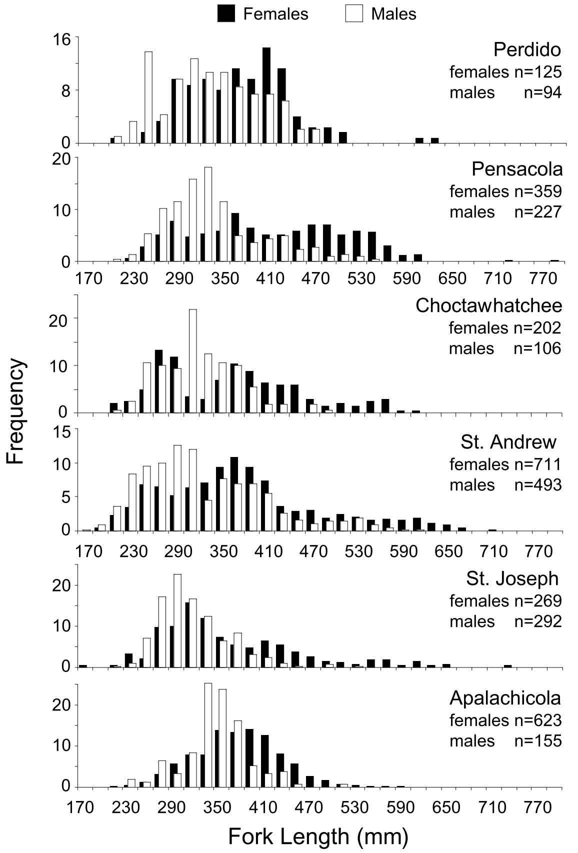

FIGURE 7.2 Total length frequency distributions by sex and estuary of spotted seatrout used in reproductive analyses and to generate age-length keys.

highest from late April through July. There was some evidence that the spawning season varied slightly among the estuaries. GSI data from St. Andrew and Apalachicola bays for both sexes appeared slightly bimodal, with peaks in May and July in the former and early May and August in the latter (Figures 7.3 and 7.4). GSIs for females in Pensacola Bay showed one mode in late July to early August, but this pattern was not evident for males from Pensacola. In St. Joseph Bay, GSIs for both sexes appeared to decline slowly throughout the spawning season, although there was never an obvious mode. Spawning in that estuary, and possibly in Choctawhatchee Bay, seemed to end a few weeks earlier than in the other Panhandle estuaries. No obvious modes were visible in the GSI data of either sex from Perdido and Choctawhatchee bays, nor from males from Pensacola, possibly because of small sample sizes.

Macroscopic maturity stage data from females supported the GSI results; i.e., between 59 and 85% of females were gravid (late developing) during April through August, with some evidence of activity in September as well, when 26% were gravid (Figure 7.5). The proportions were highest during May and June (85%), suggesting that spawning peaked then, with no real indication of a bimodal season. A plot of the monthly proportion of gravid females by estuary did suggest a secondary spawning peak in August in St. Andrew Bay, but this was not apparent in any of the other systems (Figure 7.6). Proportions of spent females peaked in August and September at 15 and 17%, respectively.

Using maturity stage 3 (early vitellogenesis or early developing) as our criterion for sexual maturity, logistic regression of the proportions of mature and immature fish indicated that 50% of female spotted seatrout in Choctawhatchee, St. Andrew, and St. Joseph bays are mature by the time they attain 230 mm (Figure 7.7). Size at maturity is probably similar in the other three bays. The

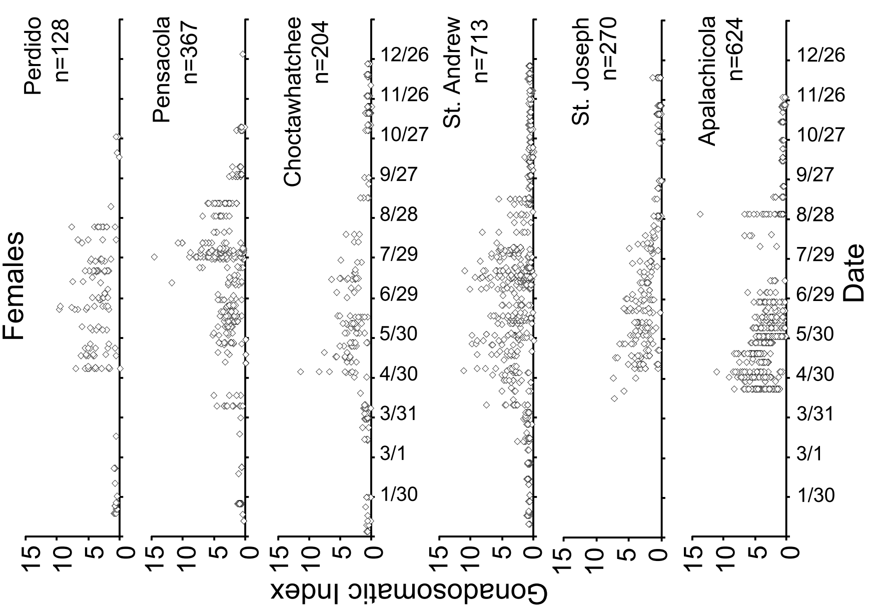

FIGURE 7.3 Plot of raw gonadosomatic indices data by day of the year and estuary for female spotted seatrout.

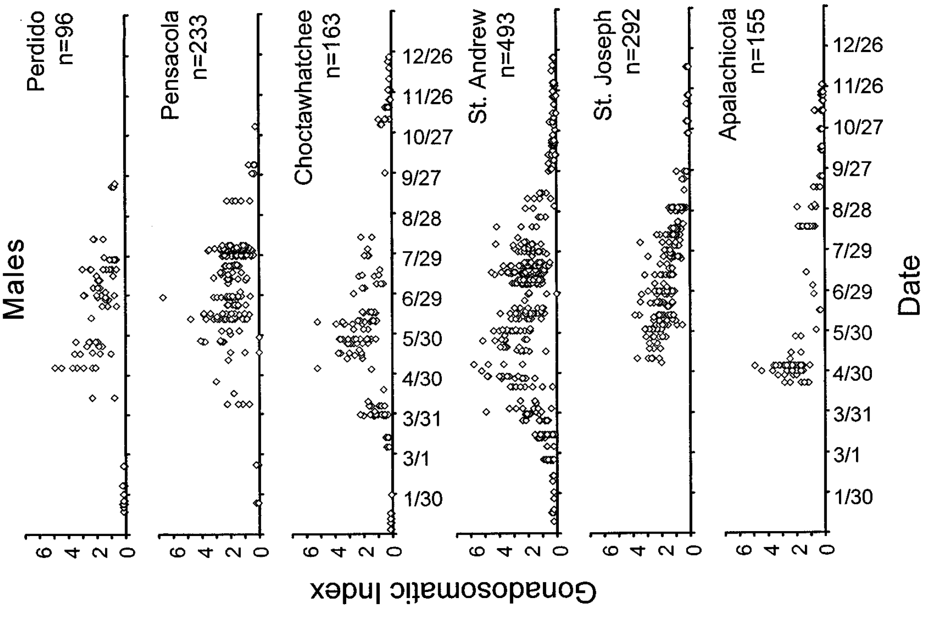

FIGURE 7.4 Plot of raw gonadosomatic indices data by day of the year and estuary for male spotted seatrout.

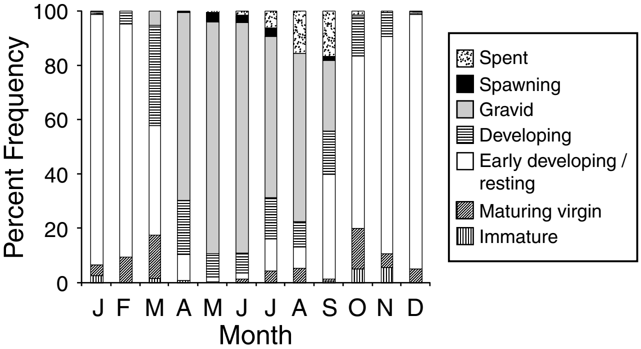

FIGURE 7.5 Monthly frequency distributions of macroscopic maturity stages of all female spotted seatrout collected from the six estuarine systems in northwest Florida.

predicted proportion of mature females in Pensacola Bay at 250 mm FL, the smallest interval with data, was 66%, so most certainly at 230 mm at least 50% were mature. All but one female from Perdido Bay and all females from Apalachicola Bay were mature; the former had three fish below the 270-mm interval, two at 250-mm, and one at 210 mm. In the latter there were three below the 250-mm interval, two at 230 mm, and one at 210 mm. At 50% maturity, a size of 230 mm equates to an age of no more than 1 year, and in some cases this would be age 0. By 290 mm, the proportion of mature females ranged from 0.78 to 1.00, and at this size almost all fish are still age 0 or 1.

Males appeared to mature at similar or even smaller sizes than females. Predicted size intervals at which 50% of the males were mature, based on logistic regression, were between 250 and 270 mm for Choctawhatchee Bay, < 190 mm for St. Andrew Bay, and < 230 mm for St. Joseph Bay (Figure 7.8). All males collected in Perdido, Pensacola, and Apalachicola bays were mature, and the smallest size interval in each bay was 230, 210, and 230 mm, respectively. Except for Choctawhatchee Bay, males of these sizes would all be age 0 or 1. In Choctawhatchee Bay, roughly 5% of males between 250 and 270 mm were age 2, while the rest were age 0 or 1.

SIZE COMPOSITION

The overall size distributions from the hook-and-line fishery were similar among the six estuaries, with recruitment occurring at about 250 mm and modes somewhere between 275 and 375 mm (Figure 7.9). The fishery was dominated by fish below 450 mm; they constituted between 87.6 (St. Andrew) and 96.5% (Pensacola) of samples. Few fish were above 550 mm (0 to 3.8%) and virtually none were above 650 mm. There were, however, some small differences among the bays. St. Joseph Bay, and St. Andrew to a lesser extent, had the most skewed distributions and were dominated by smaller fish — 250 to 350 mm. Fish > 350 mm constituted only 26 to 27% of samples from those two estuaries, compared to 42 to 45% in the other four bays. Pensacola and Choctawhatchee bays had the largest proportion of large fish, with 5.2 and 5.3% between 500 and 600 mm, compared to 0.6 to 2.4% in the other four estuaries (Figure 7.9). When the size distributions were examined by sex, there were no dramatic differences; although modal size of males was less than that of females in all but Perdido and Choctawhatchee bays, females dominated the upper ends in each system (Figure 7.9).

The size distributions of seatrout caught by project personnel and by volunteer anglers in St. Andrew Bay for use in characterizing the fishery were very similar; collection of size data by volunteers was most successful by far in that bay. In both data sets the distribution was unimodal, with a mode between 250 and 350 mm, and few fish < 200 mm or > 450 mm were caught (although volunteers

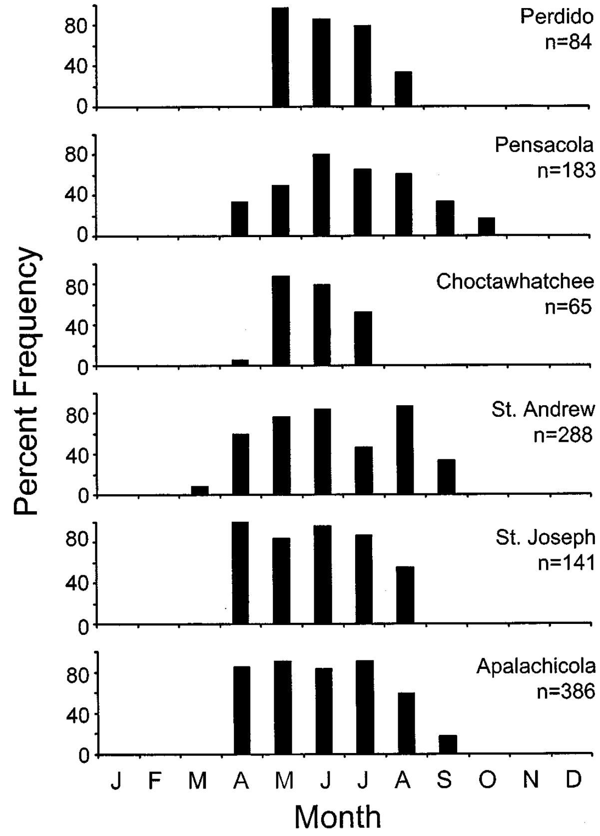

FIGURE 7.6 Monthly proportions of gravid (stage 5) female spotted seatrout by estuary.

did catch a higher proportion of those < 200 mm) (Figure 7.10). Because the distributions were so similar, we felt it was valid to pool these data for the size and age composition analysis. In Apalachicola Bay, where we had much less cooperation from recreational anglers, the size distributions of project- and volunteer-caught fish were also similar, although not quite as similar as in St. Andrew Bay. The overall size range was the same but the mode was much more defined in St. Andrew Bay (Figure 7.10); however, we still felt the distributions were sufficiently similar to allow pooling of the data.

AGE COMPOSITION

Fish ages 1 and 2 dominated and few over age 3 were taken in the recreational hook-and-line spotted seatrout fishery in the Florida Panhandle, although the age distribution varied considerably among bays and between seasons and sexes within bays (Figure 7.11). One- and two-year olds made up 88.5, 70.0, 70.9, 80.2, 69.2, and 69.3% of the catch in Perdido, Pensacola, Choctawhatchee, St. Andrew, St. Joseph, and Apalachicola bays, respectively. If age-0 fish are included, these proportions increase to 91.6, 72.8, 82.3, 87.3, 95.0, and 85.8%, respectively; when 3-year-olds are added, these numbers rise to 98.5, 86.7, 95.8, 93.8, 97.0, and 96.3%, respectively.

Within estuaries, age structure shifted seasonally and annually to varying degrees. In each estuary, young-of-the-year were caught almost exclusively during the fall-to-winter (September to February) period, as can clearly be seen in the seasonal plots from St. Andrew Bay (Figure 7.12). This pattern was most apparent in St. Joseph Bay, where 67.9% were young-of-the-year during these months. In Perdido Bay the dominant age class shifted from age 1 in summer 1995 to age 2 in summer 1996. Age-2 fish dominated in Pensacola Bay both years that it was sampled, but the proportion of age-1 fish dropped from about 35% during March to August 1994 (the period of greatest effort) to about 10% the following March-to-August period.

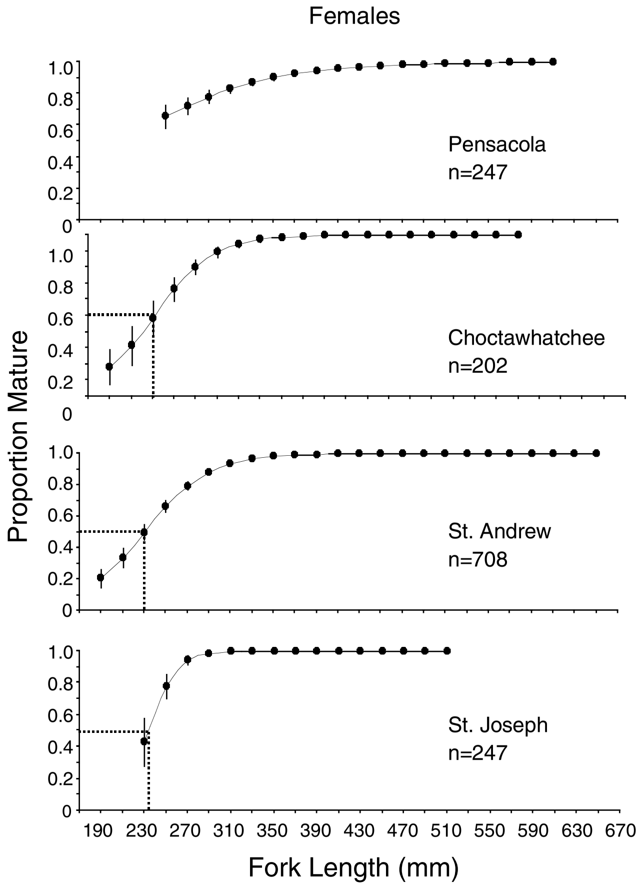

FIGURE 7.7 Predicted proportions (and standard error) of mature female spotted seatrout at size by estuary. Stage 3 or early developing fish were considered mature. The dotted line indicates the predicted size at which 50% would be mature.

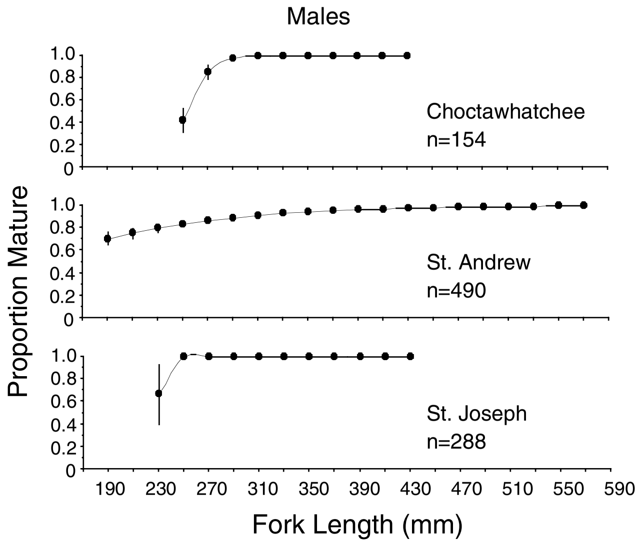

FIGURE 7.8 Predicted proportions (and standard error) of mature male spotted seatrout at size by estuary. Stage 3 or early developing fish were considered mature.

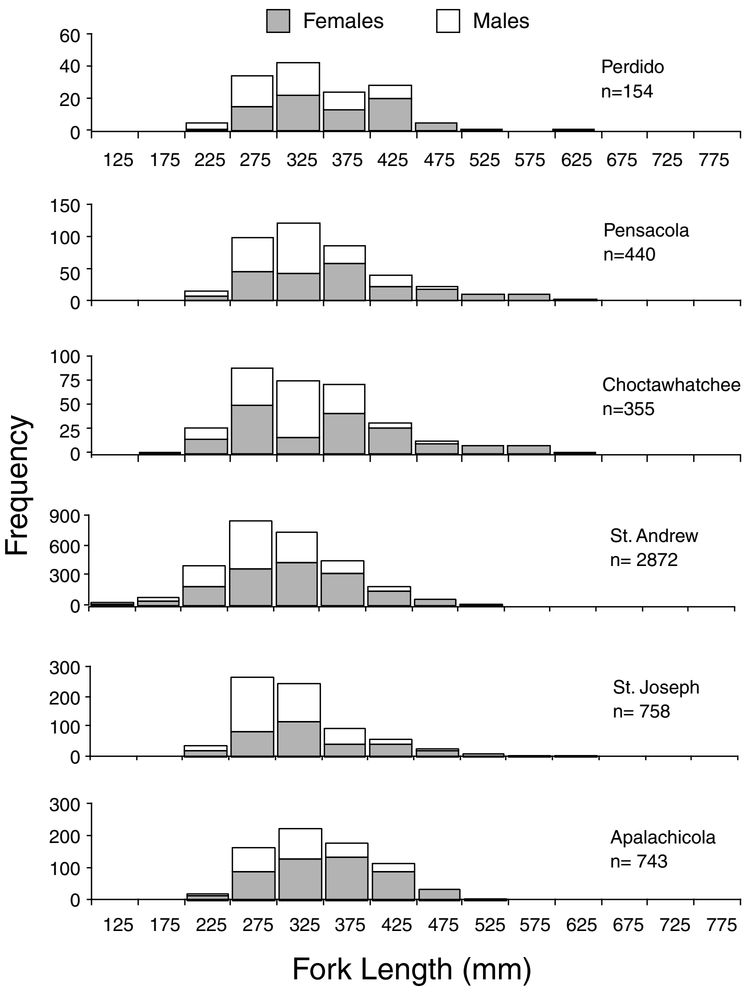

FIGURE 7.9 Overall size distributions of hook-and-line-caught spotted seatrout by estuary.

In Choctawhatchee Bay, age-1 and age-2 fish completely dominated the fishery in spring to summer 1994 (91.3%), but one year later, age-2 and age-3 fish composed 79.7%, with only about 12% constuting age 1 fish. Age-1 and age-2 seatrout dominated the St. Andrew Bay fishery both years it was sampled, but during March to August 1994, they were about equally abundant; 1 year later, age-2 fish were only about half as abundant as age-1 fish (Figure 7.12). During March to August 1994, the catch in St. Joseph Bay was almost all age-1 fish (83.3%), with age-2 fish constituting < 10%; a year later age-1 fish again predominated (60%), but age-2 spotted seatrout were much more abundant, constituting 30% of the catch. In Apalachicola Bay during March to August 1995, the mode was age 3, while during March to August 1996, most fish (81.4%) were age 1 and only 8.7% were age 3. During both fall-to-winter periods, ages 0 to 2 were all important in the fishery, while age-3 fish contributed only about 5%.

Age structure between sexes was quite variable among estuaries and ages but showed no consistent pattern (Figure 7.11). Among fish age 3 and above, the proportion of males in the catch was slightly more than twice that of females ($\overline{x} = 2.1$, SE = 0.13) at each age in Pensacola and St. Andrew bays, while in Apalachicola Bay, there were 3.2 and 6.6 times as many males as females at ages 3

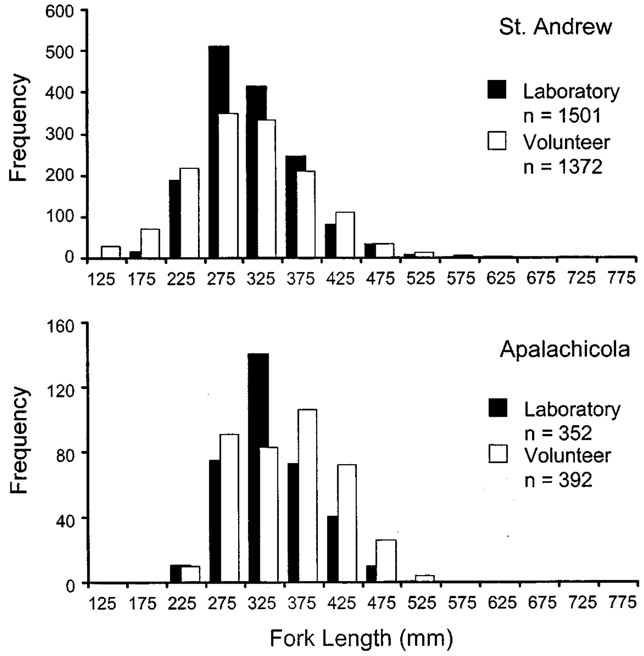

FIGURE 7.10 Total size distributions of all spotted seatrout collected in St. Andrew and Apalachicola bays by lab personnel and volunteer anglers for characterizing size and age composition of the recreational fishery.

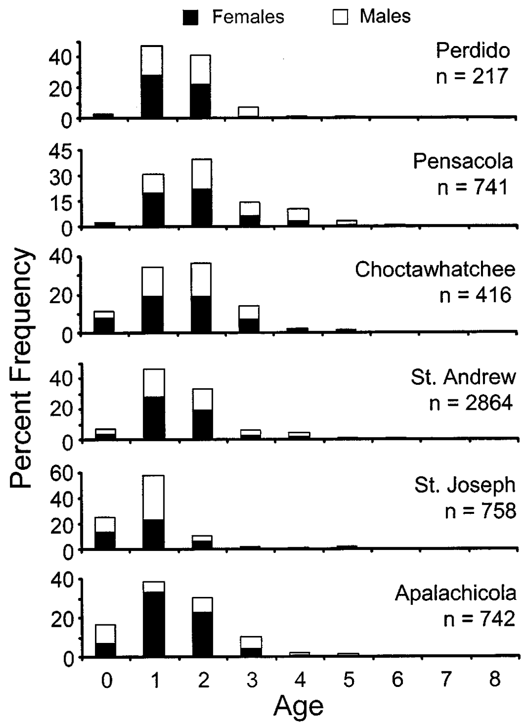

FIGURE 7.11 Total age distributions of spotted seatrout caught by hook and line, by estuary.

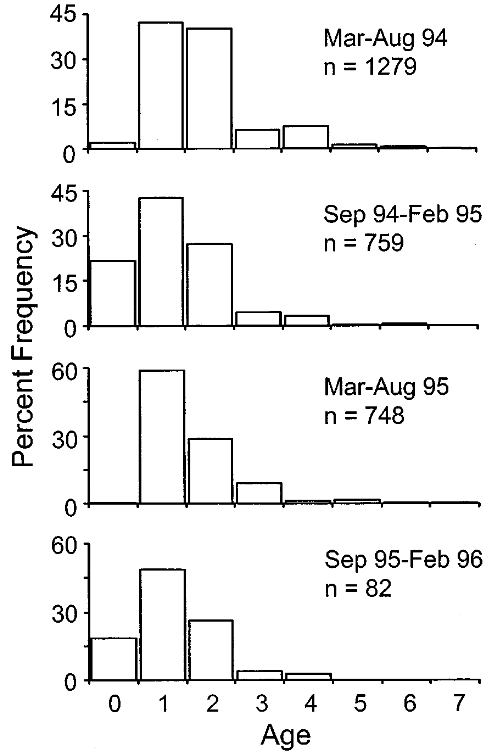

FIGURE 7.12 Seasonal age distributions of spotted seatrout caught by hook and line in St. Andrew Bay.

and 4 and only males at age 5. In contrast, in St. Joseph Bay, females at ages 3, 4, and 5 were 2.3, 11, and 2.2 times as abundant as males, respectively. In Perdido and Choctawhatchee bays, the pattern was mixed, with males exceeding females at age 3 and then females exceeding or about equal to males above that age, although sample sizes were quite small for these two systems.

TOTAL MORTALITY RATES

Estimates of instantaneous total mortality rate (Z) were quite variable, ranging from a low of 0.49 to a high of 2.05 (Table 7.1). The Robson-Chapman ML and LS catch curve estimates, which ranged from 0.80 to 2.05, tended to be higher and more similar to each other than the estimates determined using the Hoenig and Royce methods, which ranged from 0.55 to 1.15 and were also similar to each other. Both ML and LS estimates of Z for sexes combined were highest for Perdido Bay (1.740 and 1.558, respectively); the lowest ML estimate came from St. Andrew Bay (0.866), while Pensacola Bay yielded the lowest (0.821) LS estimate (Table 7.1; Figure 7.13).

Of the LS estimates for sexes combined, the only statistically significant differences were between Perdido and Pensacola bays ($p = 0.019$) and between Perdido and St. Andrew bays ($p = 0.037$) (Table 7.2). Among the ML estimates for sexes combined, 95% confidence limits did not overlap between 1) Perdido and Pensacola, Choctawhatchee, St. Andrew, and Apalachicola bays; 2) St. Andrew and Choctawhatchee, St. Joseph, and Apalachicola bays; and 3) Pensacola and Choctawhatchee, St. Joseph, and Apalachicola bays (Table 7.1). Although not true statistical tests, these nonoverlapping confidence intervals certainly suggest differences in mortality rates of spotted seatrout among these estuaries. Confidence intervals of the LS estimates were much larger (96 to 565%, $\overline{x} = 367\%$) than those of the ML estimates.

Estimates of total mortality by sex showed no consistent pattern. Robson-Chapman ML estimates of Z ranged from 0.676 to 2.054 for males and from 0.683 to 1.299 for females. Males had a higher mortality rate than females in Perdido and St. Joseph bays, while females had higher rates in

TABLE 7.1

Estimates of Instantaneous Total Mortality Rate (Z) Derived from Four Methods for Spotted Seatrout from Perdido (PDO), Pensacola (PEN), Choctawhatchee (CHW), St. Andrew (SAB), St. Joseph (SJB), and Apalachicola (APL) Bays in Northwest Florida

						Least Squares		Hoenig							
				Robson-Chapman		Catch Curve		Females		Males		Royce			
Bay	Ages	Sex	n	Z	95% CL	Z	95% CL	Z	Max Age	Z	Max Age	Z	Yrs3	Z	Yrs3
PDO	2–5	F+M	109	1.740	1.418–2.218	1.558	0.678–2.438	0.869	5	0.727	6	1.15	4	0.92	5
PDO	2–3[1]	F+M	106	2.023	1.640–2.654										
PDO	1–2[1]	F	109	0.683	0.497–0.911										
PDO	2–3[1]	M	56	1.179	0.963–1.454										
PEN	2–6	F+M	494	0.918	0.835–1.007	1.075	0.556–1.593	0.727	6	0.624	7	0.92	5	0.77	6
PEN	2–5[1]	F+M	491	0.936	0.852–1.028	0.821	0.287–1.356								
PEN	2–5[1]	F	237	1.128	0.984–1.296	1.046	0.570–1.521								
PEN	2–5[1]	M	254	0.809	0.710–0.920	0.840	0.078–1.252								
CHW	2–6	F+M	227	1.189	1.034–1.372	1.231	0.899–1.563								
CHW	2–5[1]	F+M	226	1.214	1.055–1.404	1.146	0.461–1.830	0.727	6	0.869	5	0.92	5	1.15	4
CHW	2–4[1]	F	226	1.299	1.065–1.606	1.205	0.122–2.532								
CHW	2–3[1]	M	104	0.676	0.443–0.980										
SAB	1–72	F+M	2660	0.866	0.831–0.901	0.978	0.816–1.141	0.548	8	0.488	9	0.58	8	0.51	9
SAB	1–6[1,2]	F+M	2656	0.872	0.838–0.907	0.937	0.708–1.167								
SAB	1–6[1,2]	F	1472	0.971	0.920–1.026	1.041	0.740–1.341								
SAB	1–6[1,2]	M	1184	0.774	0.729–0.822	0.845	0.637–1.052								
SAB	2–6[1]	F+M	1315	1.168	1.102–1.239	0.995	0.627–1.363								
SJB	1–6	F+M	562	1.367	1.249–1.500	1.050	0.552–1.548	0.548	8	0.869	5	0.58	8	0.92	5
SJB	1–5[1]	F+M	561	1.385	1.266–1.520	0.943	0.124–1.762								
SJB	1–5[1]	F	249	1.104	0.966–1.264	0.795	0.147–1.443								
SJB	1–3[1]	M	307	2.054	1.808–2.381	1.989	1.674–2.304								
APL	2–5[1]	F+M	332	1.198	1.067–1.349	1.089	0.514–1.664	0.869	5	0.869	5	1.15	4	1.15	4
APL	1–3	F	442	1.074	0.972–1.187	1.031	-3.754–5.818								
APL	2–5[1]	M	130	0.807	0.670–0.965	0.663	0.010–1.316								
APL	1–5[1,2]	F+M	620	0.834	0.768–0.906	T0.931	0.550–1.311								

Note: Bays are listed in geographic order from west to east.

[1] Samples which included only age classes with at least 5 fish. [2] Samples which included an aditional younger age class because identification of the first fully recruited age class was not obvious [3] Number of years used to calculate Z, i.e. number of years from first fully recruited age to maximum age.

the other four bays (Figure 7.13). In estuaries with enough age classes to calculate them, LS estimates showed the same patterns. The difference between sexes was greatest in St. Joseph Bay, where Z for females was 1.104 vs. 2.054 for males; however, the 95% confidence intervals did not overlap in any of the estuaries. Estimates of Z calculated using the methods of Hoenig and Royce also showed no consistent differences between sexes, and the patterns they did show differed from those from ML and LS methods. Male mortality rates exceeded those for females in Choctawhatchee and St. Joseph bays, while the rates in Apalachicola were equal (Table 7.1).

DISCUSSION

REPRODUCTION

GSI data indicating that spotted seatrout spawned from April through August were consistent with previous studies. In the northeastern Gulf of Mexico, Klima and Tabb (1959) reported that spawning occurred from late April through September in Apalachee and Apalachicola bays, with a possible peak in late May or early June; Moffett (1961) found spawning from May through September in Cedar Key and Fort Myers, with a peak during summer. Brown-Peterson et al. (in review) documented an April-to-August season, peaking in June, in Apalachicola Bay and a March-through-September season, with no obvious peak, in Charlotte Harbor in southwest Florida.

Based on GSIs and visual and histological staging, Overstreet (1983) reported that seatrout in Mississippi spawn from May through August. More recently, Brown-Peterson and Warren (2000) reported a mid-April to mid-September season in that state, based on GSI data. Studies in south Texas (Brown-Peterson et al., 1988) and east Texas (Maceina et al., 1987) found significantly higher GSIs among spotted seatrout from April to September and concluded that spawning occurred during those months. The bimodal pattern in spawning activity found in St. Andrew and Pensacola bays has been documented in several other studies along the Atlantic and Gulf coasts (Stewart, 1961; Hein and Shepard, 1979; Brown-Peterson and Thomas, 1988; Brown-Peterson et al., 1988).

The significance of the differences in temporal GSI distributions (Figures 7.3 and 7.4) among estuaries is unclear. Although differences in spawning activity among these estuaries are likely, the

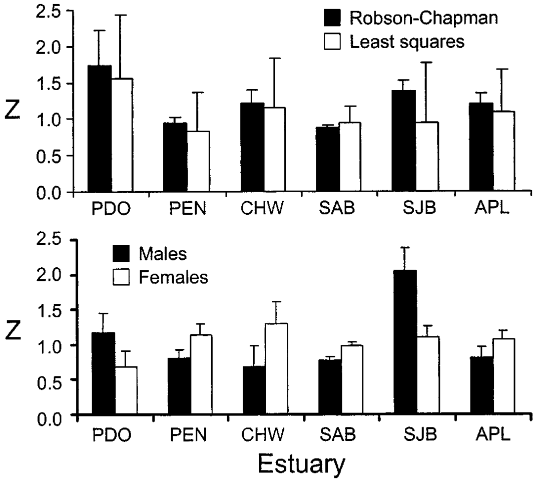

FIGURE 7.13 Estimates of total instantaneous mortality (Z) of spotted seatrout by estuary. Top panel: estimates of Z calculated using the Robson-Chapman and least squares methods. Bottom panel: Robson-Chapman estimates of Z by sex. Error bars = 95% C.L., PDO = Perdido, PEN = Pensacola, CHW = Choctawhatchee, SAB = St. Andrew, SJB = St. Joseph, and APL = Apalachicola.

TABLE 7.2
Results of F Tests for Differences in Total Instantaneous Mortality Rate Z Derived from Catch Curves (equality of slopes in the ln percent frequency on age relationship) Between Spotted Seatrout from Different Pairs of Bays

			Bay				
Bay	**Ages Incl.**		**APL**	**SJB**	**SAB**	**CHW**	**PEN**
PDO	2–5	F	3.68	2.62	10.2	2.53	9.47
		Pr>F	0.128	0.166	0.019	0.187	0.037
PEN	2–5	F	2.15	0.11	0.49	2.58	
		Pr>F	0.217	0.749	0.508	0.184	
CHW	2–5	F	0.07	0.31	1.38		
		Pr>F	0.799	0.604	0.284		
SAB	1–6	F	0.82	0.00			
		Pr>F	0.401	0.982			
SJB	1–5	F	0.16				
		Pr>F	0.702				
APL	2–5						

Notes: APL = Apalachicola, SJB = St. Joseph, SAB = St. Andrew, CHW = Choctawhatchee, PDO = Perdido, and PEN = Pensacola. Values in bold indicate pairs with statistically different slopes.

data are confounded by unequal sampling effort and sample size as well as the logistic necessity of sampling different bays in different years. Brown-Peterson and Warren (2000) noted that the rapid increase in GSI during the spring (indicating the beginning of spawning activity) occurred in Mississippi about one month earlier in 1999 than in 1998.

Time of day at which the fish were collected may also have confounded the findings. For example, for logistic reasons, sampling of St. Joseph Bay occurred primarily from early morning to early afternoon. Because this species apparently spawns in the evening (Brown-Peterson et al., 1988), it is not surprising that no spawning (hydrated) females were collected there and, therefore, that fish had lower GSIs than in almost all the other estuaries. Differences in the size distribution of the samples among estuaries at a given time are still another possible confounding factor; i.e., most of the fish from an estuary in a given month were so small that many were immature, GSI estimates could be affected greatly. Spotted seatrout tend to school by size, especially at smaller sizes; these smaller fish seem to be easier to catch by hook and line, so they might be overrepresented at some times in some places.

Size-at-maturity estimates from this study are consistent with those of Klima and Tabb (1959) but somewhat lower than those of Brown-Peterson et al. (in review) — the only other data available from the region. Size at 50% maturity was about 230 mm FL for females in three of the six estuaries, and data from the other three suggest similar sizes. At 290 to 310 mm FL, virtually all females were mature. Klima and Tabb (1959) did not define a "mature" fish but stated that all females from Apalachicola and Apalachee bays were mature by the time they were 27 cm SL (314 mm FL). Brown-Peterson et al. (in review) estimated that 50% of female spotted seatrout from Apalachicola Bay matured by 300 mm TL (298 mm FL), which is about 70 mm larger than our estimate; their smallest was 285 mm TL. This difference may reflect differences in our definitions of maturity or in methodology or possibly temporal variation, as our study occurred 8 to 10 years after theirs.

Our data suggest that males mature at slightly smaller sizes than females; Klima and Tabb (1959) found that all males were mature by about 25 cm SL (292 mm FL). Overstreet (1983) found gravid (stage 5) females as small as 189 mm SL (226 mm FL) and males down to 201 mm SL (239 mm FL) in Mississippi. In a recent study in Mississippi, Brown-Peterson and Warren (2000) estimated size at 50% maturity of females to be 230 mm SL (270 mm FL), with the smallest mature female at 225 mm SL (265 mm FL); however, only 3% of the 432 females collected were immature, so their estimate may have been biased. In South Carolina, Wenner et al. (1990) reported that 83.3% of six males < 238 mm TL (237 mm FL) were mature, as were all males above that size. Among females 273 to 284 mm TL (271 to 282 mm FL) they found 63.6% were mature, as were 100% of those larger than that size. The smallest ripe male and female collected in Florida Bay by Rutherford et al. (1982) were 237 mm SL (278 mm FL) and 230 mm SL (270 mm FL), respectively.

Using age–length keys, we estimated that close to 100% of male and female spotted seatrout mature by age 1. Klima and Tabb (1959) reported that males may mature "by the end of their first year of life" (late age zeros?), females may mature by the "end of the second year of life" (late age 1?), and all fish spawn by age 3 (age 2?). Wenner et al. (1990) found that 409 of 410 age-1 males and 97.1% of 930 age-1 females in South Carolina were mature. Brown-Peterson and Warren (2000) reported that 80% of age-1 females from Mississippi were mature, and all 117 of the males they collected were mature, with the smallest being 201 mm SL at age 1.

SIZE COMPOSITION

The skewed size distributions with a dominance of smaller fish that we observed in St. Joseph and St. Andrew bays may reflect the impact of higher exploitation rates in those two systems, although this is certainly speculation at this point. The truncation of the size and age structure is a typical response of fish populations to fishing. Based on our observations, the exploitation rate appears to be much higher in St. Joseph and St. Andrew bays than in Apalachicola Bay, where the proportion of larger fish was much greater. This difference in exploitation rates is probably related to the fact that the former two bays are much closer to a populated area (Panama City), are aesthetically much more attractive, and, because of water clarity, are much easier for a person unfamiliar with the bay to find productive fishing sites. A note of caution is warranted for the Apalachicola data. Many of the more successful catches there were dominated by fish in a rather narrow size range, and certain sites seemed to produce fish of certain sizes, so the choice of fishing sites could definitely affect the size composition data. In addition, many of the sites fished were learned about from guides, who obviously would want to avoid areas where smaller trout tended to occur. The broader size structure seen in Pensacola and Choctawhatchee bays suggests that the exploitation rates in those two systems were lower than in the other four, although this is just speculation since we did not estimate this parameter. One other weakness with the overall size distribution data is that they are affected by the temporal distribution of the samples, which, if not distributed proportionately to the temporal distribution of effort in the fishery, can introduce biases.

Surprisingly, the size composition of seatrout collected with hook and line in Apalachee and Apalachicola bays in 1957 and 1958 (Klima and Tabb, 1959) was very close to what was observed almost 40 years later in most of the estuaries in this study; their modal size was about 320 mm FL and the range was 230 to 450 mm FL. Similarly, the size distribution of fish collected for a tagging study in Apalachicola Bay in 1958 and 1959, primarily by hook and line, ranged from roughly 200 to 500 mm FL with a mode around 350 to 375 mm FL (Moffett, 1961). The size distribution of spotted seatrout caught recreationally in Everglades National Park from 1978 to 1980 was also quite similar to that found in northwest Florida, ranging from about 260 to 540 mm FL with a mode around 350 mm (Rutherford et al., 1982: Figure 2). That the size distributions of spotted seatrout from 35 to 40 years ago are so similar to the ones found in this study during 1994 to 1996 suggests that the species is capable of sustaining a considerable amount of fishing mortality, given that a noticeable truncation in the size structure — with the possible exception of St. Joseph and St. Andrew bays — has apparently not occurred.

The collection of size structure data from volunteer anglers was quite successful, especially in St. Andrew Bay, as evidenced by the similarity between those data and data collected by study personnel and the fact that volunteers basically doubled the sample sizes for at least two estuaries. This method of collecting valuable size structure data was extremely cost effective and yielded apparently unbiased data of considerable value for stock assessment. Another benefit of this method is that it provided information that could not be obtained by dockside sampling about numbers and size structure of fish outside the size limits.

AGE COMPOSITION

The variation in overall age structure among the six estuaries in northwest Florida further confirms the hypothesis that the nonmigratory nature of this species will tend to produce populations with unique demographics in each estuary because of varying environmental factors and exploitation rates. Given that only two age classes (ones and twos) constituted 69 to 89% of the total recreational catch in all six systems, and assuming larval recruitment varies spatially and temporally, one would predict that these unique demographics are quite dynamic. This prediction is confirmed by the annual variability in age structure seen within each estuary. Murphy and Taylor (1994) found significant differences in the age structure between seatrout from Apalachicola Bay and Indian River Lagoon, Florida, which the authors said suggested that the populations were responding independently to local fishing pressures. Because the age composition values from this study were based on all spotted seatrout caught, including those released, they provide an estimate of the age structure of the population, not just of the legal catch.

In contrast, other studies that have sampled only the retained catch had a 305-mm (12-in.) size limit in effect. Klima and Tabb (1959) reported that age-3 and age-4 spotted seatrout dominated the commercial hook-and-line catches in Apalachee and Apalachicola bays in the late 1950s. In the Everglades National Park, age-3 and age-4 fish also dominated the recreational catch, constituting 45 and 29%, respectively (Rutherford et al., 1982). They noted that anglers frequently caught small, young fish below the 305-mm (12-in.) size limit and released them. In spite of a 305-mm (12-in.) limit, 72 to 77% of the spotted seatrout landed by South Carolina anglers during 1986 to 1988 were age 1 and 94 to 97% were under age 3 (Wenner et al., 1990).

The recruitment of large young-of-the-year during fall and winter was quite evident in the seasonal age distribution data from each estuary (Figure 7.12). This phenomenon underscores the importance of sampling throughout the year to get a true idea of the age structure in a spotted seatrout fishery.

TOTAL MORTALITY RATES

The large range and significant differences in estimates of Z found among six northwest Florida estuaries support the hypothesis that different exploitation rates and environmental factors in each estuary can result in differences in demographics and population parameters of this nonmigratory species, even within geographically close systems at similar latitudes.

The LS estimate of Z for males in Apalachicola Bay (0.66) from this study was considerably less than the 1.63 that Murphy and Taylor (1994) estimated from fish collected there in 1986 to early 1988. Their estimate was based on ages 1 to 4, while ours included ages 2 to 5. It seems more likely that much of this difference reflects sampling differences — Murphy and Taylor (1994) included fish caught by haul seine, as well as hook and line, in their estimate — because it is unlikely that mortality rates decreased that much in less than 10 years. Our overall range in ML and LS estimates of Z of 0.80 to 2.05 for sexes combined was similar to results from other investigations in the Gulf: Everglades National Park, Z = 1.31 and 1.43 (Rutherford et al, 1982), and Bastrop Bayou, Texas, Z = 1.13 to 1.61, based on a tagging study (Baker et al., 1986). Murphy and Taylor's (1994) estimates from Charlotte Harbor, Florida (1.24 for females and 0.65 for males), were quite similar to some of the estimates from this study.

Although we do think that there are real differences in mortality rates of spotted seatrout among estuaries in northwest Florida, it is important to remember the basic assumptions of these estimation procedures: that all fully recruited age classes are equally vulnerable to the sampling gear; that survival is constant across ages; and that recruitment is constant. It is almost certain that none of these assumptions is completely met with spotted seatrout. In this study, sample size varied widely (106 to 2660) among estuaries; it is likely that the estimates from those with the smaller sample sizes (Perdido, Choctawhatchee, and possibly Apalachicola) may not be accurate. Also, hook-and-line sampling is subject to considerable variability from factors such as differences in angler skill and knowledge of the water body. The fact that this species tends to school or at least aggregate by size, as well as the fact that bait preferences vary with size, can also complicate sampling and bias results. Larger, older fish tend to be more solitary and wary and are probably underrepresented in the collections; this would result in overestimates of mortality.

It is somewhat puzzling that females had a higher mortality rate than males in Pensacola, Choctawhatchee, St. Andrew, and Apalachicola bays, while males had a higher rate in Perdido and St. Joseph bays. Because of small sample size, the Perdido Bay estimates may be inaccurate, but the St. Joseph Bay estimates, which were highly different from each other, were based on fairly large numbers (females = 249; males = 307). Intuitively, one thinks that this difference must reflect a real difference in the fisheries among estuaries, since it is very unlikely that natural mortality rate patterns would differ that much. The higher total mortality rate of females in four of the estuaries could reflect that the faster-growing females are being recruited to the fishery at a younger age and thereby are being exposed to increased fishing mortality. Murphy and Taylor (1994) found higher mortality rates for females than males in Charlotte Harbor and Indian River, Florida. In contrast, Rutherford et al. (1982) reported lower mortality rates for females than males in Florida Bay.

CONCLUSIONS

The use of life history parameters of spotted seatrout as an indicator of environmental health among estuaries, or within an estuary over time, has merit; however, some caveats must be considered with this method. Reproductive parameters in particular, such as GSI, annual or batch fecundity, spawning frequency, and fertilization rates, may provide some evidence of differences or changes in environmental quality among or within estuaries, although it is important to consider the possibility of latitudinal variation (Brown-Peterson and Thomas, 1988; Conover and Present, 1990). Size at maturity has been demonstrated to decline as a result of fishing, so it would be of less utility unless effort was constant. Natural mortality rates would be much less useful. Difficult to estimate accurately in a fished population, these rates can also be affected by such factors as recruitment variation, which is common among teleost fishes, population variation of their predators and prey, and possibly genetic differences (which could also confound interpretation of reproductive differences).

Focusing on fish below the size of recruitment to the fishery would greatly reduce, if not eliminate, effects related to fishing, but it would not help with other confounding factors. Using some other abundant, widely distributed, strictly estuarine, and, most importantly, unfished (even as bycatch) species of teleosts would be a better alternative. However, this would still not solve most of the problems associated with natural mortality rates or, even reproductive parameters if there are genetic differences among estuaries. In the southeastern U.S., some possible candidates might be found among the blenniids (blennies), gobiids (gobies), cyprinodontids (killifish), or batrachoidids (toadfish). A few other suggestions which would improve an interestuarine study of this type include 1) to sample all estuaries during the same years, to eliminate confounding from annual variation; 2) to expend equal amounts of effort and collect similar sample sizes in each system; 3) to be aware of diel effects on GSI, fecundity, and spawning frequency data; and 4) to consider possible effects related to salinity, distance from inlets, and other environmental and hydrological factors when designing the sampling plan and analyzing the results.

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8

The Reproductive Biology of Spotted Seatrout

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CONTENTS

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ABSTRACT

The reproductive biology of spotted seatrout, *Cynoscion nebulosus*, throughout their range is summarized. Most spotted seatrout attain sexual maturity by age 1 and 250 mm TL, although regional differences exist and males always attain sexual maturity at a younger age and smaller size than females. The contribution of age-0 and age-1 females to the spawning population is significant in many areas. Spotted seatrout have an extended reproductive season, ranging from 3 months in Chesapeake Bay, Virginia, to year round in the Bay of Campeche, Mexico; a 5- to 6-month spawning season is typical in most areas. Females produce multiple batches of eggs during the spawning season, and histological evidence shows that an individual can spawn, on average, every 4 to 5 days. Batch fecundity is related to female size and ranges from 12,600 to 797,000, with total annual fecundity estimates of 3 to 52 million. Final oocyte maturation occurs within 14 h and is induced by 17α,20β,1-trihydroxy-4-pregnen-3-one (20β-S). Spotted seatrout spawn at dusk in estuarine areas near channels when temperatures range from 22 to 34°C. Reproductive differences among estuaries throughout the range should be taken into account when regional management plans are devised.

INTRODUCTION

The reproductive biology of fish of the genus *Cynoscion* has been well documented, although most research has concentrated on only a few species. Various aspects of reproduction are similar among species in the genus, such as multiple spawning, an extended spawning season, and achieving sexual maturity at a relatively small size and young age; however, there are some species-specific differences. This chapter will concentrate on the reproductive biology of the spotted seatrout, *Cynoscion nebulosus*, the most extensively studied *Cynoscion* species. The reproductive biology of *C. regalis*, a species which co-occurs with *C. nebulosus* along the Atlantic coast of the U.S., is also well known (see Merriner, 1976; Shepard and Grimes, 1984; Taylor and Villoso, 1994; Connaughton and Taylor, 1995, 1996; Lowerre-Barbieri et al., 1996a, 1996b). The reproduction of other, smaller *Cynoscion* species that co-occur with *C. nebulosus* in the Gulf of Mexico has not been as well described. There is little current information on the reproduction of *C. arenarius* (see Pitre and Landry, 1981; Shlossman and Chittenden, 1981; Sheridan et al., 1984) and *C. nothus* (see DeVries and Chittenden, 1982; Sheridan et al., 1984; Barrera et al., 1997) in the Gulf of Mexico.

The major difference between *C. nebulosus* and the other congeners within its range is that the spotted seatrout spends its entire life history within estuarine waters (Tabb, 1958, 1966). Thus, while most sciaenids, including other *Cynoscion*, spawn offshore and allow currents and water movement to carry their eggs and larvae into the estuarine nursery areas, spotted seatrout actually spawn within the estuary. The tendency of spotted seatrout to stay within their natal estuary has been demonstrated by tagging studies (Iversen and Tabb, 1962; Music, 1981; Baker et al., 1986).

Recent genetic analysis suggests that *C. nebulosus* in the northern Gulf of Mexico are spatially divided into discrete subpopulations (Gold et al., 1999). The separation of subpopulations among estuaries suggests subtle differences in the reproduction of spotted seatrout among estuaries, as demonstrated by Brown-Peterson et al. (2002).

This chapter will summarize recent and historical information on the reproductive biology of spotted seatrout and discuss the implications that potential regional differences in reproduction may have on management decisions.

SIZE AND AGE AT SEXUAL MATURITY

SUMMARY OF AVAILABLE DATA

Spotted seatrout grow rapidly during their first several years of life (see Chapter 6) and achieve sexual maturity at a relatively small size and young age. There have been numerous reports, some conflicting, regarding the size and age of sexual maturity for males and females. However, general agreement in the literature is that males reach sexual maturity at a smaller size than females. The most current information on age and size at sexual maturity is summarized by geographic region in Table 8.1. In general, male and female spotted seatrout reach sexual maturity throughout their range at age 1, although variations in the size at 50% maturity, as well as in the size of the smallest sexually mature fish, exist.

DETERMINATION OF SEXUAL MATURITY

The literature contains some disagreement on when spotted seatrout should be considered sexually mature, particularly for females. Histological inspection of ovarian or testicular tissue is the most accurate method to determine sexual maturity, although the histological criteria are not consistent among studies. The appearance of cortical alveolar stage oocytes, indicating the beginning of glycoprotein and lipid synthesis and gonadotropin-induced ovarian growth (Tyler and Sumpter, 1996) has been used as evidence of sexual maturity in several studies (Brown, 1981; Brown-Peterson et al., 1988; Brown-Peterson and Warren, 2001; Roumillat and Brouwer, in preparation).

Other authors (Nieland and Wilson, 1993; Lowerre-Barbieri et al., 1996a; Crabtree and Adams, 1998; Bumguardner et al., 1998) consider females to be sexually mature with the appearance of yolked (vitellogenic) oocytes in the ovary, a stage of development more advanced than the cortical alveolar stage oocytes (Tyler and Sumpter, 1996). The presence of oocytes in the cortical alveolar stage suggests that the ovaries have begun growth and maturation; these oocytes must continue through vitellogenesis, hydration, and ovulation or undergo atresia, since oocytes in this stage cannot overwinter until the next reproductive season. Thus, ovaries with oocytes in this stage constitute the broadest definition of sexual maturity. However, ovaries containing primary and cortical alveolar oocytes macroscopically appear similar to regressed or immature ovaries containing primary oocytes only. For this reason, the presence of vitellogenic oocytes has been used as an indication that a fish is sexually mature and will spawn during that reproductive season, since vitellogenic oocytes are easy to distinguish macroscopically and microscopically.

Additionally, small females with ovaries containing only cortical alveolar oocytes at the end of their first summer may not spawn during that season. Thus, there appears to be a difference between biological sexual maturity, indicating growth and maturation of the oocytes, and functional sexual maturity, suggesting that the fish will actually spawn during that reproductive season. In practical terms, the differences among authors in reported size at sexual maturity may be partially related to considering fish of a slightly smaller size to have attained sexual maturity when using the cortical alveolar rather than the vitellogenic oocyte criteria.

REGIONAL COMPARISONS OF SEXUAL MATURITY

Historical size at maturity data for northwestern Florida, including the Panhandle, compares favorably with more recent reports. Klima and Tabb (1959) reported 50% sexual maturity at 250 mm TL for females and 215 mm TL for males, whereas DeVries et al. (see Chapter 7) reported slightly smaller sizes for both males and females (Table 8.1). Moody (1950) found females to be 50% mature at 240 mm TL in Cedar Key, along the west coast of Florida, while males achieved sexual maturity between 200 to 240 mm TL. This appears to be a smaller size at sexual maturity than current reports for western Florida from Charlotte Harbor (Brown-Peterson et al., 2002), where the smallest sexually mature female captured was 245 mm TL (Table 8.1).

Disparity in the size of the smallest sexually mature female captured in the Everglades area of Florida also exists; Stewart (1961) found the smallest mature female to be 206 mm TL, whereas Rutherford et al. (1982) found the smallest female in the same area to be 272 mm TL and the smallest male to be 280 mm TL. However, the largest disparity in Florida occurs along the east coast in the Indian River Lagoon area. Tabb (1961) reported the size at 50% maturity to be 409 mm TL for females, with a suggested age at maturity of 3 or 4 for females and 2 or 3 for males.

TABLE 8.1
Estimated Size and Age at 50% Sexual Maturity and Smallest Sexually Mature Male and Female Spotted Seatrout from Various Regions within the Southern U.S.

Region	Female			Male			Reference
	Size 50% Maturity	Age 50% Maturity	Smallest Mature	Size 50% Maturity	Age 50% Maturity	Smallest Mature	
Chesapeake Bay, Virginia	300 – 350	2 or 3	290 (age 2)	< 250	< 2	250	Brown, 1981
North Carolina	280 mm FL	0	241 mm FL	241 mm FL	0	231 mm FL	Burns, 1993
South Carolina	280	1	225	< 200	1	197	Wenner et al., 1990
Georgia		1	263	–	1	263	Lowerre-Barbieri et al., 1999
Florida, West Coast	280	1	245	–	–	—	Brown-Peterson et al., 2002
Florida, Panhandle	230 mm FL	0 or 1	210 mm FL	< 235 mm FL	0 or 1	< 190 mm FL	DeVries et al., 2002
Alabama	–	–	300	–	–	–	Van Hoose, 1987
Mississippi	272[a]	1	267[a]	< 239[a]	0 or 1	239[a]	Brown-Peterson and Warren, 2001
Louisiana		1	247		0 or 1	210	Nieland et al., 2002
Texas	280	1	270	—	1	—	Bumguardner et al., 1998

Note: All lengths are TL in mm unless otherwise indicated.

[a] Converted from SL to TL using mm TL = 1.1399 (mm SL) + 10.26 (Murphy and Taylor, 1994).

In contrast, Crabtree and Adams (1998) found females to be mature at 200 to 250 mm TL, corresponding to age 0 or age 1, although they did not sample enough fish < 200 mm TL to determine size or age at 50% maturity. Sampling techniques appear similar between the two studies, suggesting a potentially significant decrease in size and age at maturity over the past 30 years. A decrease in size or age at sexual maturity is generally considered to relate to a decrease in population size (Rothschild, 1986).

Historical studies in Louisiana and Texas suggest no major changes in size at maturity over time. Hein and Shepard (1979) found the smallest sexually mature female in Louisiana was 246 mm TL and the smallest male was 196 mm TL. These numbers agree almost exactly with the recent findings of Nieland et al. (2002; Table 8.1). In Texas, Pearson (1929) reported female spotted seatrout attained sexual maturity at 2 or 3 years of age, while males were mature by age 2. Miles (1951) also reported 50% maturity by age 2 for females, at a size of 250 mm TL. Brown-Peterson et al. (1988) found the size at 50% maturity for females to be slightly larger, at 278 mm TL, although the smallest male captured (201 mm TL) had achieved sexual maturity. The size at 50% sexual maturity for females reported 10 years later by Bumguardner et al. (1998; Table 8.1) is virtually identical to the Brown-Peterson et al. (1988) findings. However, aging by Bumguardner et al. (1998) suggests fish of this size are age 1, a difference of 1 or 2 years when compared to Pearson (1929) and Miles (1951). The earlier studies used scales to age the fish, which, for spotted seatrout, have been shown to overestimate ages by 1 or occasionally 2 years when compared to otoliths (Cottrell, 1990). Thus, it appears that the size and age at sexual maturity for spotted seatrout in Texas has remained relatively consistent over the past 70 years.

Information on size or age at maturity for spotted seatrout along the east coast of the U.S. north of Florida is less abundant than similar data from the Gulf of Mexico. Brown (1981) reported that female spotted seatrout from Chesapeake Bay, Virginia, reached 50% sexual maturity between 300 and 350 mm TL, with the smallest mature female reported to be 290 mm TL (Table 8.1). These corresponded to age-2 or age-3 fish, the oldest reported age at first maturity. However, the ages of these fish may be overestimated, as scales were used rather than otoliths. Burns (1993) aged fish using the left saggita and found that both male and female spotted seatrout in North Carolina first mature before age 1, with 70% of females and 90% of males that are mature at age 0 corresponding to sizes < 260 mm FL. By age 2, 100% maturity was found for both sexes.

Wenner et al. (1990) found that all age-1 males and 97% of age-1 females from South Carolina had reached sexual maturity, based on otolith aging. In Georgia, both males and females mature by age 1 and are as small as 263 mm TL; the contribution of age-0 fish to the spawning population is unknown (Lowerre-Barbieri et al., 1999). Regardless of potential aging problems, spotted seatrout in the northern portion of their range in Chesapeake Bay clearly reach sexual maturity at a larger size than those from South Carolina, Georgia, Florida, and the Gulf Coast (Table 8.1). Sampling bias may account for part of this difference due to an underrepresentation of small fish in commercial and recreational catches; however, clinal variation in size at sexual maturity is also suggested (Brown-Peterson and Thomas, 1988). This is not a phenomenon unique to *C. nebulosus* and has been reported in both marine (Parsons, 1993; Peterson-Curtis, 1996; Yamaguchi et al., 2000) and freshwater (Jonsson and Abée-Lund, 1993; Snyder and Peterson, 1999) species of fish.

REPRODUCTIVE CONTRIBUTION OF YOUNG FISH

The potential for small, age-1 fish to become reproductively active during the spawning season has long been acknowledged, but the historical view was that these fish contributed very little to the overall yearly reproductive effort (Moody, 1950; Tabb, 1961; Sundararaj and Suttkus, 1962). These findings may be partially due to inaccurate aging based on scales. Recent research, however, suggests that age-1 females do make an important contribution to the total spawning biomass. Brown-Peterson and Warren (2001) found that 80% of the age-1 females in their sample of Mississippi fish were sexually mature, with 62% of those fish showing evidence of recent or eminent spawning in the form of postovulatory follicles (POFs) or oocytes undergoing final oocyte maturation (FOM). Similarly, 96% of females from Louisiana approaching or at age 1 were sexually mature, and 100% of females ≥ 250 mm TL were mature (Nieland et al., 2002). In Texas, 68% of age-1 females were sexually mature (Bumguardner et al., 1998), although the smallest mature fish in Texas were 270 to 279 mm TL, larger than those from Mississippi and Louisiana. In the Florida Panhandle region, 78 to 100% of females were sexually mature by 290 mm TL, corresponding to age-0 and age-1 fish (DeVries et al., see Chapter 7).

Small spotted seatrout also contribute significantly to the reproductive population along the east coast of Florida in the Indian River Lagoon. Some age-0 females were sexually mature and spawned during their first season, and 27% of age-0 females contained either hydrated oocytes or fresh POFs (Crabtree and Adams, 1998). However, the age-0 fish from the Indian River Lagoon ranged from 237 to 480 mm TL (Crabtree and Adams, 1998), a size range that includes age-1 fish from other studies. In South Carolina, no age-0 fish were sexually mature, although 40% of the actively spawning stock were age-1 females, and this group of fish dominated the spawning stock from June through August (Wenner et al., 1990). In Georgia, young fish dominated the spawning population, as 94% of the female fish collected in spawning condition were age 1 (Lowerre-Barbieri et al., 1999). In South Carolina, the total annual reproductive output by age-1 females was estimated to be 25% of the total spawning population (Roumillat and Brouwer, in preparation). In North Carolina, the population was dominated by age-0 and age-1 fish, of which almost all were sexually mature (Burns, 1993).

Regardless of aging discrepancies among studies, it is clear that recent research has unequivocally shown that small age-0 and age-1 spotted seatrout are important to the overall spawning population. Furthermore, age-0 female spotted seatrout made up from 4 to 11% of the total population in Florida (Murphy and Taylor, 1994), while the percentage of age-1 females varied from 15% in Louisiana (Nieland et al., 2002), to more than 45% in several estuaries in Florida (Murphy and Taylor, 1994), 63% in South Carolina (Wenner et al., 1990), and as high as 73% in Georgia (Lowerre-Barbieri et al., 1999). Thus, the importance of spawning in age-1 fish is considerable when considering the overall age distribution of spotted seatrout populations throughout the southeastern U.S.

SPAWNING

SPAWNING SEASONALITY

Spotted seatrout have an extended spawning season across their range, with spawning occurring throughout the summer in most areas. The wide distribution of the species results in differences in the duration of the spawning season, from 3 months at the northern portion of their range in Chesapeake Bay, Virginia (Brown-Peterson and Thomas, 1988) to year-round at their southern limit in the Bay of Campeche, Mexico (Coto and Argudín, 1991). Table 8.2 summarizes the most current information on spawning seasons for each region.

Various methods have been used to determine the duration of the spawning season. While histological inspection of the ovaries remains the best method for determination of spawning seasonality, use of the gonadosomatic index (GSI) or macroscopic inspection of gonadal development provides a quick and useful reference. However, the reliability of GSI as an accurate indicator of ovarian maturity has been questioned (Jons and Miranda, 1997), and Brown-Peterson and Warren (2001) have shown that GSI is not independent of female body weight in spotted seatrout from Mississippi. Thus, while GSI may be adequate as an indicator of spawning seasonality, it may not be suitable for comparing or predicting maturity classes of fish, even for the same species from different areas (Jons and Miranda, 1997). In any case, the presence of vitellogenic oocytes in the ovary and mature sperm in the testis indicates that fish are reproductively active and probably have the ability to spawn.

Using the presence of larvae to estimate the spawning season is not as accurate as quantifying ovarian development but is often the only information available from an area. Spotted seatrout eggs hatch within 24 hours (Holt et al., 1985) and the larvae grow rapidly. Thus, collections of preflexion

TABLE 8.2
Spawning Seasonality of Spotted Seatrout Throughout Their Range

Region	Season	Method	Reference
Chesapeake Bay, VA	May to July	GSI, histology	Brown, 1981
North Carolina	May to August	GSI	Burns, 1993
South Carolina	late April to early September	GSI, histology	Wenner et al., 1990 Roumillat and Brouwer, in prep.
Georgia	late April to mid-September	GSI, histology	Lowerre-Barbieri et al., 1999
Florida, east coast	April to September	GSI, histology	Crabtree and Adams, 1998
South Florida	February to September and November to December	larval collections	Rutherford et al., 1989
Florida, west coast	mid - March to early October	GSI, histology; larval collections	Brown-Peterson et al., 2002; McMichael and Peters, 1989
Florida, Panhandle	April to August	GSI	DeVries et al., 2002
Mississippi	April to early September	GSI, histology	Brown-Peterson and Warren, 2001
Louisiana	April to September	GSI, histology	Nieland et al., 2002
Texas	April to September	GSI, histology	Brown-Peterson et al., 1988
Campeche, Mexico	Year-round	larval collections	Coto and Argudín, 1991

larvae suggest that spawning has occurred within the past 7 days (Fable et al., 1978) and can be an accurate indicator of the initiation and duration of the spawning season. Indeed, Stewart (1961) estimated a February through November spawning season for spotted seatrout in Everglades National Park, using macroscopic inspection of the gonads and GSI values; Powell et al. (1989) found a January through October season for the same area based on larval collections. However, estimating the beginning of the spawning season from larval collections may also result in inaccurate data. Based on the appearance of larvae and young juveniles in Alabama, Van Hoose (1987) surmised a 4-month spawning season in that area, from June through September (Table 8.2). This seems unrealistically short, considering that spotted seatrout in Mississippi and the Florida Panhandle, areas adjacent to Alabama, begin spawning by April (Table 8.2).

SPAWNING PEAKS

Although spotted seatrout appear to spawn throughout the summer in most of their range, there have been reports of single or bimodal spawning peaks, suggesting times of more intense spawning during the reproductive season. In Texas, Pearson (1929) reported peak spawning in April and May, while Miles (1951) found that peak spawning occurred in July. Both Brown-Peterson et al. (1988) and Colura et al. (1988) found evidence of bimodal spawning peaks in Texas in April through May and in July or August, agreeing with the two previous reports of peak spawning time.

There appears to be consistent evidence for bimodal spawning peaks in Louisiana. Hein and Shepard (1979) first reported a March through September spawning season, with distinct peaks in May and July to August. Wieting (1989) found an April through September spawning season and also reported spawning peaks in May and August. Most recently, Nieland et al. (2002) have confirmed the April through September spawning season and report two spawning peaks: the first in April through May and the second in August. Larval collections from Alabama also suggest two major spawning peaks in that area, one in mid-June or early July and a larger peak in early September (Van Hoose, 1987). However, apparently little evidence exists of bimodality in spawning in Mississippi, which has very similar conditions and spawning habitats to those of Louisiana (Brown-Peterson et al., 2002) and Alabama. Overstreet (1983) reported spawning of spotted seatrout from May through August in Mississippi, with no indication of spawning peaks. More recently, Brown-Peterson and Warren (2001) have extended the Mississippi spawning season to April through August and report peak spawning in May.

The great variety of habitats and temperature ranges along Florida's coast, from warm–temperate in the Panhandle to tropical in Florida Bay, has resulted in a wide array of spawning seasons and peak spawning times. Initial reports of spotted seatrout reproduction from the Indian River Lagoon area of eastern Florida suggested a shortened, mid-April through late July season (Tabb 1961). However, more recent studies have shown an April through September season (Crabtree and Adams, 1998). Indirect confirmation of the spawning season in Indian River Lagoon has been reported by Mok and Gilmore (1993), who documented spotted seatrout drumming sounds commencing in mid-March and extending through their May sampling season. However, in all cases, no distinct spawning peaks have been reported.

In northwest Florida, Klima and Tabb (1959) reported an April through September spawning season, with a peak in late May or early June. DeVries et al. (see Chapter 7) also found peak spawning in May along the Panhandle of Florida but reported an April through August spawning season, although some spotted seatrout in Pensacola Bay remained in reproductive condition through September (DeVries et al., see Chapter 7). Along the west coast of Florida, the spawning season appears to be more extended, from late March through October, as reported by both Moody (1950) and Brown-Peterson et al. (2002). While Moody (1950) found peak spawning in July in the Cedar Key area, spawning appeared to remain relatively consistent throughout the summer in Charlotte Harbor, based on GSI values (Brown-Peterson et al., 2002). However, analysis of larval collections from Tampa Bay by McMichael and Peters (1989) suggested an April through September spawning season, with peaks in May through June and August through September.

Spawning appears to occur nearly year-round in south Florida in Florida Bay and the Everglades National Park. Initial reports by Stewart (1961) of a February through November reproductive season were confirmed by Rutherford et al. (1982), based on observations of gonadal maturation, and by Rutherford et al. (1989) and Powell et al. (1989), based on larval collections. All researchers report an apparent bimodality in spawning in south Florida, with peaks in spring (April or May) and late summer (July, August, or September).

Information on spawning seasons and peak spawning times is much less abundant for the southeastern U.S. In Georgia, the spawning season begins in April, peaks in May, and continues into August (Mahood, 1975; Music and Pafford, 1984), based on macroscopic gonadal observations. More recent investigations confirm the late April through mid-September spawning season in Georgia, based on GSI values, histological samples, and acoustical surveys of spawning aggregations (Lowerre-Barbieri et al., 1999). The spawning season in South Carolina appears to begin in late April and continue until early September, with peak activity in May, based on histological examination of gonads (Wenner et al., 1990; Roumillat and Brouwer, in preparation). Spawning in North Carolina begins in May and extends through August, with an apparent peak in May, based on macroscopic observations and GSI values (Burns, 1993). The northernmost report of spotted seatrout spawning is in Chesapeake Bay, Virginia, where Brown (1981) found a May through July reproductive season, with bimodal peaks in May and July. In general, the spawning season is shorter along the Atlantic Coast than along the GOM, a difference most likely related to the shorter summers and cooler mean water temperatures along the Atlantic coast (Brown-Peterson and Thomas, 1988).

One consequence of an extended spawning season is the production of different cohorts of fish. For instance, fish spawned early in the season (April or May) have the entire summer to grow, resulting in the potential to attain sexual maturity by the beginning of the next reproductive season. In contrast, fish spawned toward the end of the season will not be able to attain sexual maturity by the beginning of the next spawning season but may attain maturity midway through that reproductive season. This later attainment of sexual maturity by a younger and smaller cohort of fish has been suggested as one factor contributing to an apparent late season spawning peak (Brown, 1981; McMichael and Peters, 1989). Wenner et al. (1990) noted that immature age-1 females were found only during April and May in South Carolina and that the contribution of age-1 fish to the spawning stock was 20 to 30% lower during the early portion of the reproductive season. In contrast, Lowerre-Barbieri et al. (1999) noted that, in Georgia, age-1 fish contributed to the spawning population throughout the reproductive season and did not mature later in the reproductive season than older fish.

SPAWNING SITE CHARACTERISTICS

Spotted seatrout encounter a wide variation in physical and chemical characteristics throughout their range, due in part to their tendency to remain within estuaries for their entire life cycle. While information on the temperatures and salinities necessary for spawning has been documented throughout their range, there is less direct evidence regarding actual spawning locations. The earliest reports of spotted seatrout spawning confirmed that the species spawns in bays and lagoons at depths ≤ 5 m (Smith, 1907; Pearson, 1929). However, recent evidence from Florida suggests that some fish may spawn adjacent to barrier islands at the mouth of a pass to the Gulf of Mexico in an area associated with a steep drop-off (S. Lowerre-Barbieri, personal communication). Moody (1950) postulated that spotted seatrout spawn over grassy flats in Florida, and Brown (1981) found running ripe females over grassbeds in Chesapeake Bay, Virginia.

More recent reports have confirmed that spawning in Texas takes place over grassbeds near shallow (2-m) channels, based on capture of spawning individuals (Brown-Peterson et al., 1988) and newly fertilized eggs (Holt et al., 1985). Mok and Gilmore (1983) also found that spotted seatrout in the Indian River Lagoon, Florida, spawned in the Intracoastal Waterway adjacent to seagrass beds, based on male drumming sounds. Further evidence of the importance of a channel to spawning locations was provided by Saucier and Baltz (1992), who identified large drumming aggregations of spotted seatrout near bulkheads adjacent to the Charleston, South Carolina, ship channel. In Louisiana, large drumming aggregations of spotted seatrout were found in passes between barrier islands and in dredged or natural channels in Barataria Bay (Saucier and Baltz, 1993). Thus, the availability of a deeper area within the estuary seems to be important for successful spotted seatrout spawning.

The presence of submerged grassbeds may not be as critical, however, because many spawning areas do not contain grassbeds (i.e., Louisiana, Mississippi, and South Carolina). In the absence of submerged aquatic vegetation, spotted seatrout appear to spawn near rubble or pilings (Saucier and Baltz, 1992), sand and shell reefs (Hein and Shepard, 1979), soft bottoms (Sackett and Hein, 1977; Brown-Peterson and Warren, 2001), or manmade structures such as docks or pilings (Lowerre-Barbieri et al., 1999) A more complete discussion of spotted seatrout spawning habitats can be found in Chapter 11.

The appropriate temperature appears to be crucial to the initiation and cessation of spotted seatrout spawning. Temperatures > 21°C appear to be necessary for successful spotted seatrout spawning in Georgia and Mississippi (Music and Pafford, 1984; Lowerre-Barbieri et al., 1999; Brown-Peterson and Warren, 2001), although McMichael and Peters (1989) have reported the occurrence of larval spotted seatrout at temperatures as low as 17.5°C. Recently, there is evidence of limited spawning at temperatures as low as 19°C in South Carolina, although 75% of the spawning occurred when temperatures were > 25°C (Roumillat and Brouwer, in preparation). Nieland et al. (2002) and Crabtree and Adams (1998) found evidence of spotted seatrout spawning at temperatures > 22°C in Louisiana and Florida, while Brown-Peterson et al. (1988) postulated that temperatures > 23°C were necessary for the initiation of spawning in Texas. Saucier and Baltz (1993) reported that temperatures between 30 and 31°C appeared optimal for spotted seatrout spawning, based on intensity of drumming aggregations. These field observations are higher than the 26 to 28°C reported temperatures for successful spawning of spotted seatrout in captivity (Colura, 1974; Arnold et al., 1978; Wisner et al., 1996). There is less information on the upper temperature limits for successful spawning. Saucier and Baltz (1993) found no spawning aggregations at temperatures > 33°C in Louisiana, while Crabtree and Adams (1998) reported that 34°C appeared to be the upper temperature limit for spawning in Florida. Thus, spotted seatrout appear to have a spawning temperature range from 22 to 34°C.

Spotted seatrout are an estuarine species and can tolerate large fluctuations in salinity. Evidence of spotted seatrout spawning has been reported from salinities of 7 (Saucier and Baltz, 1993) to 37% (Brown-Peterson et al., 1988; Tucker and Faulkner, 1987). Optimal spawning salinities for each area appear to be related to the hydrographic conditions of the area (Holt and Holt, 2002). For example, in freshwater dominated systems, optimal spawning salinities were found to be 15 to 18% (Louisiana; Saucier and Baltz, 1993), and spotted seatrout with ovaries containing postovulatory follicles, indicating successful spawning, have been found at 10% (Mississippi) (Brown-Peterson and Warren, 2001). However, in more marine-dominated systems, spawning was not observed at salinities below 20% (Texas) (Brown-Peterson et al., 1988), 26% (Georgia) (Music and Pafford, 1984), or 28% (Florida) (Tucker and Faulkner, 1987). Low salinity may reduce the fecundity of spotted seatrout (Brown-Peterson et al., 2002) as well as adversely affect the survival of eggs and larvae (Alshuth and Gilmore, 1994). A complete review of the effects of salinity on larval spotted seatrout may be found in Chapter 9.

GONADAL MATURATION AND HISTOLOGY

MALES

Testicular Morphology

The spotted seatrout has a lobular, unrestricted, continuous, spermatogonial testis type, as described by Grier (1981), which has been shown to be typical of higher perciform fishes (Grier, 1993). Spermatocysts containing synchronously developing germ cells surround the perimeter of a series of lobules that end blindly at the periphery of the testis. A main longitudinal duct extends the entire length of the testis, which gives rise to a radial system of efferent ducts from which the lobules extend.

When immature, spotted seatrout testes are small, have an elongate triangular shape with smooth walls, and are translucent white in color. As the testes undergo maturation, the triangular shape becomes more pronounced, the walls remain smooth and firm, and the color becomes bright white. During the reproductive season, the testes rarely account for more than 2% of total body weight, and this percentage declines to ≤ 1% by the end of the spawning season.

Testicular Maturation

There has been little focus on testicular maturation in male spotted seatrout, as most authors have concentrated on the reproductive biology of females. Brown (1981) described maturation classes for spotted seatrout from Chesapeake Bay; Overstreet (1983) discussed testicular development in Mississippi fish; Brown-Peterson et al. (1988) documented the seasonal cycle of spermatogenesis in south Texas; and Brown-Peterson and Warren (2001) have recently described testicular maturation classes for Mississippi male spotted seatrout. Terminology describing the various maturation classes has not been consistent in the literature and has often been more appropriate for the description of female rather than male maturation classes. The recently developed terminology of Grier and Taylor (1998) defines male reproductive classes as they relate to spermatogenesis and changes in the germinal epithelium; this classification system should be used in all future work. This system is particularly good for describing testicular changes in fish with an extended reproductive season and has been used with spotted seatrout (Brown-Peterson and Warren, 2001).

Spermatogenesis is a continuous process in the spotted seatrout testis. Spotted seatrout in the early maturation class (Figure 8.1A) undergo active spermatogenesis throughout the testis, and all stages of spermatogenesis are present. Spermatocysts completely line the walls of lobules throughout the testis, resulting in a continuous germinal epithelium. Primary spermatogonia at the testis periphery indicate growth and elongation of the testis; these spermatogonia are eventually enclosed within a lobule and begin meiosis and development into mature sperm. Spermatogonia are found throughout the testis during early maturation; however, spermatozoa are in the lumen of the lobules and in the ducts, and the fish are capable of spawning in this maturation class. This definition of early maturation is in contrast to previous terms of maturing (Brown 1981), developing (Brown-Peterson et al., 1988), or developing III (Overstreet, 1983), which indicate active spermatogenesis but the lack of mature sperm in the testis.

Spermatogenesis becomes slightly reduced as spotted seatrout enter the mid-maturation class. Testis in mid-maturation (Figure 8.1B) continue to undergo active spermatogenesis, but few primary spermatogonia are present and testis elongation ceases. Secondary spermatogonia can be seen in spermatocysts at the periphery of the testis. A continuous germinal epithelium is still present at the periphery of the testis, but spermatocysts do not completely line the walls of the lobules near the ducts, resulting in a discontinuous germinal epithelium in the proximal portion of the testis. The lumen of lobules near the ducts as well as the ducts are full with mature spermatozoa, indicating spawning. The mid-maturation class is similar to the previously described mature (Brown, 1981; Brown-Peterson et al., 1988) or developing IV (Overstreet, 1983) class, with the exception that fish in the mid-maturation class have sperm in the ducts.

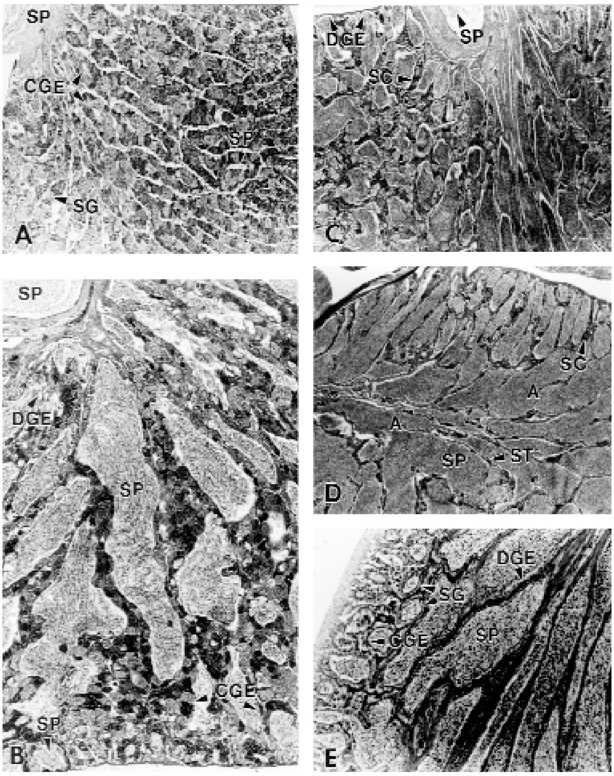

FIGURE 8.1 Histological sections of testicular tissue from spotted seatrout in various maturation classes. A. Early-maturation class; all lobules have a continuous germinal epithelium (53× magnification). B. Mid-maturation class; lobules near the ducts begin to develop a discontinuous germinal epithelium (74× magnification). C. Late-maturation class; all lobules have a discontinuous germinal epithelium, although spermatogenesis is still evident (53× magnification). D. Regression class; spermatogenesis is greatly reduced, and lobules begin to fuse due to an anastomosing network (61× magnification). E. Regressed class; a continuous germinal epithelium of only primary spermatogonia begins to develop in lobules in the periphery of the testis; no spermatogenesis is present in the testis (152× magnification). KEY: SP — spermatozoa; CGE — continuous germinal epithelium; SG — spermatogonia; DGE — discontinuous germinal epithelium; SC — spermatocytes; A — anastomosing lobules; ST — spermatid.

As the testis progresses from the mid-maturation to the late-maturation class, spermatogenesis is noticeably reduced and the primary function of the testis becomes sperm storage. There is a discontinuous germinal epithelium throughout the testis in the late-maturation class (Figure 8.1C), a result of the combination of spermiation from spermatocysts and lack of recruitment of spermatogonia to form new spermatocysts. Spermatogonia are only occasionally seen at the periphery of the testis, and most spermatocysts contain spermatocytes, spermatids, or spermatozoa. Lobular walls begin to thin and fuse, resulting in an anastomosing network of sperm-filled lobules. Spermatozoa are found in the lumina of all lobules and the ducts. The late-maturation class is most similar to the previously used ripe, running ripe, or gravid classes (Brown, 1981; Overstreet, 1983; Brown-Peterson et al., 1988), in that the defining characteristic of the older terms is spermatozoa in the ducts. Historically, spotted seatrout have been considered to be ripe, running ripe, or spawning for the entire reproductive season (Mahood, 1975; Hein and Shepard, 1979; Brown, 1981; Rutherford et al., 1982; Overstreet, 1983; Brown-Peterson et al., 1988), indicating the presence of spermatozoa in the ducts.

The regression class in spotted seatrout is characterized by greatly reduced spermatogenesis in the form of widely scattered spermatocysts containing predominantly spermatids and spermatozoa

(Figure 8.1D). The germinal epithelium is discontinuous throughout the testis, and the anastomosing network of lobules first observed during late maturation becomes more pronounced. There is no evidence of spermatogonia. The major function of the testis during regression is sperm storage, and lobules appear to be partially empty of spermatozoa as this class progresses. Spermatozoa remain in the ducts and the fish continue to spawn as long as there are reproductively active females. Spotted seatrout in the regression class have historically been considered to be spent (Brown, 1981; Overstreet, 1983) or partially spent (Brown-Peterson et al., 1988).

The regressed class in spotted seatrout is characterized by the reappearance of a continuous germinal epithelium consisting exclusively of primary spermatogonia (Figure 8.1E). The defining characteristic of the regressed class is that spermatogonia are the only germ cells present. Some regressed testes may contain residual spermatozoa, including spermatozoa in the ducts, but the fish are probably not spawning. The regressed class is a time of active spermatogonial proliferation, in preparation for the next reproductive season. As the fish first enter the regressed class, primary spermatogonia may only be seen lining the lobules in the peripheral portion of the testis (Figure 8.1E). As the class progresses, all lobules within the testis will become lined with primary spermatogonia; however, spermatocysts are not present. Historically, fish in the regressed class have been classified as recovering (Brown, 1981), resting (Overstreet, 1983), or spent and regressed (Brown-Peterson et al., 1988).

Immature males have testes that are indistinguishable from the regressed class, except that immature males do not have residual spermatozoa. Primary spermatogonia are the only germ cell type present, and they are present in a continuous germinal epithelium throughout the testis. Young-of-the-year fish captured at the end of the reproductive season or during their first winter should be considered immature rather than regressed. However, the small size at maturity for male spotted seatrout can make determinations between immature and regressed fish challenging for males < 240 mm TL.

Seasonality of Maturation

Numerous authors have reported that male spotted seatrout are in reproductive condition earlier than females and remain in reproductive condition longer (Moody, 1950; Tabb, 1961; Hein and Shepard, 1979; Brown, 1981; Brown-Peterson et al., 1988; Brown-Peterson and Warren, 2001). Using the reproductive classes described above, the seasonal maturation of spotted seatrout from Charlotte Harbor, Florida (Figure 8.2A; data from M. Murphy and R. Taylor, Florida Marine Research Institute, St. Petersburg, Florida), shows that males are in potential spawning condition (i.e., spermatozoa in the testis) throughout the year. However, there is a seasonal progression of maturation classes, with fish in the early-maturation class appearing in significant numbers by December, dominating in January and February, and then disappearing by June. The disappearance of the early-maturation class corresponds with the cessation of testicular growth and elongation and the general disappearance of primary spermatogonia. Interestingly, primary spermatogonia also disappeared by June in spotted seatrout from south Texas (Brown-Peterson et al., 1988), a location at a similar latitude to Charlotte Harbor, Florida.

Males in the mid-maturation class were dominant during March and April (Figure 8.2A), the beginning of the spawning season in Charlotte Harbor (Brown-Peterson et al., 2002). There appears to be an increase in males in the mid-maturation class during July and August, corresponding with the brief reappearance of fish in the early-maturation class in July (Figure 8.2A). This may represent recruitment into the spawning population by small, young fish that did not achieve sexual maturity by February or March. This supports the speculation that the observed peaks in GSI may be related to the entry of later-maturing fish into the reproductive population.

Testes in the late-maturation class were first observed in April in Charlotte Harbor, Florida (Figure 8.2A), signifying the slowing of spermatogenesis; males in this class were dominant in May, August, and September. Spermatogenesis appeared to cease in some males by May, with the appearance of the regression class (Figure 8.2A), and the regression class was dominant in June and

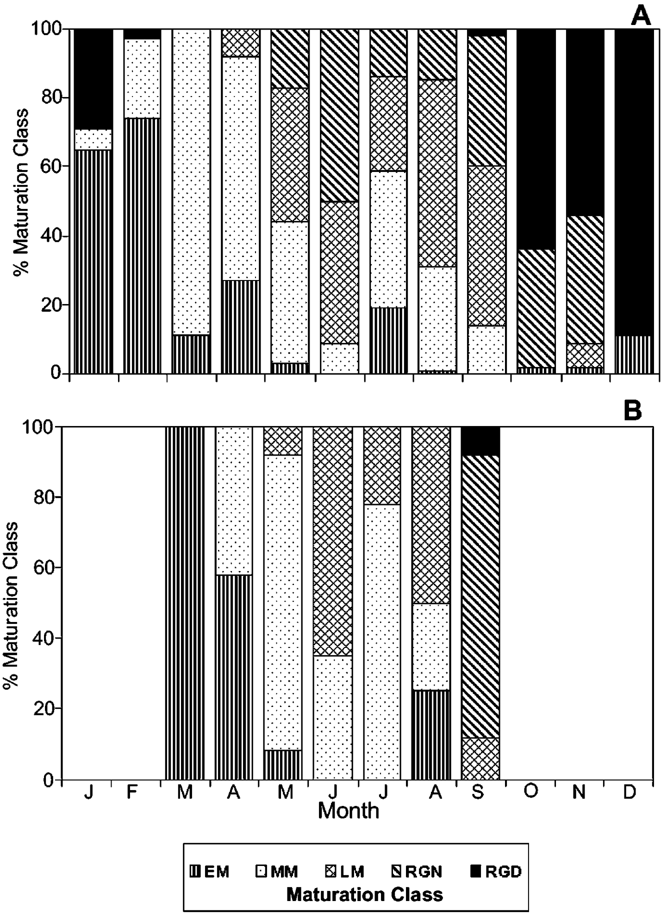

FIGURE 8.2 Monthly occurrence of spotted seatrout male maturation classes, expressed as a percentage of all males. A. Data from Charlotte Harbor, Florida. B. Data from Mississippi Gulf Coast. KEY: EM — early maturation; MM — mid-maturation; LM — late maturation; RGN — regression; RGD — regressed.

September. Spermatogonial proliferation was first observed to recur in September in a few fish in the regressed class, and the regressed class was dominant during October through December as the testis prepared for the subsequent reproductive season. Interpretation of the seasonal cycle of spermatogenesis presented for south Texas males (Brown-Peterson et al., 1988) suggests that fish from that region were also in the regressed class from October through January, based on the presence of only spermatogonia and residual sperm during those months.

The seasonal testicular cycle in Charlotte Harbor, Florida (Figure 8.2A), is similar to that of the Mississippi Gulf Coast (Figure 8.2B; data from Brown-Peterson and Warren, 2001), although the appearance of the mid- and late-maturation classes are delayed by 1 month in Mississippi, no doubt due to cooler water temperatures at the slightly higher latitude. The possibility of a second cohort of young fish recruiting into the spawning population is also evident in Mississippi, with more than 20% of the males in August in the early-maturation class. In Mississippi, males in the regression class did not appear until September, the same time as the first regressed males.

Figure 8.2 shows the importance of a classification system based on spermatogenic stages and the germinal epithelium for species with an extended reproductive season. If traditional classification systems had been used, almost 100% of males from March through September or October would have been classified as ripe or gravid, resulting in a reduced understanding of the dynamics of spermatogenesis in male spotted seatrout. Seasonal changes in the testes of spawning males were previously noted by Brown-Peterson et al. (1988), but the classification system used here clearly shows the dynamics of the reproductive cycle in males. The subtle changes in male reproduction throughout the spawning season can now be correlated more closely with the female cycle.

FEMALES

Ovarian Morphology

The spotted seatrout ovary has two lobes of about equal size suspended by mesentaries that join anterior to the cloaca. The ovarian lobes contain lamellae that project into the central lumen. In immature fish, the ovaries are small, cylindrical, and translucent pink in color, due to a complex network of small capillaries on the surface. As ovarian development occurs, the color changes from pink to yellow and the ovary takes on a granular appearance upon macroscopic inspection. The network of capillaries becomes more pronounced as the ovary increases in size, and a mature ovary can account for 4 to 8% of the total body weight. Immediately prior to spawning, mature oocytes within the ovary hydrate, giving the ovary a translucent, pinkish appearance. Upon hydration, the ovary can account for up to 18% of the total body weight of the fish.

Ovarian Maturation

More attention has been given to ovarian than to testicular maturation in the literature. Various descriptions of ovarian development have been presented (Moody, 1950; Tabb, 1961; Stewart, 1961; Mahood, 1975; Brown, 1981; Overstreet, 1983; Brown-Peterson et al., 1988; Bumguardner et al., 1998; Brown-Peterson and Warren, 2001), resulting in a wide variation of terminology for similar classifications. Additionally, several authors have discussed oocyte stages as they relate to different maturity classes (Brown-Peterson et al., 1988; Wieting, 1989; Crabtree and Adams, 1998; Nieland et al., 2002). Finally, oocyte development appears to be heterogeneous in the ovaries of spotted seatrout, as determined from histological inspections of various portions of the ovary (Overstreet, 1983; Wieting, 1989).

Spotted seatrout in the regressed ovarian class are characterized histologically by having only primary growth oocytes in the ovary (Figure 8.3A). In regressed fish found at the end of the spawning season, some oocytes may also be undergoing gamma or delta atresia. Macroscopically, regressed ovaries are small and pinkish, with obvious capillaries on the surface. They never occupy more than 15% of the body cavity. Differentiating histologically between a regressed female and an immature female can be challenging, as both classes contain only primary growth oocytes. However, the lamellar folds in the immature ovary are closely packed compared to the increased space between the folds in the regressed ovary. Often blood vessels are evident among the lamellae in regressed ovaries — an infrequent occurrence in immature ovaries. Additionally, immature fish do not have atretic oocytes. Macroscopically, immature ovaries are smaller than regressed ovaries and more translucent pink in color; capillaries are less evident on the surface.

Spotted seatrout in the early-maturation class demonstrate the first evidence that ovarian maturation is commencing. Macroscopically, early-maturation ovaries appear less translucent than the regressed ovary, can occupy up to 20% of the body cavity, and may begin to take on a yellow tinge. Histologically, ovaries in early maturation contain oocytes in the cortical alveoli stage (Figure 8.3B), which is distinguished by a larger size and less basophilic staining than the primary growth oocytes. Numerous yolk vesicles appear in the cytoplasm (Wallace and Selman, 1981) in the form of small, colorless spheres, giving the oocyte a speckled appearance. The nucleoli move to the periphery of the nucleus. Ovaries in the early-maturation class are committed to continue development through final maturation and spawning. Oocytes that do not progress through normal development will undergo atresia because cortical alveoli oocytes cannot overwinter and must mature during the current reproductive season.

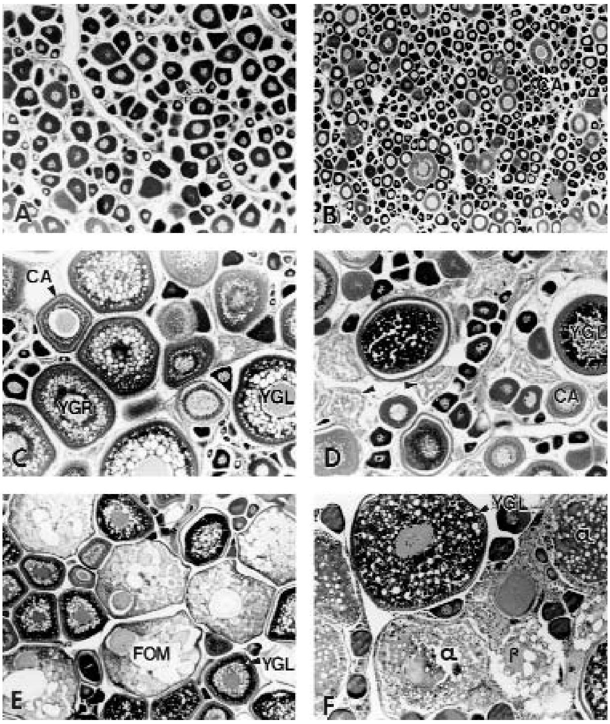

FIGURE 8.3 Histological sections of ovarian tissue from spotted seatrout in various maturation classes. A. Regressed class; only primary oocytes occur (116× magnification). B. Early-maturation class; cortical alveolar oocytes begin to develop (50× magnification). C. Mid-maturation class; vitellogenesis begins, and yolk granule and yolk globule oocytes are present. As this class proceeds to late maturation, yolk globular oocytes predominate (120× magnification). D. Late-maturation class, post-spawning; many 24-h postovulatory follicles (POF; arrows) are present, indicating recent spawning activity (124× magnification). E. FOM class; the yolk coalescence stage of final oocyte maturation (FOM). Not all yolk globule oocytes undergo FOM (124× magnification). F. Regression class; at the beginning of this class, not all yolk globule oocytes undergo atresia (128× magnification). KEY: CA — cortical alveolar oocyte; YGR — yolk granule oocyte; YGL — yolk globular oocyte; FOM — oocyte undergoing final oocyte maturation; α—oocyte undergoing α-stage atresia; ß — oocyte undergoing ß-stage atresia.

Ovaries in the mid-maturation class have begun to undergo vitellogenesis. Macroscopically, these ovaries have a noticeable yellow coloration and can occupy up to 30% of the body cavity. However, the granular-appearance characteristic of the late-maturation class is not evident. Upon histological inspection, the predominant type of oocyte in the mid-maturation class is the yolk granule oocyte (see Figure 8.3C). Yolk granule oocytes have begun to sequester vitellogenin and have numerous small, acidophilic spheres of yolk in the cytoplasm. Yolk deposition appears to occur initially in the cytoplasm toward the perimeter of the oocyte. Many cortical alveoli oocytes are still present during mid-maturation, as well as several advanced, yolk globule oocytes (Figure 8.3C). Yolk globule oocytes may be distinguished from yolk granule oocytes by their larger size and the presence of large, acidophilic spheres of yolk interspersed with lipid droplets in the cytoplasm.

Ovaries in the late-maturation class are fully developed and can occupy up to 75% of the body cavity. Macroscopically, the ovaries are often bright yellow, with pronounced capillaries on the surface and a granular appearance due to the large number of vitellogenic oocytes. Fresh ovarian tissue is generally firm but can be slightly flaccid if the fish has spawned within the past 24 h. Only females in this maturation class are capable of spawning; this is the most common maturation class during the reproductive season. Late-maturation ovaries are characterized histologically by a large number of fully grown yolk globule oocytes. However, all other oocyte stages are also present in the late-maturation ovary. Oocytes in various stages of atresia are common in this class, although the percentage of atretic oocytes is always < 6%.

Evidence of previous spawns is often seen in late-maturation ovaries in the form of post-ovulatory follicles (POFs; Figure 8.3D), which are similar to those described by Hunter and Macewicz (1985). The number of POFs visible in an ovarian section can vary greatly, but POFs within a single ovary are always in the same stage. The presence of 12- or 24-h POFs indicates that the fish has spawned within the previous 24 h. Due to rapid degeneration in the warm waters inhabited by spotted seatrout during the spawning season, 48-h POFs are often indistinguishable from gamma- or delta-stage atresia and thus cannot be used as an accurate indication of previous spawning. Recent documentation of spotted seatrout POF degeneration in warm (> 25°C) water suggests that accurate identification of POFs older than 38 h is difficult (Roumillat and Brouwer, in preparation).

Spotted seatrout ovaries in the FOM class include those with oocytes undergoing final oocyte maturation (FOM; Figure 8.3E) as well as fully hydrated and ovulated ovaries. Macroscopically, fully hydrated ovaries can occupy up to 95% of the body cavity and have a pinkish, mottled appearance; individual oocytes can be seen through the ovarian epithelium. Ovaries with oocytes undergoing FOM occupy up to 75% of the body cavity, with firm ovarian tissue, but they are often macroscopically indistinguishable from late-maturation ovaries. While hydrated oocytes or oocytes undergoing FOM are the distinguishing histological characteristic of the FOM class, the ovaries also contain oocytes in all other stages, from primary growth through the vitellogenic stage. Throughout the reproductive season, ovaries cycle continuously from the late-maturation to the FOM class and back again as batches of vitellogenic oocytes undergo final maturation and spawning.

The regresson class in spotted seatrout is a transient class, occurring only when the individual fish has finished spawning for that season. Fish in the middle of the reproductive season that have spawned but still contain numerous vitellogenic oocytes have been considered to be partially spent (Brown-Peterson et al., 1988), but this is not an accurate term due to the cyclic nature of the ovary during the reproductive season. Macroscopically, ovaries in the regression class appear flaccid, although they can still occupy up to 85% of the body cavity. The yellow coloration characteristic of the mid- and late-maturation classes has faded, but the capillaries on the surface remain prominent. Histologically, regression-class ovaries are characterized by a large percentage of oocytes undergoing all stages of atresia (Figure 8.3F). Oocytes in the cortical alveoli and vitellogenesis stages are still present in the regression class but in greatly reduced numbers; the majority of oocytes of these types are undergoing some stage of atresia.

There may be evidence of POF in the regression class. An abrupt decrease in temperature results in a cessation in spawning (Tucker and Faulkner, 1987; Brown-Peterson et al., 1988) and may initiate atresia, resulting in ovaries that appear to be in the regression class. However, it has also been postulated that a decrease in photoperiod at the end of the spawning season signals the cessation of spawning and the appearance of ovaries in the regression class (Hein and Shepard, 1979; Tucker and Faulkner, 1987; Brown-Peterson et al., 1988).

The asynchronous oocyte development of spotted seatrout is shown in Figure 8.4 (from Brown-Peterson et al., 1988) and further confirms the multiple spawning nature seen from histological sections (Figure 8.3). Distribution of oocytes is continuous, and the ovaries of a single female commonly contain oocytes in the primary growth, cortical alveoli, and vitellogenesis stages, as defined by Wallace and Selman (1981). A distinct batch of oocytes becomes obvious only during the FOM maturation class, when some vitellogenic oocytes begin FOM and become hydrated (Figure 8.4). However, even in the FOM class, a substantial number of large vitellogenic oocytes remain in the ovary, in preparation for the next spawning event.

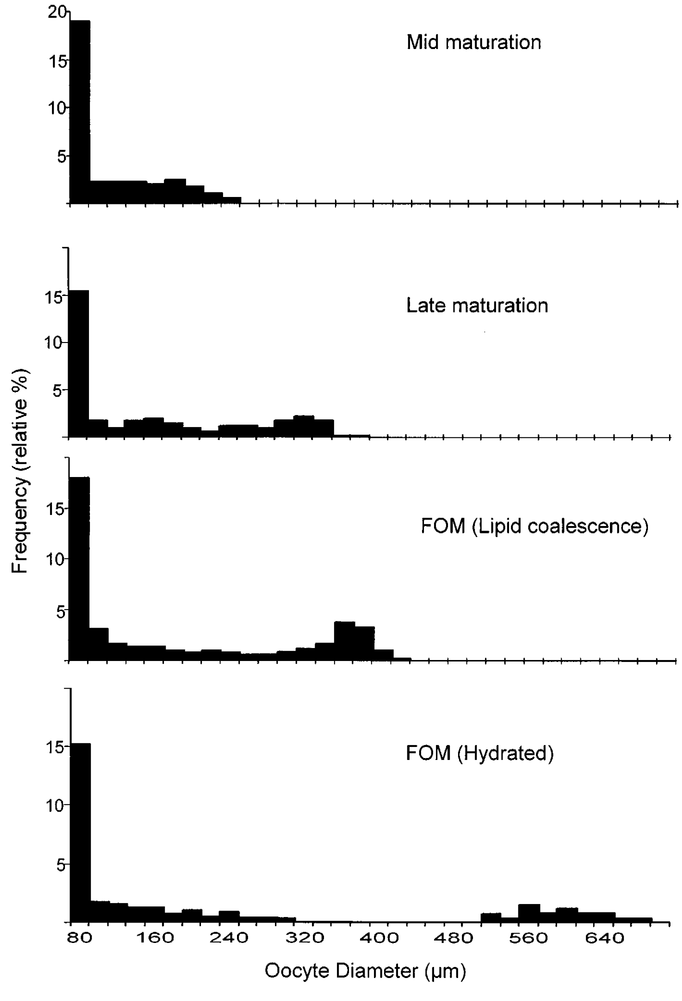

FIGURE 8.4 Oocyte distribution in the ovaries of spotted seatrout in four maturation classes. A distinct mode of oocytes is not observed until a group of oocytes undergoes final oocyte maturation (FOM) at a diameter > 350 µm. Oocyte diameters are based on oocytes preserved in Gilson's fixative.

Final Oocyte Maturation (FOM) and Timing of Spawning

Final oocyte maturation is a highly synchronous process in spotted seatrout (Brown-Peterson et al., 1988), occurring when a batch of fully grown vitellogenic oocytes (> 350 µm when preserved in Gilson's solution; Brown-Peterson et al., 1988, or > 450 µm when fresh; Colura et al.,1988) receives the appropriate hormonal stimulation. In spotted seatrout, the first evidence of FOM is the beginning of lipid coalescence. The lipid droplets move toward the center of the oocyte and begin to coalesce into one or two large droplets. This process can be seen in both histological sections as well as in cleared preparations of whole oocytes (Figure 8.5A). Immersion of fresh ovarian tissue into a 6:3:1 (ethanol:formalin:glacial acetic acid) clearing solution for 2 min clears the cytoplasm and allows easy and rapid identification of the FOM process (Brown-Peterson et al., 1988).

The next stage of FOM in spotted seatrout oocytes is germinal vesicle migration (GVM; Figure 8.5B), when the nucleus moves from the center of the oocyte toward the animal pole. Concurrent with GVM is the beginning of yolk coalescence, when the yolk globules lose their integrity and the oocyte appears to become filled with fluid yolk, a stage best seen in histological preparations

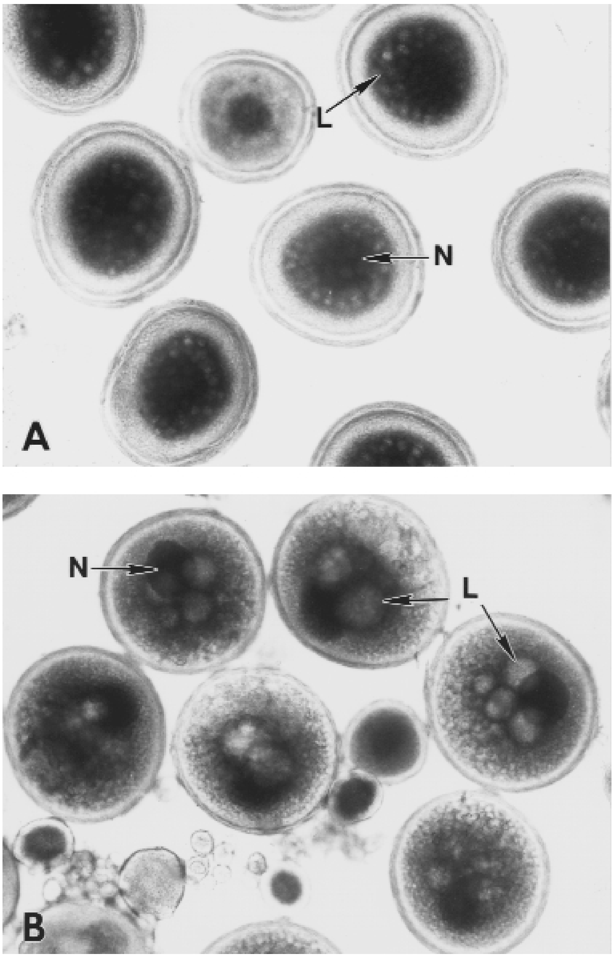

FIGURE 8.5 Cleared oocytes from spotted seatrout undergoing final oocyte maturation (FOM). A. Lipid coalescence stage of FOM; the nucleus remains in the center of the oocyte and the lipids begin to form several large lipid droplets (7× magnification). B. Germinal vesicle migration stage of FOM; the lipids have coalesced into several large droplets and the nucleus begins to move toward the side of the oocyte (7× magnification). KEY: L — lipid; N — nucleus.

(Figure 8.3E). The last stage of FOM is actual hydration, which results in a doubling in size of the oocyte to 1 mm (Holt et al., 1985) due to uptake of fluids. Ovulation occurs fairly soon after hydration, usually within 4 to 6 h.

In spotted seatrout, FOM is completed within 14 h. Brown-Peterson et al. (1988) reported that, in south Texas, lipid coalescence began at dawn (0545 h), hydration occurred by mid-afternoon (1430 h), and ovulation and spawning commenced at dusk (1930 h). Crabtree and Adams (1998) found that spotted seatrout in Indian River Lagoon, Florida, completed the final stages of oocyte maturation in 6 to 8 h, with lipid coalescence occurring at 1200 h and hydration complete by 1800 h. In Mississippi, lipid coalescence begins by 0800 h (personal observations), suggesting possible slight regional differences in the initiation of FOM. Regardless of when FOM actually begins, spotted seatrout in all areas spawn at dusk. The evening spawning activity has been confirmed by the collection of running ripe females (Brown-Peterson et al., 1988; Crabtree and Adams, 1998) and of newly fertilized eggs on the spawning grounds (Holt et al., 1985) as well as the intensity of male drumming on the spawning grounds (Mok and Gilmore, 1983; Saucier and Baltz, 1992; 1993). Spawning at dusk is a strategy common to all sciaenids and has been reported for a variety of species in the southeastern U.S. (*Bairdiella chrysoura*, Mok and Gilmore, 1983, Holt et al., 1985; *Pogonias cromis*, Mok and Gilmore, 1983, Saucier and Baltz, 1993; *C. regalis*, Taylor and Villoso, 1994; *Sciaenops ocellatus*, Holt et al., 1985)

Seasonality of Ovarian Maturation

Ovarian maturation closely mirrors the GSI profile for spotted seatrout, and the duration of the reproductive season varies with region. In subtropical south Texas, a small percentage of females began early ovarian maturation in January, and by February almost 50% of females were in the early- or mid-developing maturation classes (Figure 8.6A; from Brown-Peterson et al., 1988). Females in the late-maturation class first appeared in March and were the predominant class from April through September. Fish in the FOM class occurred from April through September, providing histological verification of the 6-month spawning season in south Texas (Figure 8.6A). A small percentage of females were regressed in September, and this class was dominant from October through February.

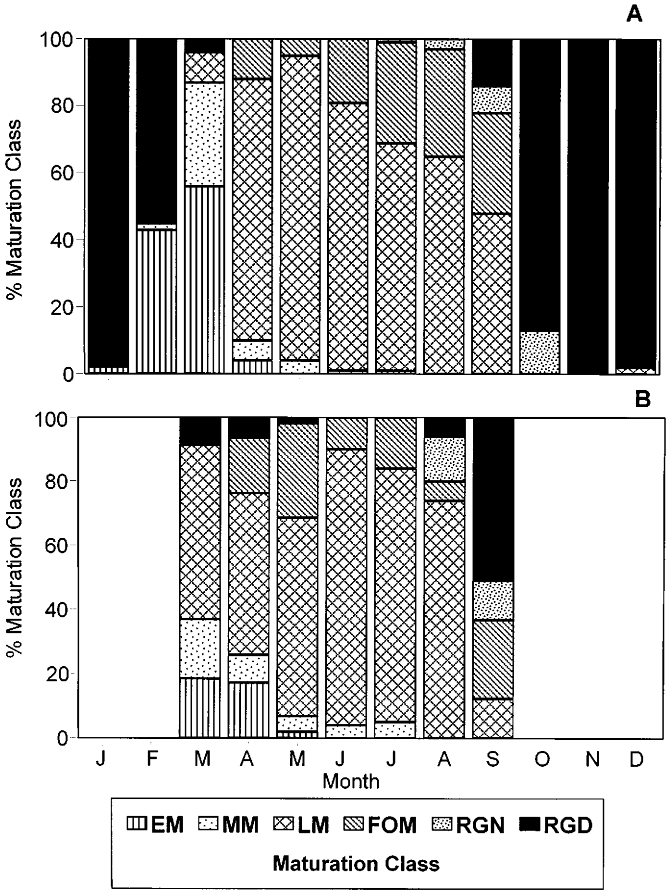

FIGURE 8.6 Monthly occurrence of spotted seatrout female maturation classes, expressed as a percentage of all females. A. Data from Redfish Bay, Texas. B. Data from Mississippi Gulf Coast. KEY: EM — early maturation; MM — mid-maturation; LM — late maturation; FOM — final oocyte maturation; RGN — regression; RGD — regressed.

The seasonal ovarian maturation pattern is similar in warm–temperate areas such as Mississippi (Figure 8.6B; from Brown-Peterson and Warren, 2001), with fish in the FOM class occurring from April through September. While females in the late-maturation class were also present in Mississippi from March through September, the percentage was lower in September than that in south Texas (Figure 8.6). Additionally, regressed fish appeared earlier in Mississippi (August), and some regressed fish were still evident in May. Overall, 90% or more of the females were in reproductive condition (late maturation or FOM) from April through September in south Texas (a subtropical area) and from May through August in Mississippi (a warm–temperate area; Figure 8.6).

REPRODUCTIVE PHYSIOLOGY

MALES

The majority of information on the reproductive physiology of spotted seatrout relates to ovarian maturation and FOM. However, there is a seasonal cycle of testosterone and 11-ketotesterone in the plasma of male spotted seatrout. Both testosterone and 11-ketotestosterone were elevated in April, at the beginning of the reproductive season in south Texas, and declined to low levels concurrent with the cessation of spawning in October (Thomas et al., 1982). This indicates that testosterone and 11-ketotesterone may be important in spring while the testis undergoes active spermatogenesis. By midsummer, when spermatogenesis is minimal, circulating levels of androgens decrease.

More recent work has shown the presence of a plasma sex steroid-binding protein in males that has an affinity for testosterone but not for 11-ketotestosterone (Laidley and Thomas, 1995). However, it is unclear if plasma steroid-binding protein levels are related to the seasonal testicular cycle, although neither the overall mean binding capacity nor the mean binding affinity of male steroid-binding protein was significantly different from that of females (Laidley and Thomas, 1997), in which a distinct seasonal sex steroid-binding protein cycle occurs.

FEMALES

Endocrine Relationships to Ovarian Recrudescence

Endocrine regulation of reproduction in female spotted seatrout can be divided into two phases: 1) ovarian maturation and oocyte growth and 2) final maturation and hydration of the oocytes. The first evidence of endocrine involvement, occurring during the early-maturation class, is an initial increase in steroid-binding protein concentration in the plasma. This increase coincided with an increased number of cortical alveolar stage oocytes prior to an increase in ovarian steroid secretion (Laidley and Thomas, 1997). Since cortical alveolar oocytes are the first gonadotropin-dependent oocyte stage (Tyler and Sumpter, 1996), steroid-binding protein may also be regulated by gonadotropin in spotted seatrout. Plasma steroid-binding protein levels increased about 50% during ovarian maturation, mirroring the increases in GSI and plasma estradiol; they appear to play a critical role in the reproductive physiology of spotted seatrout (Laidley and Thomas, 1997).

All female spotted seatrout have circulating levels of vitellogenin in their plasma, which varies from low microgram amounts in immature fish to milligram amounts in females in the late-maturation class (Copeland and Thomas, 1988). Vitellogenesis in spotted seatrout is regulated primarily by estradiol-17ß (Thomas et al., 1993). A significant increase in plasma estradiol occurs as oocytes enter the early vitellogenic stage (Laidley and Thomas, 1997), which corresponds to the mid-maturation class when oocytes begin to actively sequester vitellogenin. Estradiol levels remain elevated as spotted seatrout enter the late-maturation class at the beginning of the reproductive season but decline as the spawning season progresses (Smith and Thomas, 1991). Hepatic estrogen receptor concentrations paralleled changes in plasma estradiol titers, although the decline in receptor concentration lagged behind the decline in plasma estradiol (Smith and Thomas, 1991). In contrast, vitellogenin levels remained high in fish in the late-maturation class throughout the reproductive season (Copeland and Thomas, 1988). Since spotted seatrout are a multiple-spawning species with continuous recruitment of oocytes into vitellogenesis during the reproductive season, continuously high levels of vitellogenin in the plasma are necessary for the production of multiple batches of oocytes.

Endocrine Contributions to Final Oocyte Maturation

Endocrine regulation of FOM, hydration, and ovulation in spotted seatrout has been extensively studied in the past decade. The initial report that 17α,20ß,1-trihydroxy-4-pregnen-3-one (20ß-S) is the primary maturation-inducing steroid (MIS) in spotted seatrout (Thomas and Trant, 1989) was quickly followed by the discovery of membrane receptors in the ovary of spotted seatrout for this MIS (Patino and Thomas, 1990). Plasma levels of 20ß-S peak during the 14-h period of FOM (Thomas et al., 2001) and return to basal levels following ovulation. In addition to the induction of the lipid coalescence and germinal vesicle migration phases of FOM through an MIS membrane receptor, the MIS also induces oocyte hydration and ovulation through a nuclear receptor (Pinter and Thomas, 1995). However, before the maturation-inducing steroid can initiate FOM, a dramatic upregulation and synthesis of the MIS receptors in the ovary take place. While concentrations of the maturation-inducing steroid receptor begin to increase during ovarian recrudescence, they increase threefold to fourfold during FOM, with a decrease following ovulation (Thomas et al., 2001). If the MIS receptor is not present in sufficient concentration, the oocyte will not be competent to undergo FOM; thus, maturation-inducing steroid receptor abundance is critical for the regulatory onset of FOM (Thomas et al., 2001). An initial release of leutenizing hormone (LH, or gonadotropin II) induces the increase in maturation-inducing steroid receptors (Thomas et al., 2001) as well as initiates the synthesis of 20ß-S (Thomas et al., 1993). The increase in maturation-inducing steroid receptor concentrations during FOM is regulated by gonadotropin, which is significantly elevated in the plasma during FOM (Thomas et al., 2001).

Pinter and Thomas (1995) have proposed a model for the final stages of ovarian development in spotted seatrout. Once vitellogenesis is complete and spawning conditions are appropriate, LH is released from the pituitary and upregulates the maturation-inducing steroid receptors to induce maturational competence. Subsequently, LH induces 20ß-S synthesis. The 20ß-S acts via three pathways: 1) binding to the maturation-inducing steroid membrane receptor to initiate FOM; 2) binding to the maturation-inducing steroid nuclear receptor to initiate oocyte hydration; and 3) inducing ovulation via genomic mechanisms. In addition to the endocrine actions outlined here, RNA synthesis, protein synthesis, cAMP regulation, and Na^+/K^+-ATPase are also crucial during the final maturation process (Pinter and Thomas, 1995; Thomas et al., 2001).

BATCH FECUNDITY

DEFINITIONS AND METHODS

In multiple-spawning fishes with asynchronous oocyte development, the only accurate measurement of fecundity is batch fecundity, or the number of eggs released in a single spawning event. The annual fecundity of a female is determined by multiplying the batch fecundity by the number of times an individual fish spawns during the reproductive season. The relative batch fecundity is expressed as the number of eggs per gram of ovary-free body weight and can be used to compare fecundity values of fish of different sizes, or between fish from different regions, as it removes the confounding influence of size from fecundity estimates.

Batch fecundity estimates are usually made from a small sample of oocytes taken from one portion of the ovary, since oocyte development is homogeneous throughout the spotted seatrout ovary (Overstreet, 1983; Wieting, 1989). This is supported by findings of no significant difference in batch fecundity in different ovarian sections or between the left and right ovaries (Lowerre-Barbieri et al., 1999). However, recent data indicate a significant difference in batch fecundity determinations from six different regions of the same ovary and between the left and right ovary of the same individual (Nieland et al., 2002). Thus, batch fecundity determinations taken from a single location in the ovary may not accurately reflect the true fecundity of the individual and may help explain the large variations in batch fecundities typically seen among individuals (Brown-Peterson et al., 1988; Crabtree and Adams, 1998; Bumguardner et al., 1998; Brown-Peterson and Warren, 2001).

Accurate determinations of batch fecundity necessitate the identification and enumeration of only oocytes that will be released during the upcoming spawning event rather than all the vitellogenic oocytes in the ovary. Early estimates of spotted seatrout fecundity relied on counts of all the vitellogenic oocytes in the ovary (Pearson, 1929; Moody, 1950; Sundararaj and Suttkus, 1962) or all oocytes > 30 μm (Overstreet, 1983), resulting in an overestimation of batch fecundity. However, using these initial, inaccurate estimates, the reported fecundity of spotted seatrout ranged from 81,732 to 1,144,492 (Overstreet, 1983, and Sundararaj and Suttkus, 1962, respectively).

Traditionally, the number of hydrated oocytes in the ovary of spotted seatrout has been used to provide the most accurate estimates of batch fecundity (Brown-Peterson et al., 1988; Crabtree and Adams, 1998; Bumguardner et al., 1998; Lowerre-Barbieri et al., 1999; Nieland et al., 2002). However, in instances when females with hydrated oocytes are not available, accurate fecundity measurements can be made from fish undergoing FOM, as suggested by Hunter and Macewicz (1985). FOM is a rapid process in spotted seatrout (Brown-Peterson et al., 1988); only oocytes of a certain size that form a distinct mode (see Figure 8.4) are competent to undergo FOM (Colura et al., 1988; Thomas et al., 2001). While estimating batch fecundity from fish undergoing FOM may result in a slight overestimation when compared to the hydrated oocyte method, the inherent variability in fecundity estimations among individuals overshadows any differences between the FOM and the hydrated oocyte methods.

BATCH FECUNDITY AND FISH SIZE

The batch fecundity of spotted seatrout increases with increasing size and age of the fish. This relationship was first reported by Pearson (1929), who estimated that a 620-mm TL female had 690,000 more eggs than a 480-mm TL female. Sundararaj and Suttkus (1962) also showed a dramatic increase in fecundity from age-1 fish (283 mm TL; 140,485 eggs) to age-4 fish (504 mm TL; 1,144,492 eggs) in Louisiana. Although neither of these fecundity estimates was a true batch fecundity count, it was clear that bigger fish produced more eggs.

More recently, a significant, positive relationship between batch fecundity and fish size has been reported for spotted seatrout in a number of areas (Table 8.3). In Georgia, Mississippi, and Louisiana, fish length was the best predictor of batch fecundity (Lowerre-Barbieri et al., 1999; Brown-Peterson and Warren, 2001; Nieland et al., 2002), whereas in South Carolina, Texas, and Florida, body weight was a better predictor of batch fecundity (Roumillat and Brouwer, in preparation; Brown-Peterson et al., 1988; Crabtree and Adams, 1998). However, in all cases, fish size accounts for only some of the variation in batch fecundity (see r^2 values, Table 8.3). The best relationship reported to date is from the Indian River Lagoon, Florida, area, where ovary-free body weight explained 76% of the variation in batch fecundity (Crabtree and Adams, 1998). In contrast, SL explained only 25% of the variation in batch fecundity in Mississippi spotted seatrout (Brown-Peterson and Warren, 2001), although the regression was highly significant.

Batch fecundity counts vary widely even among similar-sized fish, which accounts for the low regression coefficients reported in all areas. Low r^2 values are a common occurrence in other multiple spawning sciaenids (Fitzhugh et al., 1993; Nieland and Wilson, 1993; Wilson and Nieland, 1994; Lowerre-Barbieri et al., 1996b; Macchi, 1998); no doubt they represent variation between successive spawns in individual fish, as a female is unlikely to spawn the same number of eggs in each batch. The number of eggs produced by captive female spotted seatrout varies among spawns (Wisner et al., 1996), suggesting that the observed variation in batch fecundity among wild fish is a normal phenomenon.

TABLE 8.3
Batch Fecundity–Body Size Relationships for Spotted Seatrout in Various Regions throughout Their Range

Region	Regression Equation	P	r^2	N	Reference
South Carolina	logBF = 3.134(log TL) to 2.653	–	0.69	134	Roumillat and Brouwer, in prep.
	logBF = 0.993(log WT) + 2.691	–	0.70	134	
Georgia	BF = 2179(TL) to 470,782	< 0.0001	0.52	41	Lowerre-Barbieri et al., 1999
	BF = 692.4(OFBW) + 11,882	< 0.0001	0.50	42	
Florida, east coast	BF = 1531(TL) to 416,965	< 0.05	0.631	82	Crabtree and Adams, 1998
	BF = 307.8(OFBW) + 5,663	< 0.05	0.761	82	
	BF = 45,585(AGE) + 120,788	< 0.05	0.13	81	
Mississippi	BF = 554.2(SL) to 88,398[a]	< 0.001	0.25	51	Brown-Peterson and Warren, 2001[a]
	BF = 78.07(OFBW) + 50,840[b]	< 0.001	0.22	51	Brown-Peterson and Warren, unpublished data[b]
	BF = 34,136(AGE) + 31,827[b]	0.013	0.12	51	
Louisiana	logBF = 3.77(logTL) to 23.65[c]	< 0.0001	0.39	52	Wieting,1989[c]
	logBF = 1.26(logWT) to 9.13[c]	< 0.0001	0.42	52	Nieland et al., 2002[d]
	logBF = 1.91(logAGE) to 2.14[c]	< 0.0001	0.36	52	
	BF = 1546(TL) to 386,168[d]	< 0.0001	0.55	25	
	BF = 249.6(OFBW) + 86,730[d]	0.0008	0.39	25	
	BF = 48,459(AGE) + 129,646[d]	0.16	0.08	25	
Texas	BF = 496(OFBW) to 56,066	0.001	0.56	32	Brown-Peterson et al., 1988

Note: BF — batch fecundity; OFBW — ovary, free body weight; WT — total body weight.

Superscript letters refer to references.

Batch fecundity varies even more with age than it does with fish size. Although spotted seatrout in Florida and Mississippi have a significant, positive relationship between batch fecundity and age (Table 8.3), age explains < 14% of the variation in batch fecundity (Crabteee and Adams, 1998; Brown-Peterson and Warren, 2001). In Louisiana, batch fecundity could not be predicted by age (Nieland et al., 2002). The greater variation in batch fecundity by age is not unexpected because of the large size range in each year class, a result of the extended spawning season. Thus, estimating batch fecundity and ultimately annual fecundity, based on the age structure of a population is not advisable.

BATCH FECUNDITY ESTIMATES

Batch fecundity estimates based on hydrated oocytes or oocytes undergoing FOM are available for six areas within the southeastern U.S. (Table 8.4). Reported batch fecundities range from 7,493 eggs/female (Crabtree and Adams, 1998) to 1,698,000 eggs/female (Wieting, 1989), with the largest variation reported from Louisiana (Wieting, 1989). However, since batch fecundity varies with size, fecundity comparisons among regions are best made using relative fecundity, which adjusts for body size. While no significant relationship existed between relative fecundity and fish length in Florida (Crabtree and Adams, 1998), Brown-Peterson and Warren (2001) found a significant, though not very predictive ($r^2 = 0.081$), relationship in Mississippi. The relationship between the two variables has not been tested in other regions.

In most regions, relative fecundity appears to vary between 300 and 400 eggs/g ovary-free body weight (Table 8.4). Brown-Peterson and Warren (2001) suggested that the low relative fecundity values reported for Mississippi fish may be related to more stressful environmental conditions, particularly the consistently low salinity in the region (Brown-Peterson et al., 2002). The high relative batch fecundity values from Texas reported by Bumguardner et al. (1998) may be an overestimation due to the histological technique used. Other reports of relative fecundity of spotted seatrout from Texas (467 ± 60 eggs/g ovary-free body weight, Colura et al., 1988, and 465 eggs/g ovary-free body weight, Bumguardner et al. 2001) are more similar to the value reported by Brown-Peterson et al. (451 ± 43 eggs/g ovary-free body weight; 1988) and probably represent a closer approximation to the true relative fecundity value for Texas.

Relative fecundity does not vary by month throughout the reproductive season in Florida (Crabtree and Adams, 1998), Texas (Brown-Peterson et al., 1988; Colura et al., 1988), or Louisiana (Wieting, 1989). In Mississippi, relative fecundity was lowest in August at the end of the reproductive season, but there were no other significant monthly differences (Brown-Peterson and Warren, 2001). Thus, while batch fecundity does vary among individuals, the overall mean reproductive effort appears to remain relatively consistent throughout the extended spawning season. Therefore, the observed seasonal peaks in GSI or larval abundance in various regions cannot be explained by seasonal increases or decreases in the relative batch fecundity.

SPAWNING FREQUENCY

METHODS OF DETERMINATION

Determination of spawning frequency in multiple-spawning species is crucial for realistic estimates of total annual fecundity. Spawning frequencies for spotted seatrout have been determined following the method of Hunter and Macewicz (1985), in which the percentage of fish in the total catch that have recently spawned is calculated and then divided by 100 to determine the number of days between spawns. Traditionally, the percentage of fish with 24-h POFs is used as an estimate of recent spawning activity and has been successfully used for spotted seatrout (Brown-Peterson et al., 1988; Crabtree and Adams, 1998; Bumguardner et al., 1998; Lowerre-Barbieri et al., 1999; Brown-Peterson et al., 2002; Nieland et al., 2002). However, POFs degenerate rapidly in spotted seatrout,

TABLE 8.4
Fecundity Estimates of Spotted Seatrout throughout Their Range

Region	Batch Fecundity	Length Range (mm TL)	Relative Batch Fecundity (0 ± S.E.)	Annual Fecundity	Reference
South Carolina	12,000 to 1,150,000	263 to 537	—	3.3 to 17.6 million	Roumillat and Brouwer, in prep.
Georgia	55,640 to 417,394	228 to 490	—	3.6 to 8.5 million	Lowerre-Barbieri et al., 1999
Florida, east coast	7,493 to 797,515	250 to 650	319 ± 10	7 to 52 million	Crabtree and Adams, 1998
Mississippi	12,633 to 354,000	361 to 588	166 ± 14	3 to 7 million	Brown-Peterson and Warren, 2001
Louisiana	28,000 to 1,689,000[a] 102,000 to 512,000[b]	275 to 463[a] 341 to 550[b,c]	— 397 ± 26[c]	0.03 to 16.9 million[a] 9 to 11 million[b]	Wieting, 1989[a] Nieland et al., 2002[b] Brown-Peterson et al., 2001[c]
Texas	178,434 to 647,434[d] 330,198 ± 12, 133[e]	386 to 553[d] 280 to 389[e]	451 ± 43[d] 1185 ± 40[e]	> 10 million[d] 4.6 million[e]	Brown-Peterson et al., 1988[d] Bumguardner et al., 1998[e]

Note: Superscript letters refer to references.

becoming difficult to distinguish from atretic oocytes after 24 h (Crabtree and Adams, 1998). Thus, only POFs ≤ 24 h should be used for spawning frequency determinations. Fish caught in the early morning have 12- to 24-h POFs that are easily distinguishable (see Figure 8.3E), making this an ideal time of capture for histological assessment of spawning frequency.

Spawning-frequency estimates have also been made for spotted seatrout using other methods. The calculation of the percentage of fish undergoing FOM, representing fish about to spawn, is also a reliable method to estimate spawning frequency, since FOM is completed in spotted seatrout within 8 to 10 h (Brown-Peterson et al., 1988; Crabtree and Adams, 1998). This method has been successfully used by several authors (Brown-Peterson et al., 1988; Brown-Peterson and Warren, 2002; Brown-Peterson et al., 2001; Nieland et al., 2002). A method similar to the FOM method is to look at the percentage of females with viable hydrated oocytes, just before or just after ovulation (Brown-Peterson et al., 1988; Crabtree and Adams, 1998; Lowerre-Barbieri et al., 1999).

Comparisons among the three methods for determining spawning frequency show that, while each gives a reasonable estimate, the spawning frequency estimate for a group of fish differs slightly depending upon the method used. For instance, the first reports of spawning frequency for spotted seatrout showed that the highest frequencies were obtained using the FOM method, followed by the hydrated oocyte method (Brown-Peterson et al., 1988). For this same group of spotted seatrout, the POF method resulted in the lowest spawning-frequency estimate. More recently, Brown-Peterson and Warren (2001) found that the POF method resulted in a more frequent estimate than the FOM method in samples from 1998 but the exact opposite in 1999 samples from Mississippi. In fish examined from Louisiana, the POF method resulted in a slightly greater rate of spawning than the FOM method (Nieland et al., 2002), similar to results from Charlotte Harbor, Florida (Brown-Peterson et al., 2001). However, fish from Apalachicola Bay, Florida, showed a more frequent spawning rate using the FOM method, although the difference was not significant from the POF method (Brown-Peterson et al., 2001). In Georgia, the hydrated oocyte method resulted in a greater estimate of spawning frequency than the POF method (Lowerre-Barbieri et al., 1999). Thus, the available data indicate no consistent, significant differences among the methods used to determine spawning frequency.

SPAWNING-FREQUENCY ESTIMATES

Most estimates of spawning frequency suggest that spotted seatrout spawn, on average, once every 4 to 5 days (Table 8.5). While some individuals may spawn more frequently, there is no histological evidence that spotted seatrout spawn daily. Estimates of the number of times an individual can spawn during the reproductive season (Table 8.5) vary from a low of 14, based on POFs of age-1 fish in Texas (Bumguardner et al., 1998), to a high of 80 for fish undergoing FOM in Texas (Brown-Peterson et al., 1988). The large variation in the number of annual spawns is related to a combination of differences among methods for determining spawning frequency and differences in the length of the spawning season among regions. However, in most regions, spotted seatrout appear to have the ability to spawn 40 to 50 times in a single reproductive season.

Some monthly differences in spawning frequency have been noted (Brown-Peterson et al., 1988; Brown-Peterson and Warren, 2001; Brown-Peterson et al., 2002; Bumguardner et al., 2001; Rouimillat and Brouwer, in preparation). Along the Gulf of Mexico, spawning frequency often decreases in the middle of the spawning season (June or July), followed by an increase in frequency towards the end of the season (Brown-Peterson et al., 1988; Brown-Peterson and Warren, 2001; Brown-Peterson et al., 2002). However, in South Carolina, spawning frequency changed with the age of the fish; peak spawning frequency for age-1 fish was in June, whereas spawning among age-2 and age-3 fish peaked in July and August, respectively (Roumillat and Brouwer, in preparation).

Spawning frequency has also been shown to vary annually in Texas (Bumguardner et al., 2001), Mississippi (Brown-Peterson and Warren, 2001), and Florida (Crabtree and Adams, 1998), as well as regionally among estuaries within Texas (Bumguardner et al., 1998, 2001), Mississippi (Brown-Peterson and Warren, 2001), and Florida (Brown-Peterson et al., 2002), and across the Gulf of

TABLE 8.5
Spawning Frequency Estimates of Wild Populations of Spotted Seatrout throughout Their Range

Region	Spawning Frequency, days			Number of Spawns/Year	
	POF	FOM	Hydrated		
South Carolina	4.4	–	–	28	Roumillat and Brouwer, in prep.
Georgia	6.5	–	2.75	19 to 44	Lowerre-Barbieri et al., 1999
Florida, east coast	3.2[a]	–	3.2[a]	56	Crabtree and Adams, 1998
Florida, west coast	5.4	14.3	–	40	Brown-Peterson et al., 2001
Florida, Panhandle	7.7	4.7	–	22	Brown-Peterson et al., 2001
Mississippi	4.8	4.7	–	31 to 51	Brown-Peterson and Warren, 2001
Louisiana	4.2	5.1	–	36 to 45	Nieland et al., 2002
	–	2.6	–	51	Bumguardner et al., 1998 Colura and Bumguardner, 1997
	7	2.3	4.6	24 to 80	Brown-Peterson et al., 1988

[a] Methods combined to produce one estimate.

Notes: POF — postovulatory follicle; FOM — final oocyte maturation; Hydrated — hydrated oocytes

Mexico (Brown-Peterson et al., 2002). In Florida, spawning frequency varies with fish age; older spotted seatrout spawn more frequently than young (age-0 and age-1) fish (Crabtree and Adams, 1998). This difference in spawning frequency based on age may help to explain the less-frequent spawning reported for Texas fish by Bumguardner et al. (1998), as their estimates were made with age-1 fish only. Spawning frequency estimates of older spotted seatrout from the same area in Texas are much greater, ranging from every 2.6 days (Colura and Bumguardner, 1997) to every 3.3 days (Bumguardner et al., 2001).

Estimates of spawning frequency have also been made from captive fish used for culture purposes. Arnold et al. (1978) manipulated temperature and photoperiod regimes and were the first to successfully spawn spotted seatrout in captivity without using hormonal injections. While spawning frequencies of individual fish are difficult to ascertain in a culture situation, a group of four females held under controlled temperature and photoperiod spawned 99 times over a 17-month period, resulting in a mean spawning frequency per individual of once every 21 days (Brown-Peterson et al., 1988). A similar mean spawning frequency of once every 17 days was observed for a group of six females held in outdoor tanks at ambient conditions (Tucker and Faulkner, 1987), while an individual female held under identical conditions spawned once every 16 days. More recently, a group of spotted seatrout held under controlled temperature and photoperiod spawned 172 times during 265 days, resulting in a mean spawning frequency of every 10.8 days for an individual female (Wisner et al., 1996). Thus, captive spotted seatrout appear to spawn less frequently than their wild counterparts, although the data are not directly comparable. However, females injected with LHRH to induce spawning did spawn on 2 consecutive days in six separate trials (Thomas and Boyd, 1988), suggesting that a high spawning frequency is possible for spotted seatrout with hormonal stimulation.

ANNUAL FECUNDITY ESTIMATES

For multiple-spawning species, the annual fecundity can be determined if the batch fecundity and the spawning frequency are known. However, annual fecundity varies with the size and age of the fish as well as the length of the spawning season. Reports of total annual fecundity for spotted seatrout (Table 8.4) vary from a low of 28,000 for age-1 fish in Louisiana (Wieting, 1989) to a high of 52 million for age-5 fish in Florida (Crabtree and Adams, 1998). Overall, fish from Mississippi appear to have the lowest annual fecundity, a result of the low batch fecundity from that area. While age-1 Texas fish had a high batch fecundity (Table 8.4), the low spawning frequency (Table 8.5) resulted in a relatively low estimate of total annual fecundity (Bumguardner et al., 1998).

Colura and Bumguardner (1997) estimated that a 1-kg fish in Texas would have an overall fecundity of 23 million eggs, remarkably similar to estimates by Brown-Peterson et al. (1988) for similar-sized fish in Texas. In comparison, a 1-kg female from Florida could spawn 20 million eggs annually (Crabtree and Adams, 1998), while the same-sized female from Louisiana could spawn 15.8 million eggs annually (Nieland et al., 2002). These total annual fecundity values are larger than annual fecundity estimates of the congener *C. regalis* in Chesapeake Bay (Lowerre-Barbieri et al., 1996b), no doubt due to the longer reproductive season of *C. nebulosus*. However, spotted seatrout have a much lower estimated annual fecundity than larger sciaenids such as red drum (Wilson and Nieland, 1994) and black drum (Nieland and Wilson, 1993), even though these larger species have a shorter spawning season than *C. nebulosus*.

REGIONAL DIFFERENCES AND MANAGEMENT IMPLICATIONS

The reproductive biology of spotted seatrout varies throughout its range, with a slightly larger size at sexual maturity and a shortened spawning season in Chesapeake Bay, Virginia, relative to Florida and the Gulf Coast (Brown-Peterson and Thomas, 1988). While variations across such latitudinal expanses are not unexpected, variations among estuaries within the same region can have significant management implications. For instance, the size and age structure of spotted seatrout varies among estuaries in Florida (Murphy and Taylor, 1994; DeVries et al., see Chapter 7), which implies that fecundity may also vary among estuaries, although this has not been investigated to date in Florida. Data presented here show that while spawning frequency is similar among the east, west, and Panhandle coasts of Florida, the number of spawns per year varies greatly, which can significantly affect spawning stock biomass estimates. The determination of length and bag-size restrictions should take into account variations in the reproductive potential of the species within each estuarine system; this makes the development of statewide and region-wide management plans challenging. Currently, Florida manages its spotted seatrout fishery on an area-wide basis within the state (Muller et al., 1997), in recognition of differences in the biology of the species in different areas.

Interestuarine differences in the reproduction of spotted seatrout have been found in Mississippi and Texas. In Mississippi, spawning frequency is significantly lower in Biloxi Bay than along the barrier islands and in St. Louis Bay, which may be related to less wind-driven water movement and greater shoreline development (Brown-Peterson and Warren, 2001). In Texas, fecundity is higher in the lower Laguna Madre than in Matagorda Bay, but spawning frequency is significantly lower (Bumguardner et al., 2001). The decreased spawning frequency in the lower Laguna Madre could be related to the greater fish population density in that area (Bumguardner et al., 2001).

Differences in the reproductive biology of spotted seatrout are also evident along the northern Gulf of Mexico. While there appears to be little difference in size or age at 50% maturity from Florida to Texas, the length of the spawning season varies among regions, as do peaks in GSI values (Brown-Peterson et al., 2001). Batch fecundity was significantly lower in Mississippi than in Texas and Louisiana, and spotted seatrout from Charlotte Harbor and Apalachicola bays, Florida, spawned significantly less frequently during March, April, and September than fish from more western areas of the Gulf of Mexico (Brown-Peterson et al., 2001). These estuarine differences in the reproductive biology may be a result of observed differences in mitrochondrial DNA throughout the northern Gulf of Mexico (Gold et al., 1999), although the relationship between reproduction and genetics has not been explored for spotted seatrout. However, the significantly reduced mtDNA diversity found in the lower Laguna Madre suggests a reduction in the number of females contributing to the reproductive population (Gold et al., 1999), which may relate to the reduced spawning frequency observed for that area. Therefore, while the population levels of spotted seatrout in the lower Laguna Madre are currently higher than in other Texas bays (Bumguardner et al., 2001), actual reproductive effort appears to be reduced, which could result in a major population adjustment in the future.

A factor which may differentially affect spotted seatrout reproduction throughout their range is the salinity profile of the spawning habitat. While *C. nebulosus* is a euryhaline species known to tolerate a wide range of salinities (Tabb, 1966), its physiologically optimal salinity is 20% (Wohlschlag and Wakeman, 1978). Furthermore, no additional energy may be available beyond that required for routine biological maintenance at salinities below 10 or above 45% (Wohlschlag and Wakeman, 1978), suggesting that reproduction would be limited at these salinity extremes. Salinity values at or near the 10% physiological limit are routinely found in Mississippi during spring (Peterson et al., 2000; Brown-Peterson and Warren, 2001; Brown-Peterson et al., 2002), the period of ovarian recrudescence. Salinities >45% can occur year-round in the lower Laguna Madre, Texas, and often persist for months (Buskey et al., 1998), which could severely restrict the energy available for reproduction and may contribute to the observed low spawning frequency for the area noted by Bumguardner et al. (2001). Furthermore, egg and larval development are impacted by the salinity in the spawning area, although there is evidence that successful spawning and larval development can occur at salinity extremes after an acclimation period (Holt and Holt, 2002).

Thus, the combination of environmental factors with the inherent estuarine nature of spotted seatrout can result in differences in reproduction among estuaries and regions that should be considered when devising management plans for the species. Current information on the age and size at sexual maturity, duration of the spawning season, batch fecundity, and spawning frequency is necessary for each region in order to design a management strategy that will best address the needs of the species for that particular region. Adoption of management strategies designed for other regions may result in unintentional negative impacts to spotted seatrout stocks.

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9 Effects of Variable Salinity on Reproduction and Early Life Stages of Spotted Seatrout

G. Joan Holt and Scott A. Holt

CONTENTS

ABSTRACT

Spotted seatrout live and reproduce in estuaries and bays, where salinity varies from brackish to hypersaline. Knowing how this species copes with such a broad range of salinity, especially during reproductive and early life stages that are particularly sensitive to altered environmental conditions, is an important consideration for their effective management. Spotted seatrout are relatively sedentary, staying within an estuarine system throughout their life. This behavior may allow the population to adapt to local salinity conditions. Spotted seatrout eggs and larvae have been found in estuarine waters ranging from 15 to 50‰.

There is evidence that spotted seatrout have adapted to estuarine ecosystems by producing eggs that are positively buoyant in their spawning salinity, thus maintaining them in a favorable environment for development. Egg diameter and wet weight are negatively correlated with salinity; the smallest eggs are produced in hypersaline water and larger eggs in lower salinity. This holds true for eggs collected from the wild and for eggs produced in captivity. The salinity range for best survival of larvae is not the same for all larvae; it is strongly biased by the spawning salinity. Larvae hatched from eggs spawned at 40‰ by fish residing in the hypersaline Texas Laguna Madre are more tolerant of higher salinities than larvae hatched from eggs spawned at 20‰ from fish resident in a polyhaline estuary. This provides evidence for some type of maternally mediated adaptation to the prevailing salinity regime.

Infrequent weather events that bring about drastic changes in salinity can result in a breakdown of this strategy. Unusually large inputs of freshwater into an estuary cause spotted seatrout eggs to sink, reducing survival of the larvae. Data collected during a major flooding event in the Aransas Estuary, Texas, showed that salinities in the low teens occurred in late spring about the time spotted

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seatrout normally begin spawning. The appearance of spotted seatrout larvae was delayed until July or even August at some locations and their eventual appearance coincided with salinity increasing to > 20‰.

Successful spawning of spotted seatrout in the laboratory also appears to be constrained by salinities below about 20‰. Laboratory manipulations to determine the flexibility of the reproductive response to salinity gave mixed results. Spotted seatrout from 30‰ were able to adapt reproductive traits to 20‰ over a period of several months. That is, the egg size and larval tolerance changed to conform to what would be expected for fish spawning at that salinity. Conversely, fish from the Laguna Madre, where the salinity is often 40 to 50‰, did not produce eggs that would float, even though the adults were maintained for 6 months in 20‰. Larvae did not show increased survival at the lower salinity as would be expected. Genetic structuring of spotted seatrout populations has been reported. There is potentially a genetic basis to the reproductive response of spotted seatrout, especially those populations living in extreme salinity environments, that allows them to be successful in those environments.

INTRODUCTION

Spotted seatrout (*Cynoscion nebulosus)* adults live in bays and estuaries and are believed to remain primarily in their natal waters throughout their life, utilizing the estuarine environment for feeding, spawning, and nursery habitat (Tabb, 1966; Baker and Matlock, 1993). Spotted seatrout is a euryhaline species found in waters ranging in salinity from 0.2 to as high as 70‰ (Simmons, 1957), but spawning is thought to occur in a more restricted range, from 20 to 37‰ (Lassuy, 1983). Despite the extensive geographic distribution of spotted seatrout, the adults do not migrate extensively. Tagging studies have shown that the majority of spotted seatrout do not migrate, even between adjacent bay systems. Iversen and Tabb (1962) found that 95% of recaptured seatrout in Florida had moved less than 48 km from their release point, and Overstreet (1983) found similar results in a tagging study conducted in Mississippi Sound. Baker et al. (1986) and Baker and Matlock (1993) reported an apparent cyclic pattern to spotted seatrout migration within the Galveston Bay system, consisting of winter and summer movements toward the bay mouth and spring and fall returns to the interior of the bay. Although the migration overlaps the spawning season, the purpose of migrating within a particular bay is not fully understood. The consistent recapture of tagged fish within the same bay system could indicate site fidelity and the potential for environmental adaptation.

Given the apparent lack of significant migration between adjacent bays, there is a potential for the spotted seatrout population to show genetic differences among bays. Weinstein and Yerger (1976) found differences in serum proteins from seatrout collected at different estuaries along the Florida coast. Allozyme analysis on spotted seatrout along the Texas coast by King and Pate (1992) identified significant differences in heterozygosity that were the result of an isolation-by-distance effect. The authors concluded that fish in adjacent bays were from a single, randomly mating population. However, due to significant clinal variation in the aspartate aminotransferase-2 locus, restocking efforts by Texas Parks and Wildlife have concentrated on three regions corresponding to the upper, middle, and lower Texas coast and a separate broodstock has been acquired for each region (King et al., 1995). The most recent evidence suggests that spotted seatrout are spatially divided into discrete subpopulations. Analyzing mitochondrial DNA, Gold et al. (1999) found significant heterogeneity between Gulf of Mexico and Atlantic coast samples and among samples from the western Gulf of Mexico. They suggested that spotted seatrout were divided into subpopulations corresponding to different bay systems along the western Gulf of Mexico and the Texas coast, including Lower Laguna Madre, Aransas Bay, and Matagorda Bay.

Since spawning occurs principally within estuaries, offspring of spotted seatrout are potentially subjected to a wide range of salinity conditions at a time when their osmoregulatory organs are poorly developed. This is especially critical when fish spawn in estuaries or bays with extreme salinity patterns. For example, in Texas, large shallow lagoons in semi-arid regions with minimum freshwater input have high evaporation rates, resulting in extremely high salinity. Spotted seatrout spawn from March to October in these habitats (e.g., Laguna Madre, Texas) in salinity as high as 40 to 50‰. They also spawn in estuaries with river input that regularly reduces the salinity to less than 20‰ (e.g., Barataria Bay, Louisiana).

Successful reproduction and larval recruitment in fishes are particularly sensitive to altered environmental conditions, including salinity changes (Billard et al., 1981). Major changes in salinity, such as alterations in freshwater inflow through upstream allocation of water, could have long-term consequences on spotted seatrout population dynamics. Although moderate increases in salinity may not be acutely lethal to the fish, the increased energy requirements for acclimation leave fewer energy reserves for growth and reproduction. This chapter will address how the spotted seatrout life-history strategy works through maternally mediated changes and adaptations that can modify the responses of eggs and larvae to variable salinity.

FIELD INVESTIGATIONS

SPAWNING

Salinity effects on spawning activity of fishes can be derived directly through laboratory experiments or through experimental or observational analysis in the field. An initial understanding of salinity tolerance can be gained by observing the salinity regime in areas where spotted seatrout are presumed to be spawning. Available evidence suggests that spotted seatrout spawn primarily within estuaries (Pearson, 1929; Miles, 1950; Tabb, 1966; Lorio and Perret, 1980; Hein and Shepard, 1979; Overstreet, 1983; Brown-Peterson et al., 1988; Peebles and Tolley, 1988; Holt et al., 1990; Alshuth and Gilmore, 1993), although evidence exists of spawning in the tidal passes and the nearshore ocean (Jannke, 1971; King, 1971; Christmas and Waller, 1973; Holt et al., 1985; Overstreet, 1983; Collins and Finucane, 1984). Early reports of spawning locations were typically based on measures of gonadal development in adults and occurrence of juveniles in nursery areas because eggs and larvae proved difficult to locate. These reports generally suggested that spotted seatrout spawn in polyhaline and mesohaline portions of estuaries, with little indication of spawning in oligohaline or tidal freshwater areas. Overstreet (1983), however, reported finding female spotted seatrout classified as "spawning" at a salinity of 10‰. He did not know the fate of the embryos or larvae spawned at that salinity.

More recently, catches of preflexion larvae (< 3.0 mm)[1] in plankton samples (McMichael and Peters, 1989; Powell et al., 1989; Holt et al., 1990) have lent credence to the suggestion that spawning occurs extensively throughout estuaries. (All lengths reported here are notochord or standard lengths unless otherwise noted.) Three-mm spotted seatrout larvae are approximately 7 days old (McMichael and Peters, 1989) and occurrence of these young larvae in plankton samples is considered a proxy for spawning sites. Although these studies generally did not take advection processes into account, they still adequately represent broad generalizations of spawning sites and thus provide an indication of salinity regimes.

Peebles and Tolley (1988) found small spotted seatrout larvae to be more abundant in Naples Bay, Florida, where salinity gradients were much steeper and mean salinity was slightly higher (33.1 vs. 29.1‰) than in Fakahatchee Bay. Powell et al. (1989) found preflexion larvae in intermediate to high salinities (station means of approximately 25 to 35‰) in the western portion of Florida Bay. Rutherford et al. (1989) also suggested that spawning was primarily in the western portion of Florida Bay, where salinities ranged from 33 to 50‰; they caught a few small larvae in the eastern portion of Florida Bay, but salinities were not reported for that site. Both research groups concluded that spotted seatrout did not spawn in the brackish portions of Florida Bay. In a follow-up study in Florida Bay, Thayer et al. (1999) found small spotted seatrout larvae (i.e., spawning) in essentially the same locations as the previous studies. However, they also found small larvae in the central portion of the bay and attributed the potential expansion of spawning area as a response to changes from "hypersalinity to more normal salinities that have occurred during the decade." In Tampa Bay, Florida, catches of small (< 2.0 mm) spotted seatrout larvae in plankton tows indicated that spawning occurred over a broad area of the bay and in nearshore Gulf waters (McMichael and Peters, 1989). Lower and middle bay stations, where surface salinities ranged from 18 to 36‰, contained the greatest abundance of small larvae and were presumed to be primary spawning sites.

In Texas bays, Holt et al. (1990) found small (< 2.5 mm) spotted seatrout larvae throughout the Laguna Madre at salinities of 35 to 48‰. Small larvae were found at the highest salinities (48‰) recorded during the spotted seatrout spawning season of March through September. Small larvae were relatively abundant at salinities up to 45‰. The location of these collections was at least 30 to 40 km from areas of more moderate salinity, and advective processes in this region are relatively weak (Ward, 1997), suggesting spawning was actually occurring at the observed salinities. Tolan et al. (1997) found small spotted seatrout in the southern portion of the same study area (Lower Laguna Madre) in salinities of 24 to 39‰, rather low salinities for this normally hypersaline lagoon. S.A. Holt (unpublished data) has recorded small spotted seatrout larvae from Aransas Bay, Texas, at salinities of 22 to 35‰ and in the Aransas Pass tidal inlet at salinities of 30 to 36‰. Immigration of small spotted seatrout through the tidal inlet indicates some spawning activity offshore in oceanic salinities of 33 to 36‰, but spotted seatrout larvae of any size are relatively rare in nearshore Gulf of Mexico samples (S.A. Holt, unpublished data).

In Louisiana, Sabins and Truesdale (1974) found spotted seatrout larvae of 2 to 14 mm (mean length = 4.5 mm, n = 748) in the vicinity of Caminada Pass and suggested that spotted seatrout were spawning there. Even though Caminada Pass connects Barataria Bay with the Gulf of Mexico, the salinity is described as "low to moderate," with salinities ranging from 8.5 to 35.5‰ and a mean of 23.4‰ during their study. Although the authors did not provide specific salinities associated with spotted seatrout collections, their results suggest that spotted seatrout may spawn at lower salinities than reported from the Florida and Texas studies. This suggestion is corroborated by data in Aransas Bay, Texas (S.A. Holt, unpublished data). Following a major flooding event in early April 1992 that lowered salinities throughout the estuary to 10‰ or less, spotted seatrout eggs and small larvae were not collected at sites that typically produced larvae until the salinity reached 20‰ or more. At some sites, apparently no successful spawning took place until August, when salinity reached 20‰. These data indicate that spawning activity or egg and larval survival in Aransas Bay, Texas, may be limited by salinities below 20‰. Conclusions supported by the results of laboratory studies are discussed below.

Collections of young larvae provide compelling evidence of spawning activity in the vicinity of the collection sites. More direct and detailed data are available from the recent employment of bioacoustic techniques that take advantage of the vocalizations of male spotted seatrout to locate spawning aggregations. The identification of spawning sounds can allow localization of spawning aggregations to within 15 to 20 m (Saucier and Baltz, 1993). Mok and Gilmore (1983) utilized this technique to locate spawning aggregations of spotted seatrout in the Intracoastal Waterway in the central portion of the Indian River Lagoon, Florida, but they did not report the salinity at those locations. Alshuth and Gilmore (1993) surveyed the same area and found spawning aggregations at salinities of 18 to 33‰. Spotted seatrout sound production ceased when salinities fell below 14‰, and spawning aggregations were displaced southward toward higher salinities near the Fort Pierce Inlet.

Saucier and Baltz (1993) used bioacoustics to locate numerous spawning aggregations of spotted seatrout in the Barataria/Timbalier Bay region of Louisiana and related aggregation size to physiochemical variables through multiple regression. Although time of day and water velocity were the most important variables, salinity made a significant contribution to the model. Drumming aggregations were located in salinities as low as 7.0‰, but 81% of the observations were at salinities between 15 and 18‰. No drumming was observed at salinities above 25.8‰, even though they sampled salinities up to 31.0‰. The authors suggested that optimum salinity for spawning was between 15 and 21‰ and found that spawning locations shifted as much as 30 km with changing environmental conditions. Saucier and Baltz (1992) found drumming aggregations of spotted seatrout inside Charleston Harbor, South Carolina, at salinities of 23 to 27‰, but failed to located spawning activity in the upper estuary at salinities < 16‰ or at high salinity sites (> 32.0‰) on barrier island beaches or tidal passes. Luczkovich et al. (1999) recorded drumming aggregations of spotted seatrout in what were described as both high- and low-salinity areas of Pamlico Sound; however, actual salinities were not reported.

These data from Florida and Texas suggest that spotted seatrout spawn in moderate to high salinities of 18 to 36‰ and are tolerant of salinities of up to 45‰. These studies are from ecosystems where freshwater inflow is relatively low and estuarine salinities are relatively high and stable. In contrast, studies from Louisiana and South Carolina estuaries, where higher freshwater inflows produce relatively low salinities and more variable conditions, suggest optimum spawning salinities in the range of 15 to 27‰ and a lack of spawning at higher salinities. In both environments, however, spotted seatrout appear to avoid low-salinity, brackish water areas as spawning sites. This argument is supported by circumstantial evidence reported by Arnoldi (1984) and Helser et al. (1993) for Louisiana estuaries that show seasonal movement of spotted seatrout toward the higher salinity coastal waters during the spring-to-summer spawning season and dispersal throughout the estuaries in the fall and winter.

EGGS

Salinity can affect marine fish eggs through a variety of means, including reducing fertilization rates, reducing hatch rates, and changing buoyancy (Holliday, 1969). Most of the information on salinity effects in spotted seatrout eggs is derived from laboratory studies (see below). A major impediment to studying salinity effects *in situ* is the difficulty in separating spotted seatrout eggs from other sciaenids or even other fish families with similar eggs (Holt et al., 1988; Daniel and Graves 1994). Fable et al. (1978) reported that hatchery-spawned spotted seatrout eggs were 0.70 to 0.85 mm in outside diameter, but spawning salinities were not reported. Laboratory studies have shown that spawning salinity has significant effects on egg size (G.J. Holt, in press). Holt et al. (1988) found that wild-caught spotted seatrout eggs were 0.60 to 0.85 mm in diameter in salinities ranging from 19 to 36‰, but the authors did not report specific egg-size/salinity relationships. Alshuth and Gilmore (1993) found that spotted seatrout eggs spawned at 34‰ were 0.73 to 0.79 mm in diameter and those spawned at 25‰ were 0.79 to 0.89 mm in diameter, while those spawned at 15‰ were 0.89 to 0.99 mm in diameter. These eggs were all collected with a 1.0-m plankton net towed at the surface, so all the eggs were apparently buoyant at their spawning salinity. Luczkovich et al. (1999) collected spotted seatrout eggs of 0.80 to 0.93 mm in diameter in surface collections in Pamlico Sound, North Carolina, but salinities at the collection sites were not reported.

LARVAE AND JUVENILES

Survival and growth of marine fish larvae is a complex interaction between the fish's physiological capabilities and its environment. These ecophysiological processes have been summarized in a conceptual model by Fry (1947, 1971) and supplemented by Neill et al. (1994), Yamashita et al. (2001), and others. This model classifies environmental factors that might act on the individual (or the population [Neill et al., 1994]) as controlling, limiting, masking, directive, and lethal. Salinity has been suggested as acting as both a masking and directive factor (Yamashita et al., 2001). Salinity acts as a masking factor by increasing osmoregulatory cost when it is outside the optimum range and as a directive factor by cueing or signaling the fish to respond to characteristics of the environment (Brett, 1979). The role of salinity in changing metabolic rate by altering osmoregulatory cost in euryhaline species may be relatively small but complex (Claireaux and Lagardere, 1999). Thus, the role of salinity as a directive factor may be more significant than its role as a masking factor under "average" estuarine conditions.

These processes are most easily understood through controlled laboratory experiments, but insight can be gained through manipulative and observational field work. Virtually all field research to date on larval and juvenile spotted seatrout has been observational. The majority of the applicable data for spotted seatrout larvae is in the form of distribution/abundance and salinity comparisons. Planktonic larvae have been found in open waters of estuaries and occasionally in nearshore oceanic waters at salinities of 15 to 45‰ (Peebles and Tolley, 1988; McMichael and Peters, 1989; Powell et al., 1989; Rutherford et al., 1989; Holt et al., 1990; Tolan et al., 1997), but most of these studies do not provide any indication of the relative condition of the larvae.

The only direct comparison among different salinity regimes was by Peebles and Tolley (1988), who found no significant difference in growth rates of larvae (< 7.0 mm) between two Florida estuarine systems that differed in mean salinity (Naples Bay mean bottom salinity = 33.1‰; Fakahatchee Bay = 29.2‰) and horizontal salinity gradient. The pooled growth rate of larvae from both systems was 0.405 mm^{-d}. McMichael and Peters (1989) estimated the growth rate of < 50-mm spotted seatrout collected at salinities of 18 to 32‰ in Tampa Bay to be 0.509 mm^{-d}. Peebles and Tolley (1988) reported a difference in the mortality rate of larvae between Naples and Fakahatchee bays, but suggested that the difference might be related to greater access to seagrass meadows in the estuary with lower mortality rather than any direct effect of salinity. In a study of small juvenile spotted seatrout (20 to 200 mm), Chester and Thayer (1990) found that salinity was not a significant factor in the distribution of these juveniles among sites throughout Florida Bay.

Although data from field studies are limited, little evidence exists that salinity plays a major role in regulating growth or general condition of spotted seatrout larvae or juveniles within areas where the fish are normally found. There are few reports, however, of larvae or juvenile spotted seatrout from low salinity areas and, thus, salinity may in fact be acting as a directive factor in the avoidance of potentially stressful conditions.

LABORATORY STUDIES OF SALINITY TOLERANCE

Several studies have investigated the salinity tolerance of spotted seatrout eggs and larvae in the laboratory, with varying results. Taniguchi (1981) reported that eggs from spotted seatrout collected in South Florida (ambient salinity of 33‰) could be fertilized in salinities of 5 to 60‰, but embryos developed only in 10 to 50‰. He determined the optimum conditions for hatch through the yolk-sac stage to be 18.6 to 37.5‰ at 28°C. Eggs stripped from adults collected in South Texas in 32‰ seawater and transferred within minutes after fertilization did not develop in 10 and 20‰, but hatched successfully in 25 to 40‰ seawater (G.J. Holt, unpublished). Egg diameters (0.72 mm) were the same in all salinities, and eggs were negatively buoyant at 25‰ or less. Eggs from the same source, transferred 12 h after fertilization, hatched in salinities ranging from 10 to 55‰ and survived to day 3 post-hatch in salinities of 10 to 40‰ at 26°C (Holt and Banks, 1988).

Gray et al. (1991) reported that high salinity adversely affected hatching success of spotted seatrout in relation to temperature of incubation. Eggs held at 26°C exhibited greater hatch rates at higher salinities than eggs incubated at higher or lower temperatures. They worked with fish from Matagorda Bay, Texas, acclimated to salinities ranging from 17 to 33‰ and suggested that spotted seatrout living in hypersaline habitats might spawn successfully in higher salinities. Fish from the Indian River Lagoon, Florida, spawned in the laboratory at salinities ranging from 24 to 27.5‰ and produced eggs that hatched in 5 to 45‰ but were negatively buoyant below 20‰, according to Alshuth and Gilmore (1994). They reported poor hatching rates at 0 and 5‰ at all temperatures and greater than 80% survival of 24 h larvae in 10 to 40‰ at 30°C. Larvae developed successfully to first feeding at 15 to 35‰.

Banks et al. (1991) reported a significant age-linked pattern in salinity tolerance of spotted seatrout larvae. Both lowest and highest salinities tolerated by larvae (spawned at 32‰) decreased from day 1 post-hatch (4 and 40‰) to day 3 (8 and 32‰) but increased thereafter. Similar changes were reported for larvae spawned in low salinity (24‰) but, in this case, there was a reduction in the highest salinity tolerated: 37‰ on day 1 and 27‰ on day 3. The authors suggest that the drop in tolerance on day 3 is associated with osmotic stresses related to first feeding. It was possible to acclimate the larvae to lower but not to higher salinity. Survival at 4‰ was increased compared to controls maintained at 32‰; however, hypersaline acclimation did not improve survival in higher salinity. In the same study, larvae from adults spawning in Copano Bay, Texas waters at 24‰ were less tolerant of high salinity than were larvae from the adults spawning in Aransas Bay at 32‰. These results indicate the possibility for parental or habitat influence on the salinity tolerance of newly hatched larvae.

In general, early egg development seems to be limited to salinities near that of the prevailing spawning condition. After formation of the embryonic axis (> 12 h), the eggs are tolerant of a broad range of salinities but are negatively buoyant in salinities below that of spawning. Size of eggs and salinity tolerance of the larvae are closely linked to the spawning salinity. Larvae from fish in low salinity hatch from larger eggs and tolerate lower salinity than do those from higher salinity. Spotted seatrout around the Gulf of Mexico and southeast Atlantic coast may be adapted to the salinity of a particular estuarine system that is reflected in the physiological responses of eggs and larvae to salinity.

FLEXIBILITY OF SPAWNING TO CHANGES IN SALINITY

Differences in salinity tolerance of eggs and larvae may be due to genetic adaptation to the prevailing salinity regime of the ecosystem in which they reside; if so, adults from different sites varying in long-term average salinity might produce offspring with different salinity responses. On the other hand, changes in egg size, buoyancy, and larval tolerance may simply be the consequence of parental acclimation to ambient salinities. To test these hypotheses, fish were brought into our laboratory and placed in salinities that differed from their origin to determine if adult fish would spawn in different salinities and to evaluate their offspring.

Spotted seatrout were captured from Aransas Bay, Texas (30‰), placed in the laboratory in 30,000-l recirculating tanks and induced to spawn, according to Arnold et al. (1976). After the fish successfully spawned at 30‰, the salinity was gradually reduced to 20‰. When spawning resumed at the lower salinity, egg hatch rate was low and many larvae were deformed. However, after several months, the percent of hatch increased and the deformities disappeared. Eggs from this low salinity spawn were large (0.87 mm in diameter compared to 0.72 mm), and larvae had a reduced range of salinity tolerance compared to the larvae from the original spawns in 30‰ (G.J. Holt, unpublished). The adult fish were gradually acclimated to approximately 40‰ over a period of 1 year. Eggs from spawns at 42‰ were small (0.6 mm), and larval salinity tolerance was again changed. Highest survival of the larvae occurred at 35 to 40‰, with less than 50% of 3-day-old larvae surviving in the original natal salinity of 30‰. These results from Aransas Bay (ambient salinity of 30 to 34‰) indicate that long term acclimation to changes in salinity can occur. But what about fish from sites that consistently have fairly high or low salinity? Are those fish able to adapt as well as the fish from more moderate conditions or has some genetic adaptation occurred? If there are subpopulations as suggested by the mtDNA analysis of Gold et al. (1999), there might be differences in salinity adaptations.

To evaluate this possibility, adult spotted seatrout were collected from two Texas bays with historically different salinity regimes; Matagorda Bay averaging 18 to 24‰ and Upper Laguna Madre with 34 to 45‰ salinity. Each group was maintained for at least 4 months in salinities of 20, 30, or 40‰ and induced to spawn. The resulting eggs and larvae were evaluated for viability, quality, and salinity tolerance. Adult seatrout from both sites successfully spawned in each of the three salinities, and the percent of viable larvae hatching from individual spawns was greater than 90% in all cases, although egg characteristics varied (Kucera et al., submitted). Diameter and wet weight of eggs of spawners from both bays increased significantly as spawning salinities decreased. However, dry weights were similar among treatments, indicating that wet weight differences were due to a difference in water content among eggs from different spawning salinities.

The increased water content of eggs spawned in low salinity resulted in neutral buoyancy (NBS) at lower salinity compared to eggs spawned in higher salinities. That is, large eggs floated in lower-salinity water than did the smaller eggs (with lower water content) spawned in high salinity. Significant differences were found in egg diameter, wet weight, and salinity of NBS in the adults spawned in 20‰. Eggs spawned by fish collected from the traditionally low-salinity Matagorda Bay and maintained in 20‰ were larger and exhibited a lower NBS than eggs spawned by fish taken from Upper Laguna Madre and acclimated to 20‰ water. In fact, eggs produced by fish from Upper Laguna Madre spawned in 20‰ were not positively buoyant in the spawning salinity. The authors suggest that the adaptability of adult spotted seatrout to different spawning salinities may not be uniformly successful, depending, in part, on parental origin.

Kucera et al. (in review) examined the hatch rate and 3-day larval survival in salinities below (hyposaline) and above (hypersaline) that of the spawning salinity for spotted seatrout from both Texas bays. While no hatching was observed at 0‰, exposure of eggs (tailbud stage) to 4 and 8‰ resulted in hatching abnormalities and deformed and nonviable larvae, regardless of spawning salinity or parental origin — with one exception. Eggs spawned in 20‰ by adults from Matagorda Bay produced a large number of normal, viable larvae at 8‰. Overall, hatching success was influenced mainly by the salinity in which the eggs were spawned, with eggs spawned at low salinity less likely to hatch in high salinities and vice versa. As was reported earlier (Banks, et al., 1991), spotted seatrout larvae showed a narrower salinity-tolerance range for 3-day survival than for hatching. The survival of larvae exposed to salinities above that of spawning increased with increasing spawning salinity, indicating that a greater proportion of larvae are able to survive at high salinity when spawned at high salinity. Furthermore, larvae from the higher saline bay (Upper Laguna Madre) were able to hatch and survive to day 3 in a wider range of salinities than larvae from the less saline Matagorda Bay. Larvae from Matagorda Bay were spawned in 20 and 30‰ and showed a reduced range of salinities for 50% survival to day 3.

The range of salinities tolerated by a particular group of spotted seatrout larvae was dependent upon the spawning salinity of the adults and the prevailing salinity regime within the natal estuary. Larvae spawned from fish captured from Matagorda Bay and subsequently adapted in the laboratoryoratory to higher salinity lost tolerance to low salinities and gained tolerance to high salinities. Similarly, larvae spawned from fish captured from Upper Laguna Madre and adapted to low salinity gained tolerance to low salinities and lost tolerance to high salinities. Changing spawning salinity of the adults alters the range of salinities tolerated by spotted seatrout larvae; however, an extreme change in spawning salinity is necessary to increase the salinity tolerance at extremely low or high salinities and shifts the entire range of salinities tolerated either up or down (Kucera, 2001).

Kucera et al. (in review) examined the acute salinity tolerance of spotted seatrout larvae (age 1 to 9 days) with respect to parental origin (Matagorda Bay or Upper Laguna Madre) and the three spawning salinities (20, 30, and 40‰). Acute salinity tolerance was evaluated by quantifying the number of larvae surviving after 18 h of exposure to ten salinities ranging from 0 to 60‰. Tolerance was defined in terms of the median lethal salinity (LC_{50}) — the salinity at which 50% of the larvae survived exposure to salinities below (hyposaline) or above (hypersaline) the spawning salinity. Larvae from Matagorda Bay fish were more tolerant of sudden drops in salinity than were larvae from Upper Laguna Madre fish, regardless of spawning salinity. Overall, larvae spawned in 40‰ were less tolerant of low salinities and more tolerant of high salinities than larvae spawned at 20 or 30‰, regardless of parental origin.

These results suggest that short-term acclimation of the parents or exposure of the embryos and larvae to specific salinities influences the response of larvae to abrupt changes in salinity. However, hyposalinity tolerance of Matagorda Bay larvae was not significantly different across all spawning salinities and may reflect a threshold for tolerance in this species. Larvae from Upper Laguna Madre, on the other hand, were significantly more tolerant of increases in salinity than larvae from Matagorda Bay, regardless of spawning salinity.

CONCLUSIONS

Early egg development of spotted seatrout is limited to salinities near that of the prevailing spawning condition. After formation of the embryonic axis (> 12 h), the eggs are tolerant of a broad range of salinities but are negatively buoyant in salinities below that of spawning. Size of eggs and the salinity tolerance of the larvae are closely linked to the spawning salinity but are influenced by the natal estuary. Fish from Laguna Madre, Texas, a hypersaline lagoon, could not produce buoyant eggs at low salinity even after 6 months or more at that salinity. Local adaptation of fish populations to a particular spawning salinity may be advantageous for long-term survival of species such as spotted seatrout that spawn over a wide range of salinities. Egg diameter, buoyancy, and larval salinity tolerance are regulated by spawning salinity; thus, the adults provide characteristics that can influence survival in a variable but predictable environment. There is potentially a genetic basis to the reproductive response of spotted seatrout, especially those populations living in extreme-salinity environments, that allows them to be successful in those environments.

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10 Spotted Seatrout Habitat Affinities in Louisiana

Donald M. Baltz, R. Glenn Thomas, and Edward J. Chesney

CONTENTS

ABSTRACT

The productivity of Louisiana's estuaries and spotted seatrout populations is probably enhanced by factors that are unusual elsewhere in the northern Gulf of Mexico: shallow, turbid waters in expansive marshes with extensive marsh edges and a miniscule tidal range. Ontogenetic habitat shifts move larvae into shallows, then juveniles move into progressively deeper waters, with changing predation pressures reflected in habitat and prey selection. Large spawning aggregations occur from May to October in a variety of habitat types when salinity, depth, and water velocity are appropriate. However, spawning sites, characterized by relatively deep, moving waters (> 15 ppt), can shift quickly up to 30 km with changing salinity conditions. Salinity-use patterns by juvenile-size classes show that the smallest (≤ 25 mm TL) are most abundant at 19 ppt but larger juveniles (> 25 mm) are abundant at lower salinities (9 ppt). Temperature patterns are more similar, with highly suitable temperatures ranging down to 24°C for juveniles ≤ 50 mm and down to 16 to 18°C for juveniles > 50 mm. Beginning in April and through the spawning season, seatrout (> 305 mm) avoided salinities below 14 ppt and favored higher salinities.

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THE LOUISIANA FISHERY

The spotted seatrout (*Cynoscion nebulosus*) has long been the most sought-after food fish in coastal Louisiana. Trends in commercial landings of spotted seatrout in the northern Gulf of Mexico (GOM) and recreational landings in Louisiana coastal waters reflect the importance and historical trends in the status of spotted seatrout since 1981 (Figures 10.1 and 10.2). Commercial landings of spotted seatrout in the GOM have dramatically declined over the last 20 years, as the fishery evolved from a significant commercial allocation to their present situation as primarily the target of sport fishermen (Figure 10.1). Restrictions on commercial gears have reduced catches to a fraction of their peak landings in the northern GOM of 3374 metric tons (t) in 1973. A shift in management from a net fishery to a predominately rod-and-reel fishery reduced total GOM commercial landings to 64.1 t in 1999 with 31.2 t landed in Louisiana waters (National Marine Fisheries Service Fisheries Statistics, 2001).

Current legal commercial gear by state in the northern GOM (Gulf States Marine Fisheries Commission, 2000) includes none in Alabama and Texas; cast nets and hook and line in Florida; and rod and reel in Louisiana. In certain waters in Mississippi, hook and line, trammel net, gill net, seine, and purse seine are included, but nets must be of approved biodegradable material (1997) and most landings are via hook and line. Recent commercial landings have been less than a quarter of the yearly commercial allocation (Louisiana Department of Wildlife and Fisheries, unpublished data).

A recent ban on the use of gill and trammel nets in Louisiana's spotted seatrout fishery caused most of these dramatic declines in commercial landings. Before 1977, mesh sizes and net lengths were regulated, but were not gear types. Monofilament webbing was banned in 1977, and additional restrictions on net construction were imposed in 1977, 1980, 1983, 1984, and 1987. A commercial size limit was established in 1984 (12 in. total length (TL), 30.5 cm TL) and increased to 14 in. (35.5 cm) in 1987. In 1988, unattended "set" nets were prohibited, a season was established, and a 1.25-million lb (567 t) quota was set. In 1992, the quota was reduced to 1 million lbs (453.5 t) (Bourgeois et al., 1996). Since 1997, the commercial fishery in Louisiana has been restricted to previously licensed commercial fishermen using only rod-and-reel gear.

Recreational fishermen have also endured some changes in fishing regulations. No bag or size restrictions were in effect before 1977, when a combined bag limit of 50 red drum *Sciaenops ocellatus* and/or spotted seatrout was imposed. In 1987, a 12-in. (30.5 cm TL) minimum length was adopted, and the following year the daily bag limit was reduced to 25 fish (Bourgeois et al., 1996).

Louisiana's sport fishermen appear to have benefited greatly from changes in management. Nearly 9 million spotted seatrout were harvested by recreational fishers in Louisiana in 2000

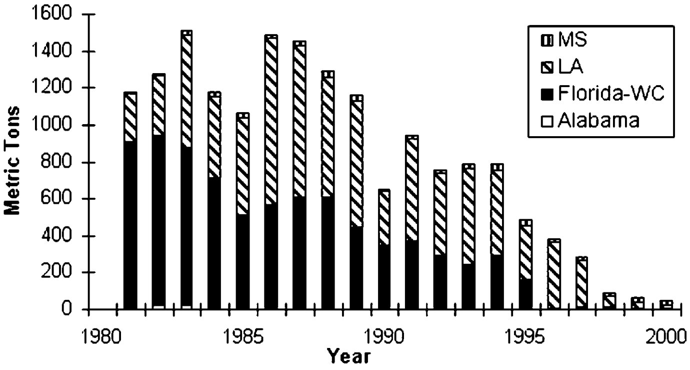

FIGURE 10.1 Trends in commercial landings of spotted seatrout within the Gulf of Mexico, by state, for the years 1981 to 2000. Commercial landings for Texas were unavailable from the National Marine Fisheries Service. (Source: National Marine Fisheries Service Fisheries Statistics, 2001; MRFSS website: http://www.st.nmfs.gov/st1/recreational/index.html).

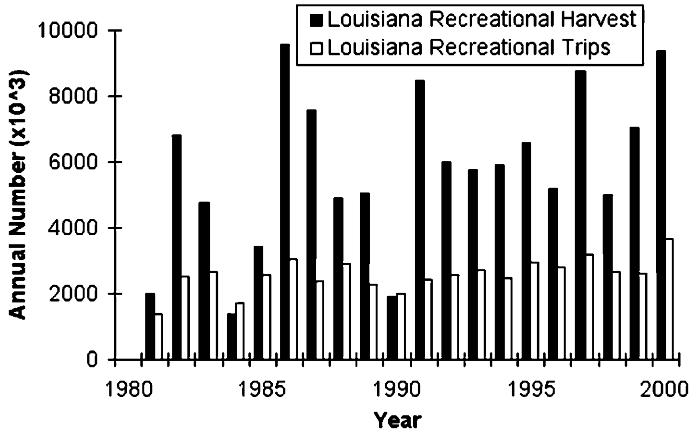

FIGURE 10.2 Annual spotted seatrout catch and effort in the Louisiana recreational fishery for the years 1981 to 2000. Solid bars represent estimates of total annual harvest of spotted seatrout in the recreational fishery, and open bars represent the estimated total number of marine recreational fishing trips in Louisiana by year (Source: National Marine Fisheries Service Fisheries Statistics, 2001, MRFSS website: http://www.st.nmfs.gov/st1/recreational/index.html).

(Marine Recreational Fisheries Statistics Survey, 2001). Trends in recreational fishery statistics (Figure 10.2) suggest that saltwater recreational fishing pressure has not increased substantially over the last 15 years in Louisiana coastal waters, while annual estimates of the numbers of spotted seatrout harvested have increased (Marine Recreational Fisheries Statistics Survey, 2001).

TROUT FISHING IN LOUISIANA

Fishing for (and dining on) spotted seatrout has been a way of life for the residents of southern Louisiana. The success rate for recreational trips is often phenomenal by the standards of other places: until recently, one major newspaper rated popular fishing areas by the number of "boxes" (i.e., 44-l ice chests) of fish reported as caught on daily trips.

The most popular baits include live shrimp, small Atlantic croaker (*Micropogonias undulatus*), and Gulf killifish (*Fundulus grandis*). Baits are often fished under a popping cork, tightlined, or attached with weights on the bottom. Historically, the most popular lure has been the "speck rig," a tandem rig with two small jigs with bucktail or soft plastic tails. Spoons, plugs, and other soft plastic lures are also used by many anglers.

The best fishing locations vary with season and weather. Subtidal oyster reefs, rock jetties, bridge pilings, and oil or gas rigs in bays or shallow coastal waters are always popular. Barrier island beaches and leeward flats can be excellent fishing locations, as can certain deep canals in the marsh. Summertime in coastal areas often produces a particularly exciting type of fishing, when schools of seatrout chase shrimp out of the water and flocks of gulls dive on the jumping shrimp; fishers can catch trout "two-at-a-time" on speck rigs.

THE HABITAT

The high productivity of Louisiana's estuaries and spotted seatrout fishery is probably enhanced by a combination of factors fairly unusual elsewhere in the northern GOM: shallow, turbid waters in expansive marshes with extensive marsh-edge ecotones and a microtidal (i.e., a tidal range of < 2 m) system easily dominated by meteorological events (Chesney et al., 2000). The role of turbidity may be the least-appreciated feature contributing to Louisiana's coastal fishery productivity, but it interacts with other features that enhance the nursery function of the estuaries, probably by enhancing the survival of early life-history stages. Turbidity is important in many systems, in that it provides cover for nekton, especially early life-history stages (Cyrus and Blaber, 1987a,b,c; Benfield and Minello, 1996). The relatively high turbidity levels of Louisiana's waters are somewhat unique in the northern GOM and are enhanced by shallowness of the system, high productivity, and fine sediments deposited by the Mississippi River that are easily resuspended. In Louisiana marshes, quantitative estimates of the abundance of small fishes are higher in nearshore shallows when the turbidity exceeds 10 nephlometer turbidity units (NTUs) and the substrate is not visible (Rakocinski et al., 1992; Baltz et al., 1993). At lower turbidity levels, the substrate is visible in water depths of 30 cm or less; fishes large enough to attract piscivorous wading birds appear to avoid these sites (Rakocinski et al., 1992; Baltz et al., 1993). Thus, turbidity influences the distribution and probably the survival of early life-history stages.

Ontogenetic shifts in habitat usage of estuarine-dependent species often move larvae into shallow water near the marsh edge; then juveniles move further from shore into progressively deeper water as they grow. By growing, they avoid being preyed upon by one group of potential predators (e.g., larger subtidal fishes such as southern flounder, *Paralichthys lethostigma*), but they become more attractive to other predators, especially those that forage visually in shallow water (e.g., intertidal wading birds). While changes in predation pressures are the ultimate factors responsible for ontogenetic habitat shifts (Kneib, 1982, 1987; Levin et al., 1997; Sogard, 1997), other influences (Peebles and Tolley, 1988) are also involved (e.g., spawning site selection, prey availability, metabolic requirements). As spotted seatrout grow, changing predation pressures are reflected in habitat selection and, in a parallel manner, they exhibit changing patterns of prey selection. Larger individuals are able to take larger prey and also a wider variance of prey sizes (Wilson, 1975).

The spotted seatrout spends its entire life cycle in or near estuaries that include the suitable habitat for all early life-history stages, juveniles, and adults (Tabb, 1966). In this review, we have endeavored to develop a "fish's eye view" of the spotted seatrout's ecological requirements (Chesney et al., 2000). We have done this by using population data to describe responses to environmental gradients while taking individual size into account. Since fishes, including spotted seatrout, continue to grow throughout their lives, each sequential life-history stage behaves essentially as a different species (Livingston, 1988), with ecological differences more exaggerated for smaller-sized classes. This is due in part to interactions between phenology and ontogeny (Miller, 1979). The short duration (< 2 seasons) of the earliest life-history stages and the unique seasonal conditions in which they occur contribute to ecological differences between size classes. However, some differences are due to changing patterns of habitat selection for subadult and adult life-history stages that experience the full annual cycle of environmental variation.

Much of the following summary of spotted seatrout ecology is based on sampling and analyses conducted using a microhabitat approach (Baltz, 1990). The ultimate microhabitat of an individual fish is the site it occupies at a given point in time (Hurlbert, 1981). This site is presumably selected by the fish to optimize net energy gain while avoiding predators and minimizing interactions with competitors (Fausch and White, 1981; Fausch, 1984; Kneib, 1987, 1993; Sogard and Olla, 1993). Because most similarly sized individuals of a species select similar microhabitats, careful measurements of the capture-site characteristics for many individuals should define the population's responses to environmental variables (Hurlbert, 1981; Baltz et al., 1987; Baltz, 1990).

Modal peaks of population abundance along environmental gradients should represent near-optimum conditions. Distributional extremes may indicate the tolerance limits of a species (Bovee and Cochnauer, 1977; Magnuson et al., 1979; Jobling, 1981, 1994), assuming that preferred microhabitats are not avoided because of predators or competitors (Werner et al., 1977; Fraser and Sise, 1980; Baltz et al., 1982) or because of unrecognized forms of habitat degradation such as substrate contamination (Engle and Summers, 1999). A microhabitat approach is also useful when defining habitat suitability and describing essential fish habitat (Magnuson-Stevens Act of 1996).

Indices of habitat suitability were calculated from patterns of resource availability and use for several spotted seatrout size classes at intervals along environmental gradients (e.g., salinity and temperature). Resource availability was estimated from the relative frequency of observations (i.e., the overall sampling program) in intervals along environmental gradients derived from the environmental data sets that included all seines, gill net sets, or drop trap samples, and all samples in which no spotted seatrout were captured. Resource use was estimated from the samples in which spotted seatrout of a given size class were collected, and was weighted for the number of spotted seatrout collected in a particular sample.

Suitability (S) is defined as: $S = P(E|F)/P(E)$ = proportional use/proportional availability (Bovee, 1982), where $P(E|F)$ is the probability of finding a particular value for an independent environmental (E) variable given (|) the presence of spotted seatrout (F), and $P(E)$ is the probability of finding that value whether or not any seatrout are present. Suitabilities were standardized to range between 0 and 1, and were calculated for biologically important periods or seasons for adult fish (i.e., spawning, nonspawning, and transitional months). High suitability values reflect favorable environmental conditions. For controlling variables such as temperature and salinity, population responses revealed as rising and falling trends in suitability values along gradients should indicate near optimum conditions as maximum values approach one; distributional extremes at the tails of population response patterns should indicate the tolerance limits of a species as suitability values approach zero (Bovee and Cochnauer, 1977; Magnuson et al., 1979; Jobling, 1981, 1994). Comparing resource use with environmental availability gives insights into patterns of habitat selection and avoidance (Baltz, 1990).

MATURITY AND FECUNDITY

The life-history characteristics of spotted seatrout in Louisiana were studied by Wieting (1989), who used otoliths to estimate lengths at age and several means to estimate age- and length-specific fecundity schedules. She found that females predominated (1.6:1) in all fishery-independent age classes and were significantly larger than males at any age. Age-specific batch and total fecundity estimates increased up to age 3, but data were too limited for analyses of older females. Fecundity estimates ranged from 3000 to 2.1 million eggs per batch and from 0.28 to 16.9 million eggs per annum, depending on female size. Recent studies suggest somewhat lower estimates of batch and annual fecundity. In Barataria Bay, Louisiana (Nieland et al., 2002), batch fecundity of 25 females age 2 to 4 years ranged from 102,000 to 512,000 (mean = 250,000) eggs per spawning event, which occurred every 4 to 5 days, yielding annual fecundity of 9 to 11 million ova. In Mississippi Sound, batch fecundity was 12,633 to 354,000 eggs per event and spawning frequency was 4 to 5 days (Brown-Peterson and Warren, 2001). Lengths at annulus formation for males up to age 5 were estimated at 213, 303, 368, 413, and 446 mm TL (ages 1 to 5, respectively), and females were always larger at the same ages: 220, 363, 453, 509, and 545 mm TL, respectively (Wieting, 1989). Juvenile growth rates have been studied by Lorica (1988).

In Louisiana, spotted seatrout have a protracted summer spawning season and form their annual growth checks in winter through early spring between December and May (Wieting, 1989; Saucier and Baltz, 1993; Nieland et al., 2002). Total lengths of individuals at the formation of the first annulus vary considerably, ranging from 115 to 306 mm TL for individuals up to 3 years old (Wieting and Baltz, 1993). Late-spawned individuals in a cohort overwinter at a smaller size and should suffer higher mortality rates and gradually diminish in the proportion of their cohort in the stock.

However, a cursory examination of available information does not support this expectation of higher mortality in late-spawned individuals. Using two separate sex-specific log–log regressions (F-values > 14.76, df > 1 and 417, $p < 0.0001$) to estimate individual lengths at the formation of the first annulus for 1-, 2-, and 3-year-old spotted seatrout examined by Wieting (1989), we found some evidence for a weakly declining trend ($R^2 < 0.0342$) in mean length at annulus one for males and females. The predicted geometric-mean lengths at age 1 for males were 214, 207, and 185 mm TL for individuals that exhibited one, two, and three annuli, respectively. For comparable females, the predicted sizes were 216, 206, and 190 mm TL, respectively. Thus, it appears that something interesting may be occurring that merits further investigation. The decline — Rosa Lee's phenomenon (Ricker, 1975; Fossen et al., 1999) — may be due to faster-growing individuals suffering higher mortality in the fishery as well as late-spawned individuals contributing disproportionately to the population. If the latter is true, fall spawning during the protracted reproductive season of spotted seatrout in Louisiana may be effective in producing recruits and is a bet-hedging strategy.

SPAWNING SITE SELECTION

The study of spawning site characteristics used by a species allows insights into important ecological niche dimensions that influence the success of populations in habitats throughout the species' range. For some fishes, reproductive success may be limited by the quantity and quality of suitable spawning habitat. Spawning site selection should place early life-history stages in or near habitat types that will foster growth and survival (Peebles and Tolley, 1988). For some estuarine-dependent fishes that spawn in low salinity coastal waters, suitable spawning conditions may be characterized by a combination of environmental and temporal variables (Peebles and Tolley, 1988; Baltz, 1990). The actual spawning sites used by a species may vary seasonally and annually because of changing climatic and hydrological conditions (Childers et al., 1990).

The sound-production ability of members of the family Sciaenidae, known generally as drums and croakers, is well known to scientists (Tavolga, 1980) and laymen. All sources of information provide evidence in the form of stories and expressions suggesting that sport and commercial fishermen (Baltz and Campos, 1996) have taken advantage of the behavior to locate spawning aggregations (e.g., "It's so quiet tonight, you can hear the croakers farting down at the York Spit," Linda Bohannon, Shacklefords, VA, personal communication). Nevertheless, scientists did not take advantage of drumming to study sciaenid reproduction until Mok and Gilmore (1983) described the repertoires of several species.

During the reproductive season, male sciaenids, including spotted seatrout, produce drumming sounds by vibrating the swimbladder with the surrounding musculature (Tower, 1908; Burkenroad, 1931; Fish and Mowbray, 1970; Tavolga, 1971). Females do not have a well-developed drumming apparatus (Tower, 1908; Pearson, 1929; Hein and Shepard, 1979), and only male sciaenids aggregate in suitable spawning habitat and drum to attract females that are ready to spawn (Pearson, 1929; Guest and Lasswell, 1978). Mok and Gilmore (1983) analyzed temporal and spatial sound production patterns by spotted seatrout (and other species) and found that sound production occurred primarily during the spawning season from dusk to midnight and that males produce four characteristic sounds, identified as: a grunt followed by a series of knocks, aggregated grunts, a long grunt, and a staccato. Since then the technique has been used to study spawning site selection for a variety of species and locations (Saucier et al., 1993; Baltz and Campos, 1996).

In Louisiana, spotted seatrout spawn from April through October (Fontenot and Rogillio, 1970), with a peak in July (Sundararaj and Suttkus, 1962). Spawning has been reported within bays and lagoons near passes to the Gulf of Mexico (Pearson, 1929); however, considerable spawning by spotted seatrout also takes place outside estuaries in the open Gulf of Mexico (Jannke, 1971). Most spawning by spotted seatrout has been reported in channels and in deep passes adjacent to open water (Tabb 1961, 1966; Tabb and Manning, 1961; Rogillio, 1975). Spawning begins when males aggregate in suitable spawning sites, usually before sunset, and croak or drum — presumably to attract females (Pearson, 1929). Tabb (1966) described spawning by spotted seatrout as constant milling of the spawning school, with light side-to-side body contact among individual fish. The fertilized eggs are buoyant and float toward the surface while the unfertilized eggs gradually sink. Fertilized spotted seatrout eggs hatch in 16 to 20 h at 25°C and larvae emerge at a length of 1.3 to 1.56 mm (Fable et al., 1978). Within 20 h of hatching, most sciaenid larvae in the northern Gulf of Mexico are identifiable by the presence of yellow chromatophores (Holt et al., 1988).

Saucier and Baltz (1993) studied spawning site selection in Louisiana by locating drumming aggregations through the use of a hydrophone (i.e. passive acoustics). From March 1987 to October 1990, 315 sound observations were made to identify and characterize spawning seasons and environmental requirements in the Barataria, Caminada, and eastern Timbalier bay systems of Louisiana (Figure 10.3). The sounds produced by the spawning aggregations were identified and verified against known recordings provided by Mok and Gilmore (1983). To characterize environmental conditions at listening locations, including suspected spawning sites, salinity, temperature, dissolved oxygen, current velocity, and water depth were measured.

DIEL DRUMMING PATTERNS

On one occasion the diel pattern in drumming activity of spotted seatrout was evaluated in a 24-h listening survey in Pass Abel (Figure 10.3), on July 26 and 27, 1989. Drumming activity was recorded between 1630 and 2330 h, but no drumming was recorded between 0100 and 1600 h. On other dates, drumming aggregations of spotted seatrout were located only between 1700 and 0100 h (Saucier and Baltz, 1993). The mean (±2 standard error of the mean, SE) time for large drumming aggregations was 2039 h (±0.29, N = 74), and 92% of the drumming took place between 1900 and 2300 h. No spotted seatrout drumming was recorded between 0200 and 1600 h. The suitability index indicates that spawning activity increased from 1800 h to a maximum between 2000 and 2100 h and decreased after 2100 h (Figure 10.4A). Mok and Gilmore (1983) recorded maximum sound production by spotted seatrout between 1930 and 2130 h.

STATISTICAL MODELS

Environmental and temporal variables were used in a statistical model to predict spotted seatrout drumming aggregation size. The stepwise regression procedure (SAS Institute Inc., 1985) selected a six-variable model, with an intercept, that included hour,^{2} hour,^{3} velocity, velocity–salinity interaction, velocity–depth interaction, and temperature.

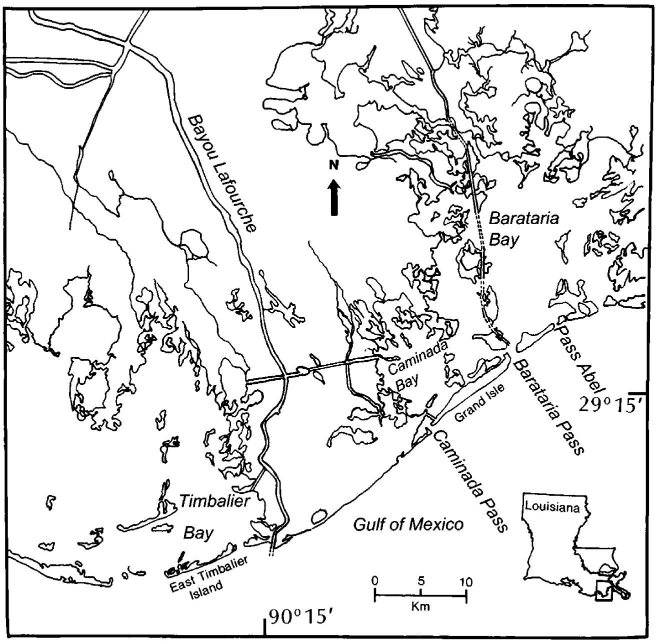

FIGURE 10.3 Study area for spotted seatrout spawning site selection. (After Saucier and Baltz. *Environ. Biol. Fish.*, 36:257–272, 1993.)

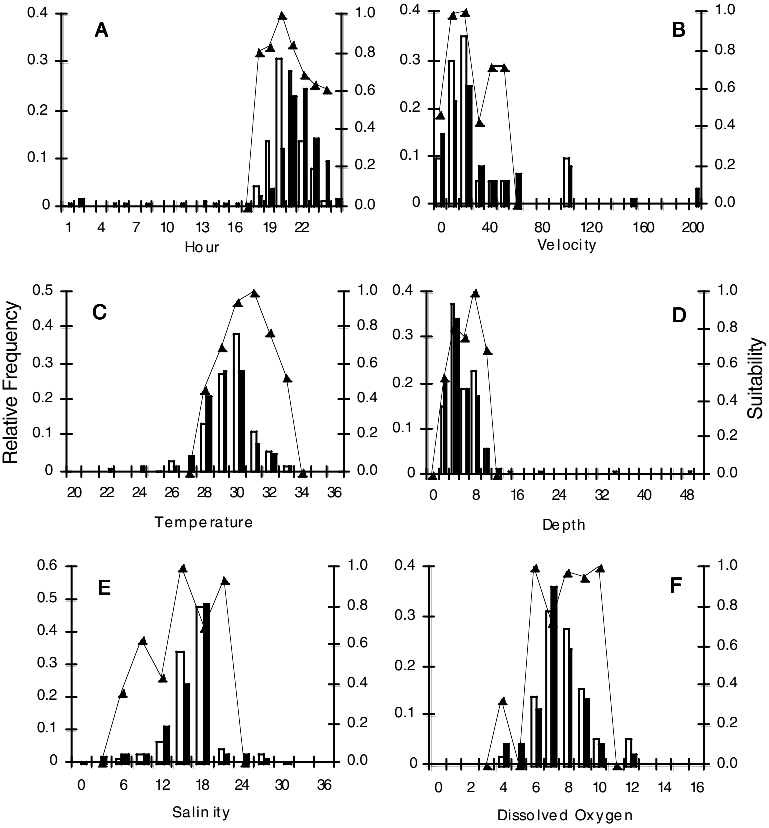

FIGURE 10.4 Patterns of resource use (open bars, spawning sites), availability (solid bars, all sites), and suitability (solid lines and triangles) for spotted seatrout spawning site selection. (After Saucier and Baltz. *Environ. Biol. Fish.*, 36:257–272, 1993.)

Of the physical variables, velocity, velocity–depth interaction, and temperature were important in predicting drumming aggregation size in the stepwise-regression model. For all spotted seatrout drumming sites, current velocity ranged from 3.0 to 100.0 cm sec^{-1}. Large aggregations were found in sites with velocities between 5.0 and 100.0 cm sec^{-1}; the majority of these (65%) were in velocities from 10.0 to 20.0 cm sec^{-1}. Although locations with higher velocities were sampled on three occasions, no drumming was recorded where the current velocity was greater than 100.0 cm sec^{-1}. Suitability for current velocity was high, between 10.0 and 20.0 cm sec^{-1} (Figure 10.4B).

Water temperature ranged from 24.5 to 33.5°C, with 83% of the spawning site observations taking place in water from 28.0 to 30.0°C. The mean (±2 SE) water temperature at sites of large aggregations was 29.7°C (±0.31, N = 73). Drumming was not observed in temperatures below 24.5°C. Suitability analysis for temperature indicated that spotted seatrout selected warmer waters and optimal spawning temperature exists between 30.0 and 31.0°C (Figure 10.4C). Water depths ranged from 1.2 to 34.1 m; most of the moderate and large drumming aggregations (91%) were observed in water depths between 2 and 10 m. The mean depth was 5.2 m (±0.55, N = 74) for large drumming aggregations and 5.7 m (±0.88, N = 92) for moderately sized drumming aggregations. Although water as deep as 48.0 m was sampled, no large aggregations were observed in depths greater than 10.0 m. Suitability for depth was high between 4.0 and 8.0 m (Figure 10.4D).

Of the chemical variables, salinity, dissolved oxygen, and the interaction of salinity and velocity made significant contributions to the prediction of spotted seatrout drumming aggregation size. Drumming took place in salinities ranging from 7.0 to 25.8 ppt, but 81% of the observations were in salinities between 15.0 and 18.0 ppt. Large drumming aggregations occurred at a mean (±2 SE) salinity of 16.6 ppt (±0.75, N = 73). Although a wide range of salinities were sampled up to 31.0 ppt, drumming was not observed in salinities greater than 25.8 ppt. Suitable spawning salinities were high between 15.0 and 21.0 ppt (Figure 10.4E). Dissolved oxygen concentrations for spawning aggregations of moderate to large size ranged from 4.4 to 12.0 mg l^{-1}, with 73% of the observations occurring at levels between 7.0 and 9.0 mg l^{-1}. The mean DO at sites where there was no drumming was 7.5 mg l^{-1} (± 0.23, N = 28). The mean DO for moderately sized aggregations was 7.1 mg l^{-1} (±0.44, N = 53), and for large aggregations, the DO mean was 7.9 mg l^{-1} (± 0.38, N = 58). Suitability for dissolved oxygen was highest at saturated levels between 6.0 and 10.0 mg l^{-1} (Figure 10.4F).

In Louisiana, the spawning sites selected by spotted seatrout can be characterized by the ranges and means of temporal and environmental variables recorded at the times and places where moderate and large aggregations of actively drumming males occur. Velocity, interactions of velocity with salinity and depth, and temperature are important environmental variables in determining spotted seatrout aggregation size (Saucier and Baltz, 1993). Mok and Gilmore (1983) found that the spawning seasons of soniferous sciaenids coincide with peak sound production by males. Saucier and Baltz (1993) verified spawning activity at drumming sites on several occasions by capturing recently spawned eggs and rearing them to identifiable larvae. The high density of buoyant eggs captured downstream from sites were in the cellular division and morula stages (< 3 h old), indicating that they were recently spawned and not eggs from other spawning sites or eggs that remained in the water column from the previous night's spawn (Holt et al., 1985).

In Louisiana, moderate and large drumming aggregations of spotted seatrout were located from late May through early October. The spawning season for spotted seatrout varies throughout its range, from April to October in Texas (Pearson, 1929; Brown-Peterson et al., 1988), and from February to October in south Florida (Powell et al., 1989) with spawning peaks in the late spring and summer (Sundararaj and Suttkus, 1962; Brown-Peterson et al., 1988; McMichael and Peters, 1989; Wieting, 1989). Photoperiod is probably the major determinant of the initiation and duration of the spawning season (Arnold et al., 1978; Hein and Shepard, 1979; Brown-Peterson et al., 1988).

Previous reports that spotted seatrout spawn in a wide range of habitats (Pearson, 1929; Tabb, 1961; Tabb, 1966) were corroborated by Saucier and Baltz (1993) in Louisiana. Gunter (1938) suggested that, in Louisiana, spotted seatrout spawn in the inshore waters of Barataria Bay and not in the Gulf like most other sciaenids. Saucier and Baltz (1993) located large spawning aggregations in passes between the barrier islands (Grand Isle, Grand Terre, and Timbalier Islands) and in dredged or natural channels in Barataria Bay and adjacent to Bayou Lafourche. During their study, spawning locations shifted spatially as much as 30 km in concert with changing environmental conditions over temporal spans as brief as 1 to 2 weeks.

Spotted seatrout probably also spawn in coastal waters that were not safely accessible at night in the small boats used by Saucier and Baltz (1993). Spawning site selection depends, at least in part, on salinity gradients, and highly suitable spawning salinities may occur in various locations inside or outside estuaries (Peebles and Tolley, 1988; McMichael and Peters, 1989). Salinities at most spawning aggregations in Louisiana ranged from 15.0 to 18.0 ppt (Saucier and Baltz, 1993); however, eggs and larvae have been captured at higher salinities of 25.0 to 36.0 ppt (Tabb, 1966; Arnold et al., 1978; Tucker and Faulkner, 1987; Rutherford et al., 1989a).

Salinity and temperature are important factors that affect egg hydration, buoyancy, and survival. Of naturally spawned eggs, 99% are fertilized (Arnold et al., 1978; Tucker and Faulkner, 1987). From laboratory studies, the limits of suitable spawning salinities range from a low of 5 ppt up to 45 ppt (Gray and Colura, 1988). A significant increase in hatching occurs between 15.0 and 25.0 ppt. Eggs hatch after 16 to 22 h between 25.0 and 27.0°C (Holt et al., 1985). Only buoyant eggs incubated in ambient sea water in which the salinity ranged from 12.9 to 27.0 ppt and temperatures ranged from 28.0 to 31.0°C were successfully hatched by Saucier and Baltz et al. (1993). Brown-Peterson et al. (1988) determined 23.0°C as the critical minimum spawning temperature, while others suggest minimums of 25.6°C (Tabb, 1966) and 26.3°C (Rutherford et al., 1989a).

The physical variables, current velocity and depth, may have significant effects on the spawning-site selection (Rutherford et al., 1989b). Peak spawning activity may coincide with water movements associated with moon phase and tidal amplitude (McMichael and Peters, 1989). Current velocity was statistically significant in the predictive model for spotted seatrout (Saucier and Baltz, 1993), and drumming aggregations were frequently located in channels and passes where substantial water movement was associated with ebbing or flooding tides. The selection of deeper spawning sites with high current velocities, which are limited in Louisiana's estuaries, may serve to concentrate individuals in well-oxygenated water and to disperse fertilized eggs.

REPRODUCTIVE STRATEGIES

Dusk and evening spawning is a reproductive tactic for temperate sciaenids, which are not dependent on light for courtship because they use sound to locate mates (Holt et al., 1985). Spawning in darkness has advantages that may include reducing predation on eggs and adults, higher DO concentrations, and avoiding the effects of sunlight on eggs (Holt et al., 1985). In a diel plankton sampling study, Holt et al. (1985) observed peak abundance of newly fertilized spotted seatrout eggs between 2030 and 2300 h. Hour of day had a significant effect in a predictive model for spotted seatrout drumming activity (Saucier and Baltz, 1993). While sound production occurs before, during, and after spawning (Mok and Gilmore, 1983; Tucker and Faulkner, 1987), Saucier and Baltz (1993) suggested that the male sciaenids typically arrive considerably earlier (i.e., near dusk) at drumming sites and begin drumming to attract females.

The maximum life span of spotted seatrout is about 10 years (Tabb, 1961). The spawning season of the spotted seatrout is long in contrast to some other large sciaenids such as red drum and black drum. Individual females spawn an average of once every 21 days, or about eight times per season (Arnold et al., 1978; Tucker and Faulkner, 1987; Wieting, 1989), although Nieland et al. (2002) found more frequent spawning, approximately once every 4 to 5 days, in Barataria Bay, Louisiana. Estimates of total egg production by spotted seatrout range from 2.3 million (Wieting, 1989) to 9 to 11 million (Nieland et al., 2002).

Growth rates between male and female spotted seatrout differ (Tabb, 1961; Sundararaj and Suttkus, 1962; Hein and Shepard, 1979; Brown-Peterson et al., 1988; Nieland et al., 2002). Sexual maturity in the spotted seatrout may be reached as early as age 1 (Sundararaj and Suttkus, 1962; Nieland et al., 2002). Saucier and Baltz (1993) hypothesized that the sex-specific difference in spotted seatrout growth rates is the result of the excessive time and energy expended (or forgone) by the males' drumming on the spawning grounds to attract females. If females participate in evening spawning only once every 4 to 21 days, and males participate each day during the prolonged spawning season, the investment in reproduction by males, in terms of time and energy, probably exceeds that of females and is reflected in the reduced growth rates of males. In contrast, other large sciaenids with shorter reproductive seasons do not exhibit significant sex-specific differences in size at age (Beckman, 1989; Murphy and Taylor, 1989; Fitzhugh et al., 1993).

ICHTHYOPLANKTON STAGE

Only limited ichthyoplankton research in Louisiana waters has focused specifically on spotted seatrout eggs and larvae. A more comprehensive study of the habitat requirements of larvae and recruitment bottlenecks is needed. Two studies of estuarine ichthyoplankton provide some insights into their distribution and occurrence in Louisiana's estuaries (Sabins and Truesdale, 1974; Raynie and Shaw, 1994).

Sabins and Truesdale (1974) studied the diel and seasonal occurrence of small fishes (postlarvae and juveniles) in Caminada Pass, Louisiana, over a 15-month period. They captured 748 spotted seatrout postlarvae ranging in size from 2 to 14 mm SL, and observed the highest abundance in August. They noted that Caminada Pass and its immediate environs were generally lower in salinity and devoid of beds of submerged vegetation that characterize interior bay spawning and larval habitat used by spotted seatrout in Texas and Florida.

Raynie and Shaw (1994) collected ichthyoplankton along a transect off Oyster Bayou into Fourleague Bay, Louisiana. This area may be characterized as a shallow turbid environment with strong salinity gradients ranging from near zero at the upper bay station to 30 ppt at the offshore stations (Raynie and Shaw, 1994). At the offshore stations, spotted seatrout larvae were collected only in August and their highest abundances were associated with intermediate salinities (5 to 27 ppt). Within Fourleague Bay, spotted seatrout were collected only from the seaward-most stations and when salinities exceeded 5 ppt (Raynie and Shaw, 1994). Larval spotted seatrout collected in tidal transport samples were significantly more abundant during flood tide, near the bottom. Larvae were also significantly larger when collected at night.

JUVENILE MICROHABITAT SELECTION, FOOD, AND GROWTH

Juvenile spotted seatrout were quantified along the marsh-edge ecotone from multiple drop samples (Rakocinski et al., 1992; Baltz et al., 1993), and their immediate environments were characterized by a suite of physical and chemical variables along with substrate type and *Spartina* stem density (Table 10.1). Differences in microhabitat use among the three juvenile-size classes (i.e., ≤ 15, > 15 and ≤ 30, > 30 and ≤ 100 mm SL) were not detectable (Baltz et al., 1993), probably due in part to small sample sizes. Juvenile spotted seatrout ranked 13th in overall abundance in marsh-edge samples, but were relatively uncommon and occurred in only 9% of the samples. When juveniles were present, (i.e., at capture sites) their mean (±1 SE [and maximum]) seasonal densities were low (winter: 0 ± 0, spring: 2.0 ± 0.42 [3], summer: 2.2 ± 0.36 [10], and fall: 2.2 ± 0.57 [8] individuals m^{-2}). Juvenile spotted seatrout occurred significantly more frequently than expected in samples with emergent stems (Rakocinski et al., 1992).

TABLE 10.1
Means ± SD of Microhabitat Measurements for Three Size Classes of Juvenile Spotted Seatrout in the Barataria Bay System, Louisiana

Variable	< 15 mm	15 to 30 mm	> 30 to 100 mm
Median depth (cm)	39.9 ± 10.9	33.3 ± 8.7	38.8 ± 12.6
Distance from shore (m)	1.4 ± 2.1	1.1 ± 1.2	1.2 ± 1.3
Substrate code	2.0 ± 0.9	2.3 ± 0.9	1.8 ± 0.8
Salinity	16.8 ± 4.1	16.6 ± 3.4	16.8 ± 3.0
DO (mg l^{-1})	6.5 ± 1.3	6.1 ± 1.1	6.7 ± 1.5
Temperature (°C)	29.5 ± 2.2	29.3 ± 2.4	29.8 ± 1.8
Turbidity (NTU)	18.6 ± 10.2	18.2 ± 9.8	14.6 ± 6.8
Velocity (cm s^{-1})	2.5 ± 2.4	1.4 ± 1.1	4.0 ± 8.9
Spartina stem density (# m^{-2})	11.7 ± 23.8	13.2 ± 22.5	29.5 ± 56.0
N (independent observations)	35	18	14

Note: Substrates were coded on an ordinal scale of particle size: 1: fines (i.e., clay and silt = mud), 2: sand, 3: organic detritus, and 4: shell or shell fragments.

Source: Baltz et al., *Environ. Biol. Fish.,* 36:109–126,1993.

Under the assumption that growth is a good indicator of habitat quality and recruitment potential (Sogard, 1992, 1994), Baltz et al. (1998) explored relationships among microhabitat use, food habits, conspecific density, and recent growth rate for small (< 29 mm SL) juvenile spotted seatrout. A series of multiple regression analyses were used to determine how nursery habitat influences early growth (Baltz et al., 1998). The spotted seatrout model included four predictor variables — otolith radius, prey diversity, salinity, and a salinity–DO interaction term — and explained 67.9% ($p < 0.0001$) of the variation in daily growth. All variables were significant ($p \leq 0.05$) and regression slopes were positive for all variables except salinity. Density variables were not significant in the model, suggesting that density dependence was not an important influence on recent daily growth.

Nurseries for juveniles of estuarine-dependent fishes are areas that harbor relatively high concentrations of individuals compared to similar nearby habitat types (Pearcy and Myers, 1974). The ultimate factors (Mayr, 1961) responsible for concentrating early life-history stages are poorly understood (Boesch and Turner, 1984), although proximate mechanisms for transport, retention, and habitat selection (Rothschild, 1986) have been described for many species. Active selection of nursery habitat is reflected by population responses to environmental gradients (Boesch and Turner, 1984; Hettler, 1989b; Rakocinski et al., 1992; Baltz et al., 1993). Presumably, the relative fitness of individuals using nursery habitats is enhanced by higher survival or growth (Walters and Juanes, 1993; Sogard, 1994). Patterns of nursery microhabitat selection are controlled or regulated in combination by physiological constraints, prey distribution, foraging success, competitor densities, and predation pressure, all of which may influence growth and survival.

For juvenile spotted seatrout, the daily increment of growth increased significantly with otolith radius, prey diversity, and a salinity–DO interaction term; it decreased with salinity (Baltz et al., 1998) and the intercept was not significant. From an analysis of partial correlation coefficients using the final model (Baltz et al., 1998), otolith radius constituted 60.2% and the remaining three variables constituted 7.7%, together explaining 67.9% of the total variance in daily incremental growth.

By focusing on food, microhabitat, and conspecific density, Baltz et al. (1998) identified several major exogenous environmental influences that regulate growth while controlling for the endogenous intrinsic influence of body size (Wootton, 1990). Recent daily increment widths in spotted seatrout were most strongly related to otolith radius, a measure of fish size. Simply put, larger individuals grew faster, in absolute terms, than smaller individuals. Nevertheless, after the influence of size was taken into account, microhabitat and diet variables still had a significant effect on growth. For spotted seatrout, prey diversity, salinity, and a salinity–DO interaction term (Baltz et al., 1998) were significant.

Physico-chemical variables, especially salinity, temperature, and dissolved oxygen concentration, generally influenced growth more than external factors such as the number of grass stems. For a closely related species, *Cynoscion regalis*, temperature and salinity reflect the suitability of estuarine zones as juvenile nursery habitat by affecting growth and feeding rates (Lankford and Targett, 1994). Climatic variables no doubt influence growth rates, abundances, and the distribution of many estuarine species, primarily through seasonal variations in temperature and salinity, which are important factors determining the structure of Louisiana's estuarine communities (Rakocinski et al., 1992; Baltz et al., 1993).

Oxygen and temperature effects on growth have been found in numerous studies (Brett, 1979; Jobling, 1994). Low oxygen levels and diel fluctuations in concentration may alter appetite and scope for activity and slow growth rates (Andrews et al., 1973; Brett, 1979; Wootton, 1990). In shallow Louisiana estuaries, the high concentrations of dissolved oxygen found by Baltz et al. (1998) may represent supersaturated conditions associated with high diurnal algal photosynthesis; however, the same water mass may experience hypoxic conditions at night (Reinert, 1993). Oxygen concentrations along the marsh edge ranged from 2.3 mg l^{-1} near dawn to 11.7 mg l^{-1} (supersaturated) during midday in the summer and early fall months when small juveniles were most abundant.

Spotted seatrout were also found on only three dominant substrate types: fines (i.e., silt and/or clay), sand, and organic detritus (Baltz et al., 1998), where mean daily increments of otolith growth were 21.4 ± 1.99 (µ47), 19.9 ± 2.54 (µ45), and 27.8 ± 7.42 (µ6) µm, respectively. Spotted seatrout appeared to grow most rapidly on organic detritus substrates, characterized as "coffee grounds," but the statistical evidence was weak because of few samples on that substrate type.

Limited information is available on the diets of juvenile spotted seatrout from the northern Gulf of Mexico and southeastern Atlantic Coast of the U.S. (Darnell, 1961; Hettler, 1989a, b; McMichael and Peters, 1989; Mason and Zengel, 1996). In Louisiana (Table 10.2), spotted seatrout rely primarily on the calanoid copepod *Acartia tonsa* and later make an ontogenetic shift from copepods to mysid shrimp at 10 to 20 mm SL. The major prey groups, *Acartia* and the mysid species *Americamysis almyra* and *Taphromysis louisianae*, are widespread along the marsh edge where juvenile spotted seatrout are most abundant, supporting the contention (Baltz et al., 1998) that refugia and foraging sites (*sensu* Walters and Juanes, 1993) are overlapping.

Food was only included in the spotted seatrout model as a significant independent variable in the form of prey diversity. Prey diversity may have been important to spotted seatrout because samples examined included individuals collected before, during, and after the ontogenetic shift from

TABLE 10.2
Means ± SD and Ranges for Microhabitat, Food, Density, Size and Growth Variables for Juvenile Spotted Seatrout in the Barataria Bay System, Louisiana

Variable	Mean ± SD	Range
Median depth (cm)	37.3 ± 9.28	17.0–68.0
Temperature (°C)	29.5 ± 1.67	24.5–33.0
Salinity	17.8 ± 3.46	10.0–27.2
DO (mg l^{-1})	6.5 ± 1.19	4.2–8.8
Velocity (cm s-1)	1.6 ± 1.44	0.0–6.0
Distance from shore (m)	1.1 ± 1.84	0.0–9.9
Spartina stem density (# m^{-2})	24.2 ± 34.81	0.0–129.6
Substrate code	1.6 ± 0.61	1–3
Turbidity (NTU)	16.8 ± 7.89	1–100
Fullness	2.8 ± 1.88	0–5
Total prey number	2.9 ± 4.18	0–33
Total prey mass (mg)	0.6 ± 0.86	0–3.7
Prey diversity (D′)	0.06 ± 0.118	0–0.9
Number of taxa	0.9 ± 0.59	0–3
Specific density (# m^{-2})	3.8 ± 2.48	1–10
Mysid mass (mg)	0.5 ± 0.87	0–3.65
Calanoid mass (mg)	0.004 ± 0.011	0–0.084
Amphipod mass (mg)	0.001 ± 0.010	0–0.1
Harpacticoid mass (mg)	0.0001 ± 0.0004	0–0.002
Tanaid mass (mg)	0.001 ± 0.010	0–0.1
Polychaete mass (mg)	0.001 ± 0.010	0–0.1
Zoea mass (mg)	0.0001 ± 0.0007	0–0.005
Fish mass (mg)	0.01 ± 0.104	0–1
Unidentified prey mass (mg)	0.013 ± 0.0007	0–1.0
Last otolith growth increment (µm)	21.1 ± 7.93	7.6–43.9
Age (days)	19.5 ± 6.39	10–35
Otolith radius (µm)	266.2 ± 133.78	61–555
Standard length (mm)	13.22 ± 7.06	3–28.8
Sample size	98	

Note: Substrates were coded on an ordinal scale of particle size: 1: fine (i.e., clay and silt = mud), 2: sand, 3: organic detritus, and 4: shell or shell fragments.

Source: Baltz et al., *Environ. Biol. Fish.*, 53:89–103, 1998.

copepods to mysids. *Spartina alterniflora* stem density was not an important variable in the model; similar findings in the same system (Toepfer and Fleeger, 1995) for bay whiff (*Citharichthys spilopterus*) indicate that feeding is more influenced by physico-chemical factors than by stem density, suggesting that physiological condition may control feeding rate. Alternatively, gut contents at one point in time (i.e., daylight hours) may be an inadequate temporal scale upon which to base predictions of daily growth one day earlier. An estimate of daily ration should be a more meaningful measure (Juanes and Conover, 1994). Alternatively, perhaps food is not limiting (Miller et al., 1991; Kneib, 1993) because the abundance of prey is high or because physiological stressors in estuaries primarily influence feeding (Malloy and Targett, 1991; Lankford and Targett, 1994).

The microhabitat and food variables included in the final growth model were a small subset of many intercorrelated variables and should not be construed as the only combination of variables (Table 10.2) with explanatory power (Johnson and Wichern, 1988; Neter et al., 1989). Variables related to conspecific density were not selected by the model, suggesting that density dependence was not important.

These models probably best apply in Louisiana's saltmarsh estuaries where environmental conditions are distinct when compared to conditions throughout the species' range (e.g., relatively little submerged aquatic vegetation, high turbidity, fine substrates, and a microtidal range of ~ 30 cm). Nursery habitat for spotted seatrout in Louisiana is probably not composed of necessarily separate refugia and foraging sites (*sensu* Walters and Juanes, 1993) but rather as potentially contiguous or overlapping areas that generally provide simultaneous access to refuge and prey (Baltz et al., 1998). If physico-chemical variables are not sufficient to explain growth variability, then the role of refugia as a nursery function needs further consideration. Refuge may not be simply *Spartina* stems *per se* but a combination of several habitat features of Louisiana's microtidal estuaries (Rakocinski et al., 1992; Baltz et al., 1993), including shallowness, turbidity, and the availability of complex structural cover in the form of emergent vegetation or substrate microtopography.

Along the marsh edge, the substrate is usually not visible in water deeper than 30 cm because wind and wave action keep fine sediments in suspension. These shallow and turbid conditions afford some degree of refuge to small fishes from other fish and avian predators, respectively. In Louisiana's *Spartina* marshes, some emergent vegetation is almost always flooded except at extremely low water levels (Sasser, 1977). Along eroding banks that are increasing in frequency, exposed *Spartina* rhizomes and a perturbed substrate surface generally provide complex cover, even at low water levels. Contrary to the expectation that erosional banks should provide better refuge and foraging sites because of their more complex microtopography (Baltz et al., 1998), evidence from other tidal systems indicates that densities and survival rates of small fishes are higher along depositional banks in freshwater marshes (McIvor and Odum, 1988; Rozas et al., 1988).

Essential fish habitat along the marsh edge may influence recruitment of spotted seatrout during early life-history stages. Baltz et al. (1998) suggested that growth for spotted seatrout in Louisiana is primarily a function of location (i.e., microhabitat site selection rather than prey or conspecific density). Certain physico-chemical conditions favor growth, although prey choice is important during ontogenic shifts. These data (and Baltz et al., 1993) suggest that fishes likely select sites with favored physical and chemical conditions. Thus, recruitment may depend upon the availability of suitable nursery habitat that provides vital functions enhancing growth and/or survival.

Whether for feeding, refuge, or both, population numbers of spotted seatrout may suffer if marsh-edge habitat availability is limited (Browder et al., 1985; Baltz et al., 1993), and poor recruitment may result from this ecological bottleneck (Fretwell, 1972; Yablokov, 1974; Wiens, 1977; Beck, 1995). As a result, cohort success may be reduced by climatic anomalies (Wiens, 1977) that prevent fishes from occupying the most favorable sites for growth. For example, during years when tidal flooding of marshes is infrequent in Louisiana's microtidal estuaries, access to flooded *Spartina* marshes by fishes and macroinvertebrates is greatly reduced (Childers et al., 1990; Baltz et al., 1993) and may serve as an ecological bottleneck. Among-year variation in the timing and extent of high water conditions (Sasser, 1977) may help account for annual variation in post-larval recruitment

(Beckman, 1989; Childers et al., 1990). Now that important physico-chemical factors have been identified, future research may examine historical records of climatological variation, marsh flooding frequency, and year-class strength of species that use different saltmarsh habitat types to determine if access to essential habitat is limited by hydrological factors.

PREDATORS AND PREY

We used a qualitative loop model (Puccia and Levins, 1985) to summarize information on spotted seatrout predators and prey (Darnell, 1961; Peters and McMichael, 1987; Hettler, 1989a, b; McMichael and Peters, 1989; Mason and Zengel, 1996; Baltz et al., 1998) during its life cycle (Figure 10.5). In the model, direct positive effects of one variable on another are indicated by links terminating in an arrow (→), and negative effects are indicated by links terminating in a filled circle (•—). Longer pathways (i.e., loops) that return to a starting point in the model form positive and negative feedback loops that result in indirect effects of a given variable on other variables.

The model has a preponderance of negative feedback loops and proved to be highly stable (i.e., Hurwitz critera is true); however, the predictive value of the model was relatively low. Important spotted seatrout predators used in the model were the fishery on adult stages and gelatinous zooplankton on nonfeeding stages (i.e., eggs and early larvae). Seven size classes of feeding spotted seatrout shared seven prey groups (each composed of multiple species). Larval spotted seatrout depend heavily on zooplankton, especially *Acartia tonsa*, and then shift to mysids, amphipods, grass shrimp, and small fishes as juveniles. As subadults and adults, they depend on small fishes, penaeid

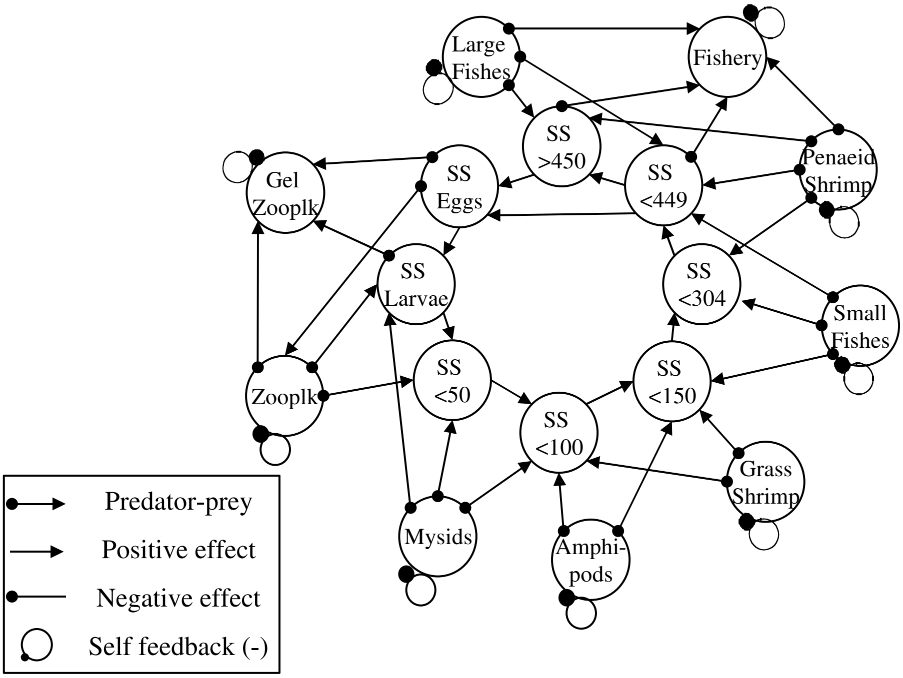

FIGURE 10.5 Loop model for spotted seatrout life-history stages, major predators, and prey showing interactions and ontogenetic shifts among seatrout size (SS) classes (i.e., generally indicated by the upper limits of nonoverlapping sizes in TL mm) and prey and predator taxa (including the fishery). Negative self feedback loops on predator and prey taxa indicate important controlling mechanisms not included in the model. Predator–prey interactions are positive at the arrowhead and negative at the closed circle, while commensal interactions are assumed to be unidirectional and positive at the arrowhead.

shrimp, and larger fishes. Ontogenetic prey shifts within and between seatrout size classes contributed to the stability of the model. Although all spotted seatrout life-history stages have direct positive influences on subsequent stages, many indirect feedback loops through shared predator and prey taxa may enhance or depress other seatrout life-history stages.

JUVENILE SEINE DATA ANALYSES

Since 1986, Louisiana Department of Wildlife and Fisheries' (LDWF) Marine Fisheries Division has conducted a statewide finfish sampling program that includes shoreline sampling with bag seines (15.25 m × 0.635 cm mesh; approx. 280 m^2 haul-sample^{-1}). Stations are sampled monthly from January to August and bimonthly from September through December. Previous analyses of these seine data demonstrated relatively high catches of juvenile seatrout at salinities lower than 10 ppt (Thomas, 1999). To examine the stratigraphy of these catches, we compared catches of juvenile spotted seatrout from 1994 to 2000 across marsh types as delineated by Chabreck et al. (1997).

Fifty-eight LDWF seine stations are located throughout the coastal zone, from Gulf barrier islands inland to the freshwater marshes (Figure 10.6). Louisiana is unique in the extent of its coastal marshes of each type (as of 1990): 163,180 ha saline marsh, 308,720 ha brackish marsh, 147,400 ha intermediate marsh, and 907,700 ha fresh marsh (LCWCRTF, 1998). Eighteen seine stations are located within the saltmarsh zone, where typical vegetation is smooth cordgrass (*Spartina alterniflora*), glasswort (*Salicornia* spp.), black rush *(Juncus roemerianus*), saltwort (*Batis maritima*), black mangrove (*Avicennia nitida*), and saltgrass (*Distichlis spicata*). Twenty-four stations are in brackish marsh, with wiregrass (*Spartina patens*), three-cornered grass (*Scirpus olneyi*), saltmarsh bulrush (*Scirpus robustus*), and widgeongrass (*Ruppia maritima*). Fourteen stations are in intermediate marsh areas, characterized by vegetation consisting of wiregrass (*Spartina patens*), deer pea *(Vigna repens*), bulltongue (*Sagittaria falcata*), Walter's millet (*Echinochloa walteri*), bullwhip (*Scirpus californicus*), and sawgrass (*Cladium jamaicense*). Two stations are in fresh marsh, with maidencane (*Panicum hemitomon*), pennywort (*Hydrocotyle* spp.), water hyacinth (*Eichhornia crassipes*), pickerelweed (*Pontederia cordata*), alligatorweed (*Alternanthera philoxeroides*), and bulltongue (*Sagittaria falcata*) (Chabreck et al., 1997). Typical salinity within each marsh zone is over

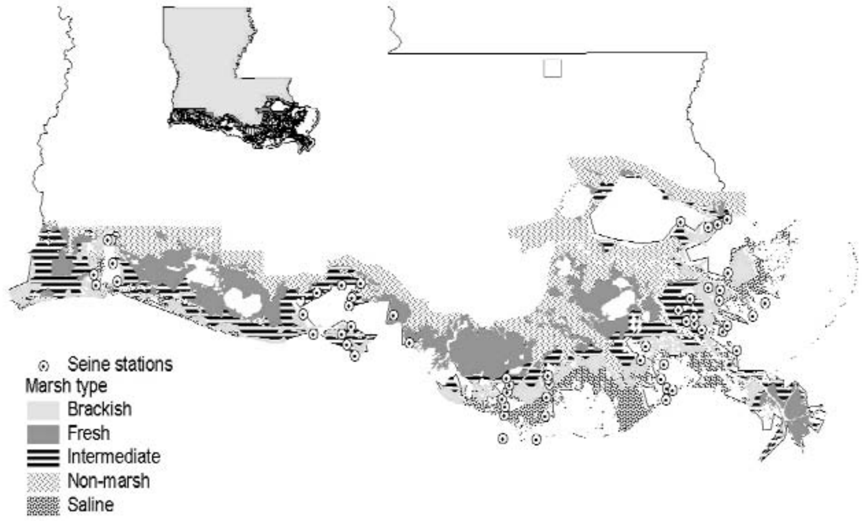

FIGURE 10.6 Louisiana marsh types showing LDWF coast-wide seine stations (after Chabreck et al., Louisiana Department of Wildlife and Fisheries, Fur and Refuge Division, and the U.S. Geological Survey National Wetlands Research Center. Lafayette, LA, 1997).

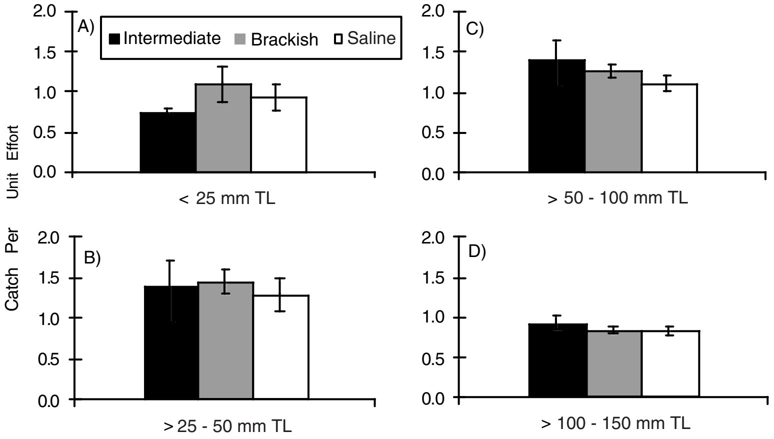

FIGURE 10.7 Juvenile spotted seatrout catch-per-unit-effort (CPUE ± 95% confidence intervals) by marsh type from LDWF coast-wide seine stations for four juvenile spotted seatrout size classes (SC): A. SC I ≤ 25 mm TL; B. SC II > 25 and ≤ 50; C. SC III > 50 and ≤ 100; and D. SC IV > 100 and ≤ 150 mm TL.

12 ppt in saline marsh, 4 to 15 ppt in brackish marsh, 2 to 5 ppt in intermediate marsh, and 0 to 3 ppt in fresh marsh (Louisiana Coastal Wetlands Conservation and Restoration Task Force and the Wetlands Conservation and Restoration Authority, 1998).

Juvenile spotted seatrout catches (Figure 10.7) from 1994 to 2000 were compared (±95% confidence intervals) between saline, brackish, and intermediate marsh types for four size classes: SC I ≤ 25, SC II > 25 and ≤ 50, SC III > 50 and ≤ 100, and SC IV > 100 and ≤ 150 mm TL. Comparison with catch data for fresh marsh was not made because of the limited number (2) of such stations. Catch-per-unit-effort (CPUE) data were transformed (L_n (x + 1)) for analysis to approximate normal distributions.

No significant differences in catch rates of juvenile seatrout were seen between marsh types for any size class except the smallest (≤ 25 mm TL), where catches were lower in the intermediate marsh zone than in brackish or saline marshes. It is possible that the greater distance of intermediate marshes from spawning areas may be controlling this apparent difference in distribution in the youngest specimens. Previous research on juvenile spotted seatrout (McMichael and Peters, 1989; Peterson, 1986) suggests that the highest affinity is to *Spartina alterniflora* shorelines. The current analysis demonstrates a relatively high occurrence of juvenile spotted seatrout in brackish and intermediate marshes. The coast-wide coverage and longer-term database of the LDWF sampling program probably account for the broader habitat-use patterns described here in contrast to earlier studies.

In addition, the low-topographic relief and microtidal nature of Louisiana's coastal zone probably favors the broader pattern. If highest-value marsh-edge ecotone (Baltz et al., 1998, 1993) occurs in proportion to total area of marsh type in Louisiana, then intermediate marshes could contribute nearly as much habitat for juvenile spotted seatrout as do saline marshes. Brackish marshes could provide almost twice the total nursery habitat as salt marshes. Further research on habitat morphology, relative growth and survival, and recruitment to nonshore-line habitat types is needed to produce a comprehensive model of juvenile spotted seatrout habitat values in Louisiana.

Habitat suitability analyses for temperature and salinity for the same four juvenile-size classes collected in marsh-edge seine catches across coastal Louisiana showed interesting annual patterns. The smallest individuals (SC I ≤ 25 mm TL) were present in low numbers from May to October, had high CPUEs in August, and had high temperature suitability values (S > 0.70) between 24 and 32°C (Figure 10.8A). Their salinity suitabilities were highest, at 19 ppt, and were high (> 0.70) between

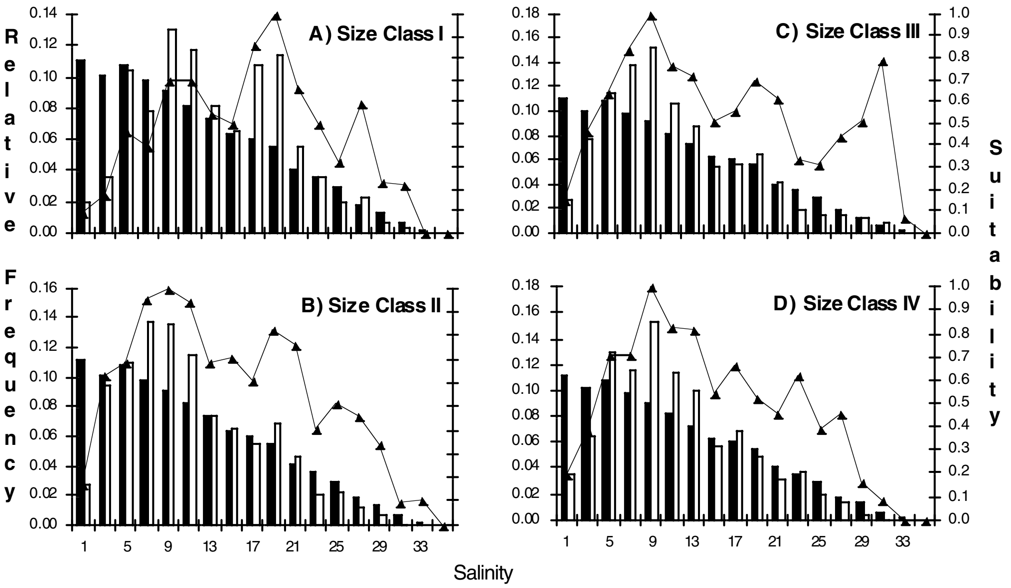

FIGURE 10.8 Patterns of resource use (open bars, occupied sites), availability (solid bars, all sites), and suitability (solid lines and triangles) for salinity selection by four juvenile spotted seatrout size classes: SC I ≤ 25 mm TL; SC II > 25 and ≤ 50; SC III > 50 and ≤ 100; and SC IV > 100 and ≤ 150 mm TL. Data are from LDWF coast-wide seine surveys.

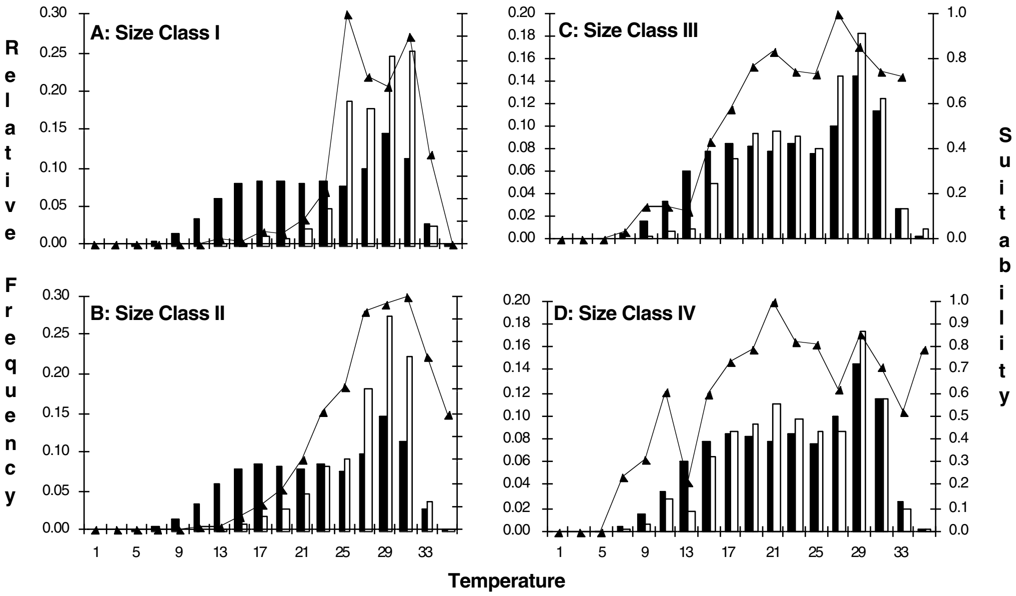

FIGURE 10.9 Patterns of resource use (open bars, occupied sites), availability (solid bars, all sites) for temperature selection by four juvenile spotted seatrout size classes: SC I ≤ 25 mm TL; SC II > 25 and ≤ 50; SC III > 50 and ≤ 100; and SC IV > 100 and ≤ 150 mm TL. Data are from LDWF coast-wide seine surveys.

8 and 22 ppt (Figure 10.9A). Their ephemeral occurrence and spawning habitat selection by adults somewhat segregates this smallest size class from other juveniles, particularly along the salinity gradient. The salinity suitabilities of other size classes peaked at a much lower salinity (9 ppt) and were high at salinities as low as 4 ppt and at salinites ranging from 16 to 22 ppt (Figures 10.8B to D).

Temperature suitabilites for all juvenile size classes were more similar, with high suitabilities ranging down to 16 or 18°C for the two larger (> 50 mm) size classes and down to 24°C for the two smaller (≤ 50 mm) size classes (Figures 10.9A to D). Individuals in size classes II and III occurred from June through November or December and their CPUEs peaked in September and October, respectively. The largest juveniles (SC IV > 100 and ≤ 150 mm TL) were captured in low numbers from July through December, with a peak CPUE in October. In general linear model (GLM) comparisons of mean salinities and temperatures used by size classes (Table 10.3), both factors were significant (salinity: F-value = 2.88, df = 3 and 3034, $p < 0.0344$; temperature: F-value = 94.28, df = 3 and 3041, $p < 0.0001$). Size class I used significantly lower salinities ($p < 0.05$) than all other size classes, but no other size classes differed. Size classes I and II did not use detectably different temperatures ($p > 0.55$), but all other comparisons were significant ($p < 0.0001$).

ADULT SUITABILITY ANALYSES OF SALINITY AND TEMPERATURE DATA

The Louisiana Department of Wildlife and Fisheries (LDWF, 1992) conducts gill net surveys across Louisiana coastal waters, a continuing sampling program begun in 1986. The surveys employ a "strike-net" approach, which entails setting a 750 × 8 ft (228.6 × 2.4 m) gill net with five 150-ft (45.7 m) panels of differing mesh sizes (1.00, 1.25, 1.50, 1.75, and 2.00 in. bar mesh to 25.4, 31.7, 38.1, 44.4 , and 50.8 mm mesh, respectively) from the stern of a boat, then running the boat around the length of the net three times before pulling in the net. Captured fishes were counted, measured, and identified. Environmental variables were remeasured at each sampling site, but station depths were recorded when the stations were first assigned and not measured for each sample as independent estimates (Baltz et al., 2000). Size classes were defined around the legal minimum size limit of 305 mm TL, with size class I ≤ 149 mm, size class II ≥ 150 and ≤ 304 mm, size class III ≥ 305 and ≤ 449, and size class IV ≥ 450 mm TL. size classes I and II were omitted from some analyses due to low number of fish collected.

A GLM approach was used to identify the influence of environmental variables on the abundance of spotted seatrout. Nonlinear terms were included in the model (second- and third-order terms) for temperature, salinity, and turbidity. Month series (from the first month consecutively numbered through the last) included higher order terms as well (first- through fourth-order) to account for long-term trends and cycles. Louisiana has four biologically meaningful seasons for spotted seatrout, and these were included in the model to identify possible shifts in environmental influences over the annual cycle: a nonspawning, overwintering season (October to March), a prespawning season (April), a spawning season (May to August), and a postspawning season (September) (personal communication, Harry Blanchet and Joseph Shepard, Louisiana Department of Wildlife and Fisheries).

TABLE 10.3
Mean Salinity and Temperature (± SE) for Size Classes of Juvenile Spotted Seatrout Captured in 9296 Monthly Seine Hauls across Coastal Louisiana between 1988 and 2000

Variable	Size Class I	Size Class II	Size Class III	Size Class IV
Salinity	13.0 ± 0.51 A	11.1 ± 0.22 B	11.3 ± 0.18 B	11.1 ± 0.24 B
Temperature	27.6 ± 0.26 A	27.3 ± 0.13 A	24.6 ± 0.14 B	23.4 ± 0.23 C

Note: Data were collected by the Louisiana Department of Wildlife and Fisheries, Marine Fish Division. Significant differences in posterior testing between means are indicated by different letters, reading horizontally.

Indices of habitat suitability were calculated from patterns of resource availability and use for each size class at intervals along salinity and temperature gradients. Resource availability was estimated from the relative frequency of observations (i.e., number of gill net sets) in intervals along environmental gradients derived from the environmental data sets (including all gill net sets, even those sets with no observed spotted seatrout). Resource use was estimated from the samples in which spotted seatrout were collected and were weighted for the number of individuals in a size class collected per net set. Chi-square values were calculated for the suitability intervals and tested for significance (Langley, 1971) to determine if spotted seatrout were more or less abundant than expected in particular salinity intervals.

In the GLM analysis to determine factors associated with seatrout abundance, environmental, spatial, and temporal variables contributed significantly to predicting the abundances of three spotted seatrout size classes and of all size classes combined (Table 10.4). When spotted seatrout size classes II through IV and all size classes combined (II through IV) were examined on an annual basis (i.e., without regard to seasons), the overall models (GLM F-value > 13.29, df = 204 and 20452, $p < 0.0001$) and most variables, with the exception of all turbidity variables, were significant. Salinity (but not its higher order forms) and temperature (including all higher order forms) were significant for all categories, as were most temporal variables and the spatial variable, station. This indicates that salinity had a linear influence but that temperature influences also included nonlinear effects.

When the same variables were examined in GLM analyses by season (i.e., overwintering, prespawning, spawning, and postspawning), fewer variables were significant, due in part to reduced variation within seasons. For size class II, station location contributed significantly to the model in every

TABLE 10.4

Significance of Variables for Predicting Spotted Seatrout Abundance by Size Classes in a General Linear Model of the Statewide Coastal Gill Net Surveys Conducted by LDWF between 1986 and 1998

	Size Class II		Size Class III		Size Class IV		All Size Classes (II-IV)	
Variable	**F-value**	**P > F**	**F-value**	**P > F**	**F-value**	**P > F**	**F-value**	**P > F**
Month-series	13.51	0.0002	31.34	0.0001	14.86	0.0001	32.57	0.0001
Month-series^2	6.94	0.0084	12.85	0.0003	15.86	0.0001	15.48	0.0001
Month-series^3	4.40	0.0359	7.00	0.0081	16.41	0.0001	9.52	0.0020
Month-series^4	3.27	0.0706	4.79	0.0287	15.76	0.0001	7.00	0.0082
Season^3	52.77	0.0001	75.09	0.0001	14.17	0.0002	88.26	0.0001
Salinity	4.37	0.0366	4.78	0.0287	4.37	0.0367	6.78	0.0092
Salinity^2	0.00	0.9662	0.08	0.7751	2.54	0.1112	0.00	0.9923
Salinity^3	3.55	0.0594	6.68	0.0098	0.68	0.4095	6.15	0.0131
Temp	10.04	0.0015	8.66	0.0033	6.25	0.0124	13.31	0.0003
Temp^2	9.62	0.0019	8.94	0.0028	6.62	0.0101	13.34	0.0003
Temp^3	6.25	0.0124	6.61	0.0102	6.28	0.0122	9.53	0.0020
Station	16.56	0.0001	17.78	0.0001	13.25	0.0001	21.81	0.0001
Turbid	0.40	0.5294	3.25	0.0714	0.84	0.3602	0.85	0.3563
Turbid^2	0.09	0.7696	1.90	0.1682	0.02	0.8854	1.06	0.3029
Turbid^3	0.05	0.8154	0.60	0.4385	0.07	0.7973	0.34	0.5614

Note: Size classes were defined around the legal minimum size limit of 305 mm TL, with size class II ≥ 150 and ≤ 304 mm, size class III ≥ 305 and ≤ 449, and size class IV ≥ 450 mm TL. The overall F-test results were significant (GLM, F-value > 13.29, df 204 and 20,452, $p < 0.0001$. Tabulated F-values are for model-order-independent analyses and have one degree of freedom (except station: df = 190).

season (GLM, $p < 0.0001$). In the overwintering period, salinity (GLM, df = 1 and 10,418, F = 6.16, $p < 0.0130$), salinity squared (GLM, df = 1 and 10,418, F = 4.42, $p < 0.0356$), and turbidity also contributed significantly (GLM, df = 1 and 10,418, F = 8.70, $p < 0.0032$). In September (postspawning transitional period), the four temporal variables also contributed significantly (GLM, df = 1 and 1523, F = 8.70 to 9.82, $p < 0.0032$) and indicated variation of a long-term or cyclical nature.

For size class III, station location and the first order temporal variable (month series) contributed significantly to the model in every season (GLM, $p < 0.0001$). In the overwintering period and in the prespawning transition period (April), the other three temporal variables also contributed significantly (GLM, df = 1 and 10,418, F = 9.36 to 16.63, $p < 0.0022$, and df = 1 and 1524, F = 9.42 to 19.30, $p < 0.0022$ for overwintering and transition periods, respectively). In the spawning period, turbidity (GLM, df = 1 and 6488, F = 16.16, $p < 0.0001$) and turbidity squared (GLM, df = 1 and 6,488, F = 8.84, $p < 0.0030$) also contributed significantly to the model. For size class IV, station location contributed significantly to the model in every season (GLM, $p < 0.0001$). In the overwintering period, all three salinity variables (GLM, df = 1 and 10,418, F = 4.46 to 6.16, $p < 0.047$) and the first- through fourth-order temporal variables also contributed significantly (GLM, df = 1 and 10,418, F = 8.73 to 14.17, $p < 0.0031$). In the prespawning transitional period, the first- through fourth-order temporal variables also contributed significantly (GLM, df = 1 and 1,524, F = 6.73 to 9.74, $p < 0.0096$). In the spawning period, the first- and fourth-order temporal variables also contributed significantly (GLM, df = 1 and 6,488, F = 9.41 and 6.94, $p < 0.0022$ and $p < 0.0085$, respectively).

Baltz et al. (2000) used habitat-suitability indices and chi-square tests to analyze habitat selection by adult spotted seatrout. In analyses of adult salinity use patterns by seasons (i.e., spawning, nonspawning, and transitional months) and size classes, several significant differences were identified between patterns of resource use and resource availability. These suitabilities are summarized graphically in Figures 10.10 through 10.12. In the nonspawning season, size class IV (Figure 10.10A) selected lower salinities (1 to 11 ppt) and had low suitabilities for most higher salinities typically encountered in Louisiana coastal waters, whereas size class III did not show a clear pattern, generally selecting higher salinities and avoiding some of the lowest salinities. In April, the selection of higher salinities increased (Figure 10.10B), especially for size class III, which selected against

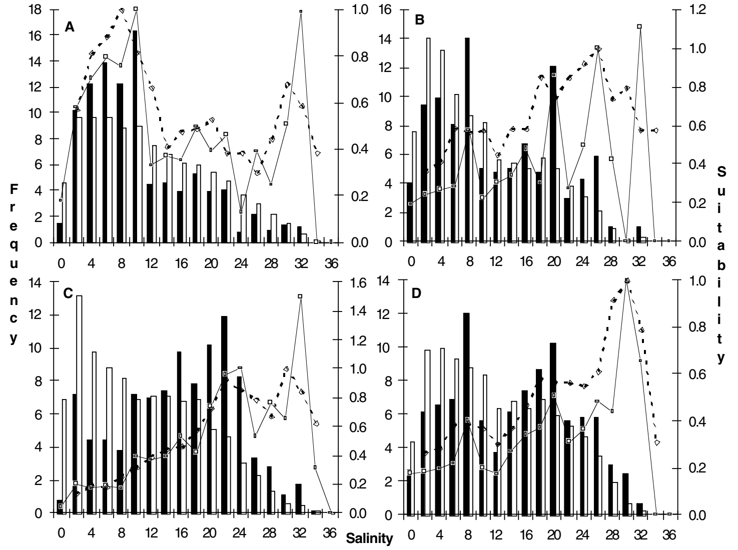

FIGURE 10.10 Seasonal patterns of resource use (open bars, occupied sites), availability (solid bars, all sites), and suitability (solid line) for salinity selection by large adult (SC IV) spotted seatrout. Dashed line is a three-interval running average used to smooth suitability curve. Data are from LDWF coast-wide gill net surveys. A. Nonspawning season; B. April; C. Spawning season; and D. September.

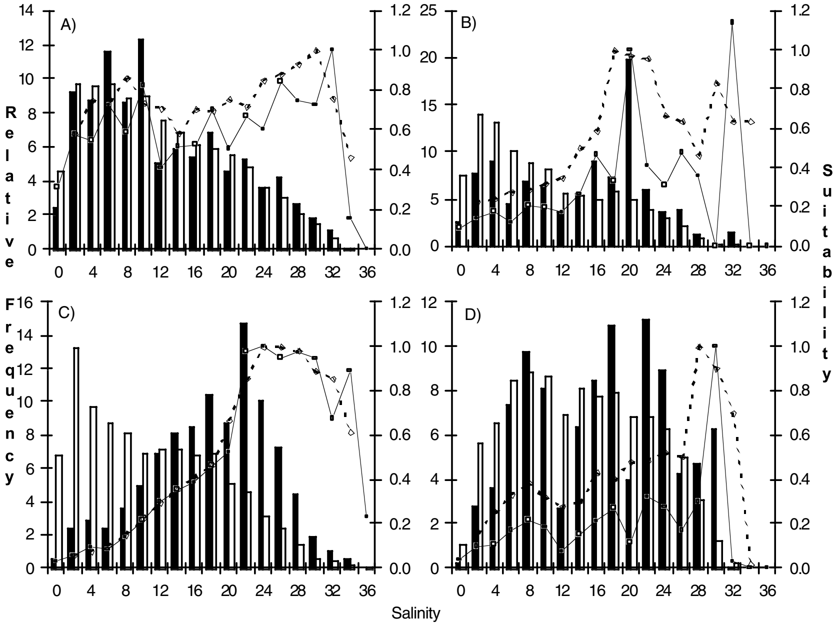

FIGURE 10.11 Seasonal patterns of resource use (open bars, occupied sites), availability (solid bars, all sites), and suitability (solid line) for salinity selection by legal-sized adult (SC III to IV) spotted seatrout. Dashed line is a three-interval running average used to smooth suitability curve. Data are from LDWF coast-wide gill net surveys. A. Nonspawning season; B. April; C. Spawning season; and D. September.

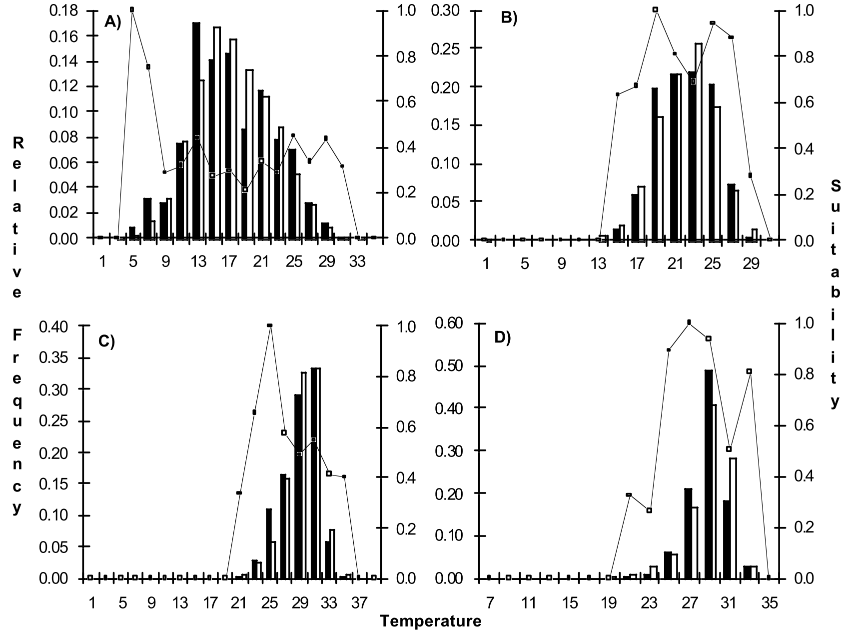

FIGURE 10.12 Seasonal patterns of resource use (open bars, occupied sites), availability (solid bars, all sites), and suitability (solid line) for temperature selection by large adult (SC IV) spotted seatrout. Data are from LDWF coast-wide gill net surveys. A. Nonspawning season; B. April; C. Spawning season; and D. September.

(chi-square = 2879, df = 16, $p < 0.001$) salinities lower than 13 ppt, and selected for most salinity intervals greater than 15 ppt. During the spawning season (May through August), selection was stronger than in the other seasons, especially for size class III, which selected strongly (chi-square = 16,729, df = 17, $p < 0.001$) against salinities lower than 11 ppt, and selected for salinities greater than 13 ppt. During the spawning season, size class IV selected against (chi-square = 660, df = 17, $p < 0.001$) salinities lower than 9 ppt, and for six salinity intervals greater than 15 ppt (Figure 10.10C). During the postspawning transitional period (September), selection by size class III was generally for higher salinities and against lower salinities, but the pattern was not as strong (chi- square = 697, df = 16, $p < 0.001$). Size Class IV selected strongly (chi-square = 126, df = 15, $p < 0.001$) for one salinity interval at 30 ppt (Figure 10.10D).

Additional analyses, conducted for all spotted seatrout of legal size (i.e., size classes III and IV combined, > 305 mm TL, ~ 12 in.) for the same seasons, also showed significant differences between patterns of salinity use and availability (chi-square > 467, df ≥ 16, $p \leq 0.001$). In the non-spawning season, legal size spotted seatrout tended to avoid the lowest salinities and select for salinities in the 6 ppt interval (Figure 10.11A), but most salinity intervals were used in proportion to availability. In April the pattern of selection was stronger in that salinities less than 13 ppt were avoided and most of those greater than 15 ppt were selected for (Figure 10.11B). In the spawning season, selection was also strong, with salinities below 11 ppt selected against and those above 13 ppt positively selected (Figure 10.11C). In September the pattern was weaker, but higher salinities were favored (Figure 10.11D).

We used habitat suitability indices and chi-square tests in analyses of temperature use patterns for adult spotted seatrout to identify several significant differences between resource use and resource availability among seasons (i.e., spawning, nonspawning, and transitional months) and size classes. For overwintering spotted seatrout in size class III, use generally exceeded availability above the 16°C interval and lower temperatures were avoided (chi-square = 1104, df = 17, $p < 0.001$). For size class IV, the pattern was significant (chi-square = 81, df = 17, $p < 0.001$) but not clear (Figure 10.12A). In April, there was strong selection for most temperatures above 24°C for size class III (chi-square = 629, df = 10, $p < 0.001$), but no significant overall pattern (Figure 10.12B) for size class IV (chi-square = 15, df = 10, $p > 0.05$).

During the spawning season, temperature use patterns differed from availability for size classes III (chi-square = 436, df = 12, $p < 0.001$) and IV (Chi Square = 73, df = 11, $p < 0.001$). For size class III, the major positive contributions to the Chi-square were for the intervals between 24 and 32°C. For size class IV selection was negative below 24°C, and it was positive between 24 and 28°C (Figure 10.12C). For the postspawning transition in September, temperature selection for Size Class III (chi-square = 436, df = 12, $p < 0.001$) was positive for temperature between 28 and 32°C, but generally negative or neutral otherwise. For size class IV, the overall pattern was significant (chi square = 17, df = 7, $p < 0.01$), and selection was positive between 26 and 30°C (Figure 10.12D).

Salinity and temperature are generally considered to be the most important physico-chemical factors that influence fish distributions between and within estuarine systems (Moyle and Cech, 2000); both are also highly correlated with other important variables. On an annual basis, both were important factors in GLM analyses (Table 10.4) of the distribution and abundance of spotted seatrout size classes in coastal gill net surveys conducted by LDWF, and this was still the case after the influence of a considerable number of other factors had been taken into account. However, when the temporal range of each analysis was reduced to biologically important seasons, these same variables — salinity and temperature — were apparently less important.

Nevertheless, salinity and temperature should be considered important from a resource management perspective when freshwater input into a coastal system has the potential to change existing salinity and temperature conditions. This view is supported by the changing patterns of resource use by size classes of spotted seatrout along salinity and temperature gradients in the suitability analyses. For controlling variables such as temperature and salinity, population responses that show peaks along gradients should represent near optimum conditions, and distributional extremes at the tails of population patterns may indicate the tolerance limits of a species (Bovee and Cochnauer, 1977;

Magnuson et al., 1979; Jobling, 1981, 1994). Nevertheless, there are numerous examples of preferred habitat types not being occupied because of the presence of a predator or competitor or low population numbers (Werner et al., 1977; Fraser and Sise, 1980; Baltz et al., 1982).

SPOTTED SEATROUT AS INDICATORS OF ESTUARINE HEALTH

Research in estuarine nurseries is needed to identify the essential habitat characteristics that facilitate the growth and recruitment potential of juvenile spotted seatrout associated with *Spartina alterniflora* marshes. Although many estuarine species may serve as potential indicators of estuarine health, juvenile spotted seatrout offer several possible advantages:

1. They are a valued resource that managers and the public alike monitor and appreciate for their importance to estuarine communities.
2. They are relatively short lived and their populations are likely to respond to changing ecological conditions within a few years.
3. The ecological requirements of all their life-history stages are generally well known so that changes in their distribution and abundance can serve as short-term indicators of changing conditions.
4. As high-level predators, they prey on a number of abundant and key prey species (i.e., shrimp and bay anchovy) and integrate information on water quality and the condition of their prey's habitat.
5. The integrated information is reflected in biological endpoints that could be used to assess local estuarine conditions.

In a recent model, Baltz et al. (1998) evaluated food, conspecific density, microhabitat variables, and fish size as independent factors predicting recent daily growth as a proxy for the recruitment potential of early juveniles. This model could be extended to include some biochemical measures of recent growth or physiological condition (e.g., electron transport system, citrate synthase, or RNA/DNA ratios) or stress (i.e., plasma cortisol) as additional response variables and an index of community health as an additional predictor variable. We suggest incorporating biochemical measures of health and condition (Avella et al., 1991; Schreck et al., 2001) to evaluate individual condition and evaluate stress of spotted seatrout juveniles in a range of habitats and incorporating an index of biotic integrity to evaluate community health. By analyzing how the recent daily growth or condition of individuals varies across environmental gradients, habitats ranging from high quality to highly degraded could be assessed to evaluate impacts on estuaries. The index of biotic integrity could be used as an independent assessment of system health (Karr and Chu, 1997). Fish require more than functional habitat; they need to be parts of healthy communities and ecosystems, and their resource needs must be met in terms of energy, materials, and sites (Hurlbert, 1981).

While focusing initially on a few key species like spotted seatrout, ultimately we would be providing a basis for identifying, enhancing, and restoring the biotic integrity of aquatic systems. Karr and Chu (1997) identified five factors — water quality, habitat structure, flow regime (e.g., freshwater management), energy source, and biological interactions —that define system quality and influence individual, population, community, ecosystem, and landscape health (Shrader-Frechette, 1994). Biological indicators that respond to gradients in habitat quality are more relevant and sensitive than simple chemical criteria (i.e., water quality or toxicological criteria), which often fail to detect degradation of biological systems (USEPA, 1992). Understanding how the growth and physiological condition of juvenile spotted seatrout respond across gradients of habitat quality and community health will enhance their value as estuarine indicator species.

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11 Sound Production and Communication in the Spotted Seatrout

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CONTENTS

INTRODUCTION TO SOUND PRODUCTION IN SPOTTED SEATROUT

Sciaenid fishes such as the spotted seatrout have been known to produce sound for centuries (Aristotle, 1910; Dufossé, 1874), and the association of sciaenid sounds with spawning has been known nearly as long (Darwin, 1874; Goode, 1887). For hundreds of years the Chinese have isolated sciaenid spawning sites from their watercraft by listening to drumming sounds emanating from the water through the hulls of their boats (Han Ling Wu, Shanghai Fisheries Institute, personal communications).

The isolation of sciaenid spawning sites using underwater technology is recent and dependent upon the availability of underwater transducers, hydrophones, and acoustic recorders used to access and study underwater sounds (Fish and Mowbray, 1970). Hydrophone tape recording of vocalizations produced by large sciaenid aggregations during spawning was pioneered by Dobrin (1948),

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Dijkgraaf (1947, 1949), Knudsen et al. (1948), Protasov and Aronov (1960), Schneider and Hasler (1960), Tavolga (1964), Fish and Mowbray (1970), and Fish and Cummings (1972).

The first isolation and description of soniferous sciaenid aggregations using mobile hydrophones moving along a sound transect at spawning sites were conducted by Takemura et al. (1978), Mok and Gilmore (1983), and Qi et al. (1984). A portable hydrophone and recording system were carried via a boat from one site to another along a measured transect, with recordings made along a preset grid or in a linear series (Mok and Gilmore, 1983; Gilmore, 1994). Recordings were made for 30 to 300 sec at each site, depending on transect length. Recorded sounds were verified by recording captured specimens identified to species and documenting specific sound types through sonographic analyses. This technique allowed spatial-temporal isolation and identification of species-specific sounds produced by sciaenid fishes, particularly under conditions of high sound attenuation for large group sounds (low-frequency, high-intensity sounds). Mok and Gilmore (1983) described the characteristic sounds of black drum, *Pogonias cromis*, spotted sea trout, *Cynoscion nebulosus,* and silver perch, *Bairdiella chrysoura,* based on detailed sonographic analyses of field recordings.

Subsequent to these observations, considerable additional work has been done on sound characterization in these species. Passive acoustic transect techniques have been used by several investigators to isolate spawning sciaenid groups in the field (Saucier and Baltz, 1992, 1993; Connaughton and Taylor, 1994, 1995; Luczkovich et al., 1999, 2000). This chapter will discuss sound production in the spotted seatrout and reveal the characteristics of its complex mating calls as well as the conditions under which these calls are produced.

PHYSICS OF SOUND PRODUCTION: WHY IS SOUND A PREFERRED ENERGY FIELD IN WATER?

Of all the energy fields detectable in aquatic habitats, sound is one of the most pervasive. Water is basically opaque to light; even in the clearest waters, most light energy is absorbed within tens of meters and is totally absent at depths of 1.5 km (Sverdrup et al., 1961; Preisendorfer, 1976; Levine and MacNichol, 1979, 1982; Kirk, 1983; MacFarland, 1991). In turbid coastal waters and estuaries, light attenuation may occur within tens of centimeters. Consequently, the optic systems of fishes are at a disadvantage in detecting objects and other organisms around them when compared to terrestrial organisms.

The opposite is true of sound energy, however; water is essentially incompressible relative to air, so sound velocity is five times faster in water (1464 to 1546 m/sec) than in air (330 m/sec at sea level) and attenuates less, particularly in oceanic waters. Low-frequency sounds carry farther than high-frequency sounds, often traveling many kilometers in open ocean basins (Richardson et al., 1995). It is not surprising that a wide variety of aquatic organisms, such as crustaceans, fish, and cetaceans, typically communicate using sound (Myrberg,1981; Richardson et al.,1995; Fay and Popper, 1998). Cetaceans are well known for their ability to broadcast high-frequency sounds and process sound reflections from objects in their immediate environment, producing acoustic images of their surroundings and prey.

The relationship between sound energy and frequency varies with aquatic environments and oceanographic and hydrological conditions. Low-frequency sounds propagate farther away from the source than high-frequency sounds; therefore, in environments where sound is most likely to attenuate rapidly, sound broadcasters are most likely to produce low-frequency sounds. Energy loss is approximately proportional to the square of the frequency. “At frequencies > 5 kHz, absorption causes significant (> 2 dB) transmission loss if range is > 10 km. At frequencies < 1 kHz, absorption is not significant at ranges < 40 km” (Richardson et al., 1995; absorption (a) = 0.036, frequency $(f)^{1.5}$ in kHz). The most significant and robust spotted seatrout sounds are at frequencies below 600 Hz (Mok and Gilmore, 1983; Gilmore,1994).

A number of physical characteristics of shallow estuarine waters create acoustic properties that may be significant to an estuarine sound producer. Because warmer water increases sound absorption, the spotted seatrout, which spawns during the warmer periods of the year (Brown,1981; Brown-Peterson et al., 1988; Brown-Peterson and Warren, 2001; also see Chapter 8 in this volume), must overcome these properties of shallow estuarine waters to propagate spawning calls. In contrast, shallow-water sound propagation could increase due to "cylindrical spreading," which causes sound to intensify and to vary inversely with distance from the source rather than inversely with the distance squared as in the "spherical spreading" typical of sound propagation in the pelagic oceanic environments (Richardson et al., 1995). With cylindrical spreading, various reflected waves combine to form a cylindrical wave spreading in all directions away from a vertical axis extending from the bottom to the surface. However, cylindrical spreading may be impeded by a wide variety of physical conditions and structures in very shallow estuaries. In shallow estuarine environments, i.e., in depths < 3 m, sound rapidly attenuates over soft mud or heavily vegetated substrates.

Mok and Gilmore (personal observation) performed a series of seatrout call attenuation experiments within the Indian River Lagoon of east central Florida. They found that 20 to 30 dB (re 1 μPa) sounds at 100 to 600 Hz frequencies were not detected 10 to 20 m from the source in shallow (< 1.5-m depth) seagrass meadows (*Syringodium filiforme* and *Halodule wrightii*). However, calls in deep, rock-lined lagoon channels, 3 to 4 m deep, allowed single, short-grunt call (20 dB re 1 μPa, 100 to 400 Hz) detection up to 100 m from the sound source. Therefore, sound propagation in shallow water is variable and site specific because it is strongly influenced by the acoustic properties of the bottom and surface as well as by variations in sound speed within the water column. Additionally, thermal, salinity, and particle discontinuities within the water column can refract, scatter, and absorb sound. For these reasons, site choice for sound production is very important to the spotted seatrout because they produce sound primarily for communication during the spawning event and require call recognition by other seatrout for effective reproduction.

WHY PRODUCE SOUND? REASONS FOR SOUND PRODUCTION BY AQUATIC ORGANISMS

Abiotic and biological sound energy is ubiquitous throughout shallow coastal environments of world oceans. Some of the most abundant and continuous sounds are produced by alpheid snapping shrimp and barnacles. Snapping shrimp produce sound through the rapid movement of their chelae, producing a vacuum and an ephemeral gas bubble that pops instantly with a loud acoustic percussion. Wherever snapping shrimp habitat exists, constant high-frequency (3-7 kHz) snaps are heard. This is the recurrent, "frying pan" sound of most coastal acoustic recordings. Barnacles and a variety of mollusks also produce sound. The ecology and behavior associated with many of these invertebrate sounds have not received adequate study.

The functions of many fish sounds have been determined through careful study of behavior associated with the sounds (Myrberg, 1981; Zelick et al., 1998). Transient or ephemeral spontaneous sounds are often produced by fish when disturbed, either to warn other individuals or to deter predators. Loud, low-frequency booms are produced by goliath grouper, *Epinephelus itajara*, when carcharhinid sharks are observed near their spawning aggregations on offshore reefs in the Gulf of Mexico (C. Koenig, Florida State University personal communication).

The most predictable and robust sounds produced by many fishes, however, are those associated with reproduction. As in many soniferous animals, it is the male that must attract a mate and induce her to donate eggs for fertilization; therefore, it is often only the male that produces sound. Males of various sciaenid species (e.g., weakfish, *Cynoscion regalis*, and silver perch, *Bairdiella chrysoura*) form large choral aggregations. Seatrout soniferous aggregations are formed specifically for attracting females with which to mate and spawn. These aggregations contribute no significant resources required by females except the males themselves (no male paternal care, no food, no nest sites) and are appropriately called seatrout "leks," such as those formed by aggregative birds and amphibians strictly for the purpose of reproduction (Höglund and Alatalo, 1995).

A lek is an arena to which females come and on which most of the mating occurs. An arena is a site on which several males aggregate, but it does not form the habitat normally used by the species for other activities such as feeding. Spotted seatrout leks are seasonal and associated with a wide variety of environmental parameters favorable for egg, larval, and adult survival. The acoustic properties of lek sites are undoubtedly favorable for mating call transmission and must have specific acoustic properties. Although many spotted seatrout spawning sites have been isolated to date, their acoustic properties have not been studied in detail (Mok and Gilmore, 1983; Saucier and Baltz, 1992, 1993; Luczkovich et al., 1999).

The spotted seatrout is not known to produce sound other than at the time of spawning. Isolated mating calls have been recorded from shallow seagrass sites early in the spawning season but probably represent only extralimital, prenuptial calls (Mok and Gilmore, 1983). Female trout do not produce sound. Male spotted seatrout produce sound — characteristic mating calls to attract females to the male aggregation and possibly to specific individual males at the spawning site (Mok and Gilmore, 1983). Aggregative calling occurs only at the appropriate time for spawning, facilitating successful mating, egg fertilization, egg and larval dispersal, and survival.

SOUND PRODUCTION MECHANISMS: HOW ARE SOUNDS PRODUCED BY SPOTTED SEATROUT?

Fishes produce sound using a variety of mechanisms, varying from the stridulation or scraping of bones, teeth, and spines to sound produced by forcing water through mouth and gill apertures. Some of the most robust and energetic sounds are produced by sonic muscles vibrating the membrane of the gas bladder. The latter mechanism is the most prevalent sound-producing mechanism in the spotted seatrout and other sciaenids. Color Figure 11.1* shows the location of the gas bladder and sonic muscles in the male spotted seatrout. Also depicted is a dorsal view of the gas bladder showing the anterior dorsal horns, which contact the skull. When a freshly captured, recently calling male seatrout is dissected, the bright red sonic muscles surrounding the gas bladder can be easily differentiated from the exterior lateral body muscles. The muscle vibratory rate is directly associated with the fundamental frequency of the characteristic seatrout call produced by the gas bladder.

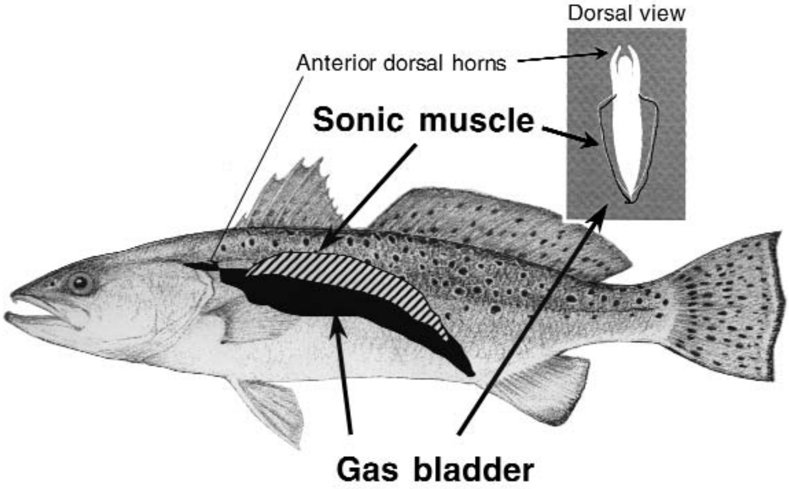

FIGURE 11.1 Position of gas bladder and sonic muscles (cross hatch) associated with sound production in male spotted seatrout. Inset reveals air bladder shape (white) and sonic muscle attachment (black with white outline) as viewed from above.

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* Color insert figures follow page 242.

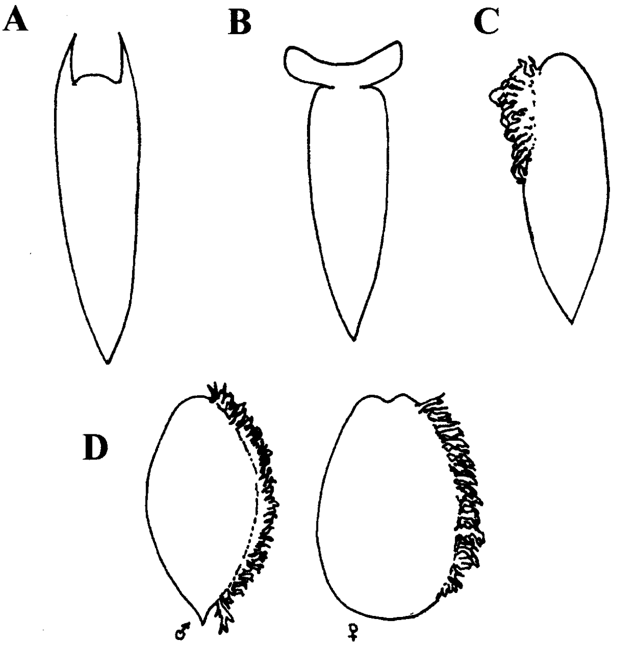

FIGURE 11.2 Variation in sciaenid gas bladder morphology. A – spotted seatrout, *Cynoscion nebulosus*; B – silver perch, *Bairdiella chrysoura*; C – red drum, *Sciaenops ocellata*; D – left male, right female, black drum, *Pogonias cromis*.

The characteristic shape of the sciaenid gas bladder is so conservative that it has been used as one of the primary characters to classify sciaenids and to determine their phyletic relationships (Chu et al., 1963; Chao 1978, 1986; Figure 11.2). Most of the 1200 species in this family produce sound using sonic muscles associated with the gas bladder. Sciaenids use the species-specific shape of the gas bladder as a sound-producing organ to produce diagnostic sounds that can be used to identify species within the family (Mok and Gilmore, 1983), as has been demonstrated in amphibians and birds (aves).

SOUNDS OF THE SPOTTED SEATROUT: CLASSIFICATION

WHAT TYPES OF SOUND DOES THE SPOTTED SEATROUT PRODUCE?

Characterization of the mechanism of sound production and sound types produced by black drum, *P. cromis*, spotted seatrout, *C. nebulosus*, and silver perch, *B. chrysoura*, was initiated by Tower (1908), Burkenroad (1931), Moulton (1964), and Fish and Mowbray (1970), but the diversity of species-specific sound types and difficulties of sound recognition under acoustically complex field conditions were not recognized. Extensive field studies, recordings, and analyses conducted by Mok and Gilmore (1983) brought about recognition of the variation and diversity of sounds produced by these species. Male spotted seatrout produce four distinct sound types, characterized by different fundamental frequencies, harmonic patterns, and different time-series pulse patterns (Table 11.1).

Spotted Seatrout Sound Classification

Spotted seatrout sounds are described in detail from a variety of graphic acoustic analyses (Figures 11.3, 11.4, and 11.5). These patterns can then be compared to analyses with historical studies of the

TABLE 11.1
Acoustic Characteristics of Indian River Lagoon Male Spotted Seatrout Calls

Sound Type	Fundamental Frequency Hz	Number Harmonic Bands	Harmonic Partial Frequencies Hz	Max Frequency Hz	Duration msec	Pulse Number
Dual-Pulse	100–175 (138)	2	200-290 (257), 380-400 (393)	850–1150 (1087)	140–210	2
Multiple-Pulse	100–175 (138)	2	200-290 (257), 380-400 (393)	850–1150 (1087)	140–450	3–5
Long-Grunt	90–110 (100)	3	190-250 (220), 310-370 (340),400, 480-700 (500)	950–1150 (1011)	175–367	1
Staccato	30–100	3	280-300, 320-400, 540-580	1300 (2340)	822.5	16+

same or similar sounds (Mok and Gilmore, 1983) to obtain the most detailed sound description. With this baseline description, a comparison was made with syntopic sound producers to isolate unique sound characteristics for spotted seatrout. The principal syntopic sound producers at study sites within the Indian River Lagoon were other sciaenids, silver perch, weakfish (*Cynoscion regalis)* black drum and red drum (*Sciaenops ocellata*) as well as the ariid catfish and the hardhead catfish *Arius felis*.

During courtship and spawning, spotted seatrout produce four major sound types (Mok and Gilmore, 1983):

1. Paired *dual-pulse* (DP) calls (= short grunts of Mok and Gilmore, 1983) (Figures 11.3 and 11.4)
2. A *long-grunt* (LG) call (Figures 11.3 and 11.5)
3. Three or more *multiple-pulse* (MP) calls (Figure 11.5)
4. A rapid series of short pulses known as the *staccato* (S) call (Figures 11.3 and 11.5)

These calls are, in turn, combined within aggregations generally classified as 1) scattered individual sounds, 2) small group sounds, and 3) large group sounds. All four seatrout call types have been recorded at the principal spawning sites, as were all of the various group sounds during long-term studies of spotted seatrout spawning activity. These studies were conducted during 1979 to 1980, 1985 to 1986, 1990 to 1994, 1995 to 1997, and 1999 to 2000 within the Indian River Lagoon system on more than 200 12- to 50-km nocturnal transects made from 26°58′ to 29°05′ N, a coastal distance of 254 km (Mok and Gilmore, 1983; Gilmore, 1994, 1996, 2000). These sounds, in addition to sounds produced by captive spotted seatrout, were used to define sound types.

Sonograms made from spotted seatrout sounds produced in Indian River Lagoon revealed energy distributed in five frequency or resonance bands, with primary band frequencies varying with the four basic sound types (Table 11.1). These five resonance bands shifted their major frequency intervals as the spotted seatrout sound type changed (e.g., dual pulse to long grunt).

The most common spotted seatrout call produced in spawning aggregations (i.e., up to 90% of the time) is the paired dual-pulse (DP) call (= short grunt of Mok and Gilmore, 1983; Figures 11.3 and 11.4; Table 11.1), consisting of two 35- to 70-msec pulses separated by an interval of 105 to 123 msec (range: 53 to 123 msec) and creating a total sound duration of 140 to 210 msec. The fundamental frequency (i.e., lowest frequency of a harmonic series, generally equal to the vibration rate of the air bladder in Hz) is 38 to 40 Hz (consequently, sound partials are at 38- to 40-Hz intervals), with major resonance bands at 85 Hz (range: 70 to 95 Hz), 135 Hz (range: 100 to 200 Hz), 250 Hz

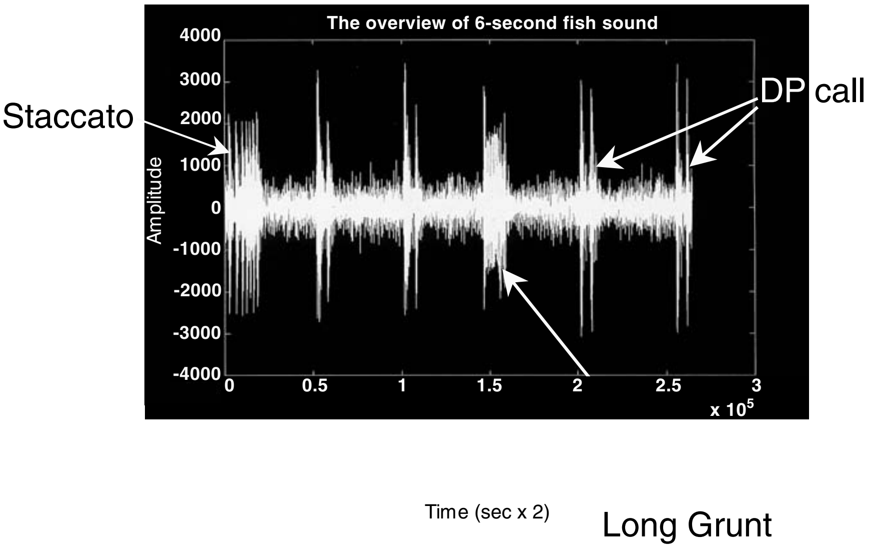

FIGURE 11.3 Oscillograph of three primary call types produced by the spotted seatrout, recorded from a single captive individual courting several females.

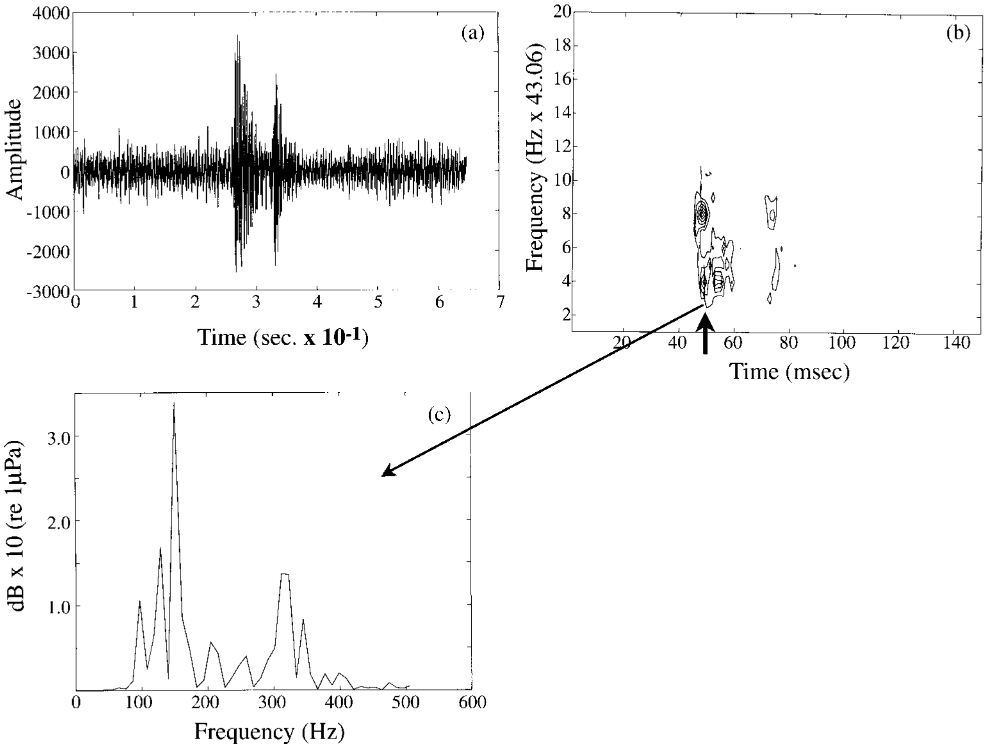

FIGURE 11.4 Spotted seatrout DP call morphology: (a) oscillograph; (b) sonograph; (c) power curve.

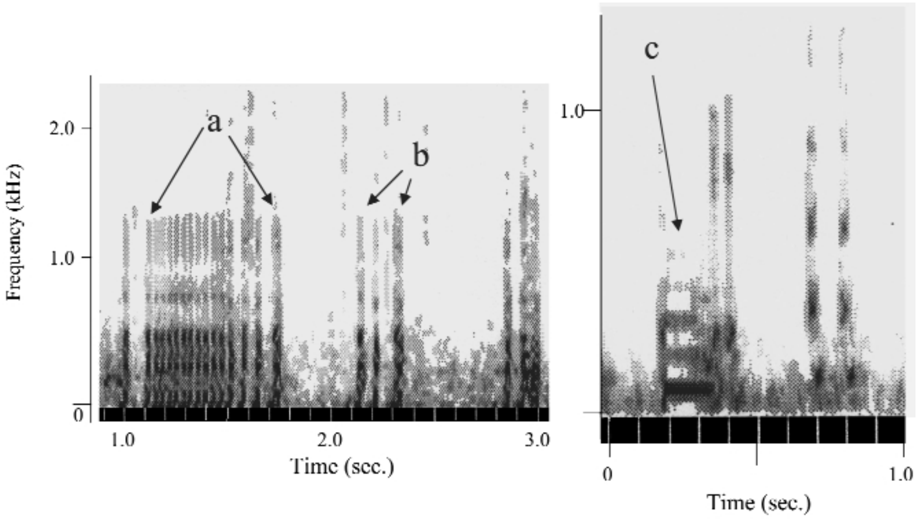

FIGURE 11.5 Sonographs of spotted seatrout: a – staccato (S); b – multiple-pulse (MP); c – long grunt (LG) calls.

(range: 220 to 270 Hz), 330 Hz (range: 320 to 350 Hz), and 460 Hz (range: 420 to 530 Hz) (Table 11.1). Most energy is centered at 135 Hz and drops off considerably at frequencies over 350 Hz. Dual-pulse call frequencies may extend to 1185 Hz, but most sound above 500 Hz is insignificant. Typically, more energy, longer duration, and higher maximum frequency (850 to 1300 Hz) are in the first pulse of the pair. The energy, major frequency bands, and harmonics for the multiple-pulse (MP) call are the same as in the DP call (Figure 11.5). MP calls may consist of between three and five pulse aggregates but never reach the rapid succession of pulses, fundamental frequency, and harmonic pattern observed in the staccato (S) call.

The long-grunt (LG; Figure 11.5) call is harmonic with fundamental frequencies at 100 Hz (range: 90 to 110 Hz), with up to four weaker resonance bands at 200 Hz (range:180 to 250 Hz), 300 Hz (range: 280 to 370 Hz), and 400 Hz, and with total sound duration of 230 to 500 msec (mean: 314 msec; Table 11.1; Figure 11.5). A 500- to 700-Hz, 40- to 50-msec duration pulse may initiate the LG call, while one to two higher frequency diffraction pulses associated with the end of the long grunt may reach 800 to 1110 Hz — or, rarely, to 1400 Hz, as described by Mok and Gilmore (1983). These diffraction pulses have a fundamental frequency of 135 to 150 Hz (mean: 145 Hz), with 35- to 53-msec duration.

The staccato (S) call typically consists of a 800- to 850-msec-duration pulse train with a major harmonic component and interpulse separation of 35 to 105 msec; most separations are 35 to 44 msec for a 16-pulse sequence (Figures 11.3 and 11.5). Initial pulse separations are greater, with 62- to 88-msec intervals for pulses 1 to 4. The last pulse is also staggered from the main train by 105 msec (Figure 11.5). Maximum frequencies are about 1500 Hz for most of the staccato call, although the third pulse reached 2340 Hz. The fundamental frequency is lower than that of other seatrout sounds and is between 30 to 33 Hz; five major resonance bands are centered at 33 to 60 Hz (range: 0 to 150 Hz), 300 Hz (range: 270 to 350 Hz), 500 Hz (range: 430 to 600 Hz), 833 Hz (range: 733 to 980 Hz), and 1200 Hz (range: 1080 to 1400 Hz).

The most energetic sounds produced by the spotted seatrout are the staccato and long grunt because muscular oscillation rates increase, as does sound duration. Consequently, fundamental frequencies decrease and frequency ranges increase, with the latter often above 1000 Hz in both sounds. With this increase in frequency range and lowering of the fundamental frequency, resonance-band distributions move to higher frequencies and harmonic frequency partials associated with these resonance bands are more evident in the sound and sonograph (Figures 11.3 to 11.5).

Because acoustic energies increase from dual-pulse (DP) to long-grunt (LG) to staccato (S) call types, it is not surprising that the DP call is produced most often. During lek call periods, spotted seatrout DP calls are produced continuously with periodic LG calls. The rarest call, the "S," is heard only during the period of maximum sound production, typically an hour or two after sunset.

ACOUSTIC AND SPAWNING ECOLOGY OF THE SPOTTED SEATROUT

WHEN AND WHERE DO SPOTTED SEATROUT PRODUCE SOUND?

Mok and Gilmore (1983) demonstrated that spotted seatrout sound production was specifically associated with crepuscular and nocturnal courtship and spawning activities. Pelagic eggs and larvae of the spotted seatrout were collected with plankton nets at spawning sites during vocalization periods (Mok and Gilmore, 1983; Alshuth and Gilmore, 1993, 1994, 1995). These same studies of soniferous spawning aggregations have demonstrated long-term spawning site fidelity, with the principal spawning sites identified by Mok and Gilmore (1983) being used for more than 20 years (Gilmore, 1994).

Because male spotted seatrout could be recognized by distinctive crepuscular calls, their presence or absence from specific locations could be determined and the percent occurrence of calls at all acoustic listening sites could be derived. In addition, the approximate size of the calling group could be estimated, based upon sound intensity (dB level, re 1 μPa) and group size estimates, using a three-part scale: 1) small group or individual callers; 2) moderate groups of several tens of callers; and 3) a large group of what appear to be hundreds of simultaneous callers. Unfortunately, mixed-species chorus behaviors were common, with *Arius felis* and *Bairdiella chrysoura* joining in with spotted seatrout calls and, therefore, elevating site-specific sound intensities and masking seatrout numbers based on sound intensity.

The percent occurrence of spotted seatrout calls at a site or time period is the most objective data used to define site and period use by seatrout leks. However, Gilmore (1994) found that spatial and temporal distributions of the estimated group size, egg and larval abundance in the water column, and percent occurrence of calling trout were highly correlated ($r = 0.92$ to 0.98 at $\alpha = 0.05$). This indicates that group-size estimates were a useful, independently derived variable that could verify calling trout distributions and relative use of specific sites or particular times of the year. These two data types have been used to isolate spawning times and locations (Gilmore, 1994).

Diel Sound Production Patterns

Mature, spawning spotted seatrout males begin to form aggregations in the late afternoon an hour or two before sunset. The pronounced diel periodicity of seatrout sound production has been demonstrated by 24-h recordings (Mok and Gilmore, 1983). Spotted seatrout initiate sound production at least an hour before sunset, but the sound is typically limited to sporadic single DP calls. It is not until after sunset that group calls become evident. Most group calls are made from sunset to 3 h after sunset, consisting of DP and LG calls with an occasional staccato (S call). Peak sound production usually occurs within 1 to 2 h after sunset. Calling sounds may be heard up to 4 or 5 h after sunset but are limited to few individuals in late evening (to 2400 h) and early morning hours (0100 to 0200 h). No male calling sounds have been heard during diurnal periods except those produced just before sunset.

Seasonal Patterns in Male Seatrout Mating Calls

Within the Indian River Lagoon system of east central Florida, calls were first heard in shallow seagrass meadows adjacent to deeper channels in February to late May and early June. Early reproductive period calls were typically from individual fish and not major group formations (Gilmore, 1994). During February, trout eggs and larvae were collected in the lagoon, indicating that these early season sounds were in fact associated with sporadic spawning activity by pairs or small groups of individuals peripheral to primary spawning sites in deeper channels.

In the southern Indian River Lagoon, the season with the most consistent and widely distributed calling male trout aggregations was late summer, August through September. Late summer group calls were heard at 38 of 47 sites (80%), particularly under spring tide conditions. Even though soniferous aggregations begin to form in April and May, they were not as ubiquitous (Gilmore, 1994). In the northern Indian River Lagoon system (i.e., Mosquito Lagoon), peak calling activity occurred earlier, from June to August, with major sound production in July (Gilmore et al., 2001). In the southern Indian River Lagoon, calling spotted seatrout were seldom heard in July after a May to June spawn but were heard at all grid transect stations made during September.

The last trout vocalizations are typically heard in October. Eleven transects consisting of 264 acoustic stations made from November 1991 through April 1992 did not record any seatrout sounds at any of the known primary spawning sites. These temporal data reveal that spotted seatrout choral activity begins in May and ends in October. Major spawning peaks occur in May to June and August to September, with the late-summer and early-fall male chorus the largest for the year.

Lunar Phase Associations

Although seatrout calling occurred on all lunar phases, it was most ubiquitous and occurred most often on the full moon or within 3 to 4 days after the full moon. The lowest call frequency of occurrence was during the last quarter. First-quarter lunar phases appeared to have higher choral activity than the new moon, though the difference was insignificant (Gilmore, 1994).

This diel pattern in sound production and spawning has several potential adaptive advantages for aggregated spawning adults as well as for egg and larval survival and dispersal. When spotted seatrout adults form large aggregations during crepuscular and dark nocturnal periods, they may avoid sight-feeding predators more effectively, due to low light levels and by aggregating. Principal Indian River Lagoon seatrout spawning sites are at least 7.5 to 100 km from the nearest ocean inlet, thus avoiding ocean inlet sites (Mok and Gilmore, 1983; Gilmore, 1994).

The primary predator on spotted seatrout within the Indian River Lagoon is the bottlenose dolphin, *Tursiops truncatus* (Barros and Odell, 1995). This predator can locate its prey by passive acoustic means (listening to trout calls) or by using active sonar (echolocation), so the absence of ambient light is inconsequential for bottlenose dolphin. However, since spawning occurs under a full moon in relatively shallow waters, nocturnal ambient light conditions are the brightest during the month then, making some sight feeding by predators more plausible.

Another potential advantage to crepuscular and early nocturnal spawning on spring tides is associated with egg and larval transport. Within the Indian River Lagoon, full- and new-moon periods are typified by flood tides from sunset to midnight, particularly within 7 to 25 km of ocean inlets. This condition would allow spring-tide-spawning spotted seatrout to disperse drifting eggs and larvae toward the upper reaches of the Lagoon prior to tidal reversal, the first ebb tide. Since Indian River Lagoon spotted seatrout prefer spawning sites greater than 5 to 7 km away from ocean inlets, this indicates a preference for egg and larval dispersal away from ocean inlets, the only seaward exits from the Lagoon system. Spotted seatrout eggs and early larvae sink within 48 h after fertilization and will go through only three to four tidal cycles before settling into epibenthic waters, insuring entrainment near the adult spawning site.

Great variations in ambient light conditions on spring tides make predator avoidance a less likely reason for seatrout spawning at night. Seatrout spawning calls increase in intensity on spring tides. Since new moon (dark nights) and full moon (brightest night) phases coincide with spring tides and since ambient light conditions differ significantly between new and full moon phases, seatrout spawning on bright full moon nights makes it less likely that predator avoidance is the primary factor influencing nocturnal timing for spawning adults. Furthermore, planktonic predators are very active during the early evening, as well, potentially consuming seatrout eggs and larvae (Day et al., 1989).

There are also acoustic advantages to nocturnal spawning, particularly for propagating spawning calls in a shallow estuarine environment. Nocturnal climatic and oceanographic conditions are generally calm relative to typically active meteorological conditions during the day. Acoustic signals attenuate less at night due to low ambient wind speed; therefore, lower wave action and surface turbulence are present than during windy diurnal periods. Not only does increased surface wave action absorb sound normally reflected off an otherwise smooth surface, but increased wave action in shallow estuaries also resuspends sediments and other particles known to absorb sound. This may be a particularly important factor in shallow coastal estuaries, where water column physics are more greatly influenced by climatic conditions. Greater nocturnal sound penetration throughout the estuary would facilitate male aggregation formation and female detection of male mating calls.

Spatial Distribution of Male Seatrout Spawning Calls

Spotted seatrout typically form soniferous leks in deeper estuarine waters. From 1978 to 2000, more than 3000 separate site location acoustic recordings were made giving detailed spotted seatrout sound distribution patterns for the Indian River Lagoon. Mean group-size estimates were calculated for each site and compared with the percentage of calling seatrout present out of all recordings made at that station during the entire survey. As presented earlier, the group-size estimate and the independently derived percent-occurrence value were highly correlated. This demonstrates that the frequency of call presence and call numbers is a good indicator of site use by calling males and, consequently, of spawning activity by attracted silent females, as demonstrated by egg and larval presence in the water column (Alshuth and Gilmore, 1993, 1994, 1995).

Calling male spotted seatrout consistently avoided specific regions of the lagoon. Spotted seatrout calls were conspicuously absent from waters adjacent to freshwater sources (rivers and canals), bridges (except a single high-span bridge on a natural lagoon channel between island formations), and ocean inlets.

Acoustic transects monitored along a 48.6-km section of the Indian River Lagoon during 1979 to 1980 and 1990 to 1993 consistently isolated nine seatrout leks. This section of the lagoon could be divided into three subregions based on spawning use, acoustic signal periodicity, and intensity (Figure 11.6). The three subregions are divided by portions of the lagoon where little or no spotted seatrout spawning activity occurs. The most consistently significant concentration of spawning spotted seatrout of these nine spawning groups is the Blue Hole Point Group (Figure 11.6). This same group was identified 11 to 12 years prior to this study by Mok and Gilmore (1983), therefore indicating consistent site-specific use by a large number of calling male spotted seatrout for two decades.

DOES SPOTTED SEATROUT SOUND PRODUCTION INCREASE THE PROBABILITY OF PREDATION MORTALITY?

Predation on spotted seatrout has been documented from a variety of sources. Egg and larval mortalities occur from a variety of invertebrates as well as from intraspecific larval cannibalism (Alshuth and Gilmore, 1993, 1994). Pelagic cnidarians, ctenophores, and chaetognaths are well known for their ability to consume large numbers of fish larvae. They are all present in estuaries throughout the range of the spotted seatrout and undoubtedly consume seatrout planktonic eggs and larvae. However, it is unlikely that any of these organisms associates mating calls of spotted seatrout at spawning sites with food resources. It is much more likely that other fish and marine mammals, most notably the bottlenose dolphin, are capable of homing in on the seatrout chorus and visiting spawning sites to consume the spawning seatrout. Barros and Odell (1995) found that the primary prey of Indian River Lagoon bottlenose dolphin populations was spotted seatrout; it was the most abundant food item in dolphin digestive system examinations.

In the summer spawning periods, seatrout diurnal behaviors do not favor bottlenose dolphin predation. During the day most larger trout are dispersed and feeding singly or in small groups in and

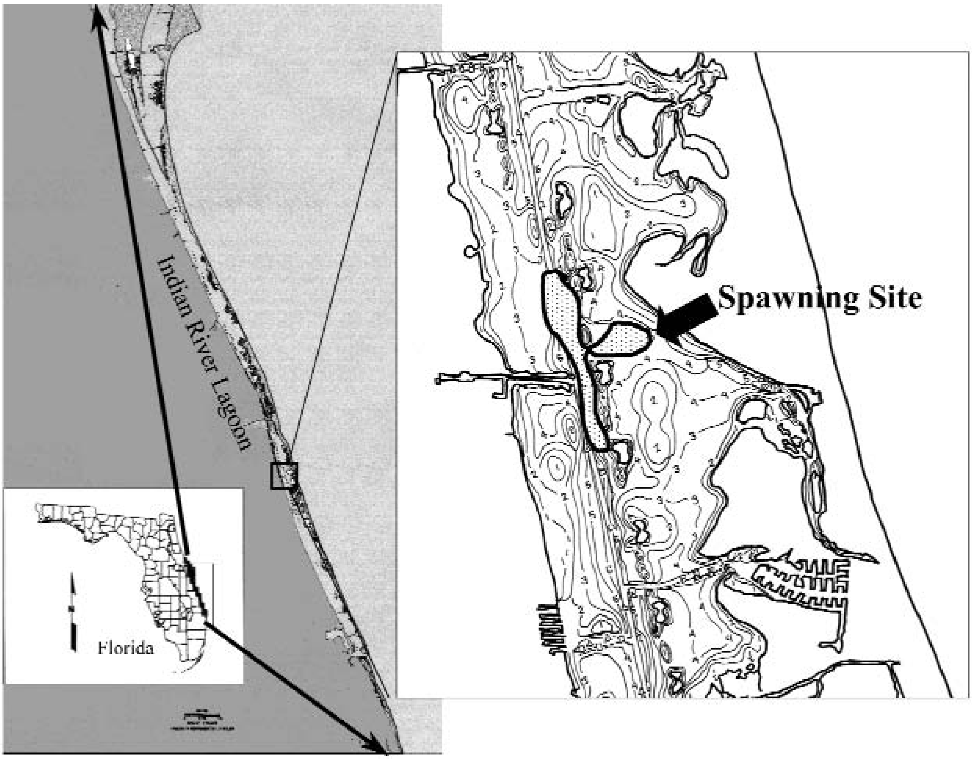

FIGURE 11.6 Contour map of Blue Hole Point spotted seatrout spawning site, Indian River Lagoon, east central Florida.

around shallow seagrass meadows and other structures. They are silent during diurnal feeding forays. Spotted seatrout are much more accessible to predators when aggregated at night. Since the bottlenose dolphin can use echolocation to find trout as well as hear trout vocalizations, it is likely that seatrout vocalizations increase chances of predation by these predators. Bottlenose dolphin have been consistently observed at several spotted seatrout spawning sites and their sonar and vocalizations recorded during the crepuscular and nocturnal seatrout chorus (R.G. Gilmore, personal observation). Although direct predation on seatrout during their spawning aggregations has not been documented, it may be assumed that this would be an advantageous time for a predator to attack seatrout — when it is aggregated and concentrating its behavioral activity on finding mates, courtship, and releasing gametes, and not necessarily on predator avoidance.

There is a similar apparent predator–prey relationship between dolphin and syntopic sciaenid, the silver perch, that reduces mating call intensity and periodicity when in the presence of bottlenose dolphin (Luczkovich et al., 2000; R.G. Gilmore, personal observation).

There is also the probability that syntopic estuarine shark populations, most notably bull sharks (*Carcharhinus leucas*), may also predate on seatrout while they are spawning. Pregnant female bull sharks enter the Indian River Lagoon each spring to release their young (Snelson and Williams, 1981) and remain in the lagoon system throughout the seatrout spawning period. Juvenile bull sharks to 1.7 m TL remain in the lagoon for several years before joining adult populations on the continental shelf (Snelson and Williams, 1981). Since sharks are capable of hearing the low-frequency calls of seatrout (Myrberg, 1978), it is possible that Indian River Lagoon bull shark populations may also take advantage of evening seatrout lek formation and may be attracted to the seatrout low-frequency, high-energy chorus.

SEATROUT FORAGING BEHAVIOR RELATIVE TO SPAWNING AND SOUND PRODUCTION

The formation of crepuscular and nocturnal spawning aggregations effectively eliminates foraging in male spotted seatrout at this time of day. Many efforts to capture male spotted seatrout on baited hooks while they were in large spawning aggregations have failed (R.G. Gilmore, personal observation). In contrast, female spotted seatrout have been readily captured on baited hooks during crepuscular periods and after sunset during the spawning season but not at the spawning site. These observations indicate possible sexual differences between evening seatrout foraging behaviors during the spawning season.

Male seatrout leks always formed near seagrass meadows, which are the preferred seatrout diurnal foraging sites in the Indian River Lagoon. Where seagrass is absent in the Indian River Lagoon, calling seatrout are absent, as well (Gilmore, 1994). This could relate to male seatrout metabolic needs after spawning and calling the previous evening. Male foraging may be intense after prolonged energy expenditures during calling and spawning. Therefore, male seatrout may require proximate quality food sources when spawning. Seagrass meadows are known to harbor a higher diversity and abundance of benthic and epibenthic invertebrates and fishes on which the spotted seatrout preys (Virnstein et al., 1983; Stoner,1983a, b; Durako et al., 1987; Patillo et al., 1997). A diverse list of stomach contents for the spotted seatrout has been compiled, revealing a wide variety of potential prey types (Table 11.2; Patillo et al., 1997). This wide range in diet indicates that seatrout optimum foraging is based on the relative abundance of potential prey. Larger juvenile and adult spotted seatrout prey principally on macrocrustaceans and fish, including cannibalizing other seatrout. Larval seatrout prey primarily on copepods (Hettler, 1989; McMichael and Peters, 1989; Peebles and Tolley, 1988). As juveniles develop they consume a variety of macrocrustaceans, amphipods, isopods, caridean, and penaeid shrimp.

During ontogeny, juveniles gradually shift to larger prey, mostly larger macrocrustaceans and some fish. Once juveniles exceed 100 mm in SL, their diet is dominated by fish (McMichael and Peters, 1989). At this point they have settled into benthic habitats, principally seagrass meadows in peninsula Florida populations (Gilmore, 1987; McMichael and Peters, 1989).

Large adults prey almost exclusively on fish, with the relative abundance of particular prey species dictated by their relative abundance within the estuary and habitat inhabited by the seatrout (Hettler, 1989). Foraging theory dictates seatrout predation on the most abundant and readily captured prey. The majority of fish consumed by adult seatrout listed in Table 11.2 associate primarily with seagrass meadow habitats in regional estuaries (Gilmore, 1987). The most notable species in seatrout diets known to numerically dominate quantitative nearshore seagrass meadow fish collections around the Florida peninsula on a seasonal basis are bay anchovy, menhaden, striped mullet, goldspotted killifish, pipefishes, pigfish, pinfish, and gobies (Gilmore, 1987; Sogard et, al., 1987).

EVOLUTIONARY SIGNIFICANCE OF SOUND PRODUCTION IN SPOTTED SEATROUT

BENEFITS OF SONIFERY IN SPAWNING AGGREGATIONS

Indian River Lagoon spotted seatrout populations are basically nonmigratory, not only remaining within the estuary throughout their entire life cycle but also typically not migrating more than 10 km from feeding and spawning sites (Johnson et al., 1999). Indian River Lagoon spotted seatrout populations actually avoid ocean inlet locations, preferring seagrass ecosystems in essentially nontidal portions of the Indian River Lagoon (Tabb, 1961, 1966 ; Gilmore, 1987). This means that movement over distances greater than 10 to 20 km is uncommon in the Indian River Lagoon and that it is likely that spawning aggregations separated by > 20-km distances do not routinely exchange gametes.

TABLE 11.2
Spotted Seatrout Stomach Contents

Larval Seatrout
- copepods

Early Juvenile Seatrout
- planktonic schizopods
- mysids*
- copepods
- isopods
- amphipods*
- gastropods
- bivalves
- Caridean shrimp*
- penaeid shrimp*
- fish

Late Juvenile Seatrout
- Caridean shrimp
- penaeid shrimp
- fish*

Adult Seatrout

Fish*

Clupeiformes
- bay anchovy, *Anchoa mitchilli*
- menhaden, *Brevoortia spp.*
- shad, *Dorosoma spp.*

Alopiformes
- inshore lizardfish, *Synodus foetens*

Batrachoidiformes
- gulf toadfish, *Opsanus beta*

Mugiliformes
- striped mullet, *Mugil cephalus*

Atheriniformes
- silversides, *Menidia spp.*
- hardhead silverside, *Atherinomorus stipes*

Cyprinodontiformes
- sheepshead minnow, *Cyprinodon variegatus*
- rainwater killifish, *Lucania parva*
- goldspotted killifish, *Floridichthys carpio*

Gasterosteiformes
- pipefish, *Syngnathus spp.*

Perciformes
- gray snapper, *Lutjanus griseus*
- snapper *Lutjanus spp.*
- pigfish, *Orthopristes chrysoptera*
- pinfish, *Lagodon rhomboides*
- silver jenny, *Eucinostomus gula*
- Atlantic croaker, *Micropogonias undulatus*
- spotted seatrout, *Cynoscion nebulosus*
- code goby, *Gobiosoma robustum*
- naked goby, *G. bosc*
- clown goby, *Microgobius gulosus*

* = most prominent prey by relative abundance (counts, gravimetric, and volumetric studies included).

Source: Compiled by Patillo, M.E. et al., ELMR Rpt. No. 11, 1997. With permission.

There is evidence that east Florida and west Florida spotted seatrout populations seldom share gametes. The Indian River Lagoon spotted seatrout populations may be considered insular from the standpoint of genetic isolation relative to other Florida estuaries (Weinstein and Yerger, 1976a, b; Ramsey and Wakeman, 1987). For this reason, the more that individual spotted seatrout can be attracted to specific spawning locations within the Indian River Lagoon, the more likely that Indian River Lagoon populations will increase their limited genetic diversity and the more likely that a female will have a variety of male characters from which to select. Females will have a greater chance to select superior male characters, whatever they may be, from larger aggregations.

It is not implausible that the characteristics of the male mating call are selected by females as in amphibians and birds. However, large mating aggregations (i.e., leks) increase the chances of male competition for females that visit the lek. Even if females may choose a specific male for spawning, sperm competition is highly likely within the lek, due to the presence of multiple spawning males. This increases the odds for ova released into the water column by a single female to be fertilized by several different males, thus increasing genetic diversity in offspring in an otherwise isolated gene pool.

Aggregative behaviors greatly benefit synchronously calling males eager to announce their readiness to spawn. Aggregations produce greater combined sound intensity levels (> 50 dB, to 90 dB, re 1 1 µPa, at 3 m) at a location than individual callers do (< 30 dB, re 1 µPa, at 3 m). This means aggregative sound energy transmitted from a soniferous male aggregation through the estuary, particularly a shallow system with high acoustic attenuation, should increase the number of receptive spawning females attracted to the aggregation.

COSTS OF SONIFERY IN SPAWNING AGGREGATIONS

While it is likely that female spotted seatrout are selecting certain male call characteristics and behaviors, it is also likely that predators preying on spawning seatrout are also selecting individuals from the soniferous aggregation, based on a successful predatory strategy. This contributes a predictable cost to the local seatrout population, as predation mortality must be accounted for in gamete production and spawning periodicity. Fecundity and spawning periodicity are relatively high in spotted seatrout (Brown-Peterson, 1988; see Chapter 8), possibly to account for spawning adult mortality as well as egg, larval, and juvenile mortalities. However, predatory selection could be a benefit to seatrout populations on the whole, as predation is now considered a coevolutionary process, with various evolutionary responses by prey populations having been observed in predator–prey interactions (Clark, et al., 1999; Post et al., 1999). Similar predator–prey relationships have been found in aquatic ecosystems (Clepper, 1979; Deeson and Smayda, 1982; Greenstreet and Tasker, 1996).

We know little of seatrout predator predatory strategies and not much about individual seatrout prey selection. The reasonable longevity of adult spotted seatrout indicates some success in coevolution under local predatory pressures. The predator–prey relationships between spotted seatrout and its predators may not be too unlike ancient predator–prey relationships in a variety of terrestrial and aquatic species whose predator–prey interactions coevolved with a variety of predation mortality-induced adaptations that have influenced population genetic structure and health over geologic time scales (Nitecki, 1983; Thompson, 1994).

The energy required for male seatrout to produce mating calls is costly. Sound transmission in shallow water is highly variable and site specific because it is strongly influenced by acoustic properties of the bottom and surface as well as by variations in sound speed within the water column. It takes considerable energy for the seatrout to produce a sound that can be transmitted the greatest possible distance in the estuary. The number of calls per unit time is temperature dependent and varies linearly with dissolved oxygen consumption. Therefore, metabolic costs of calling increase with ambient temperature. Since spotted seatrout spawn within the shallow estuaries (mean depth of the Indian River Lagoon is 1.5 m) during the warmest periods of the year, they are particularly vulnerable to the high metabolic costs of producing energetic mating calls for 180 to 240 min on consecutive evenings. Dual pulse calls are typically produced every second, so 3600 DP calls would be produced each hour and 10,800 to 14,400 would be produced each evening, as individual male seatrout call continuously at least 3 to 4 h during the evening. This acoustic effort (call rate) does not include periodic and more intense (therefore, costly) long grunts and staccatos. Metabolism in calling amphibians has been determined to be an order of magnitude over resting metabolic rates in some of the most energetic callers (Zelick et al., 1999).

Unfortunately, there are apparently no data for the metabolic costs of producing mating calls in fish. For the male seatrout to make up for this great energy expenditure, he must consume considerable food during the spawning period. If the cost of calling and migrating to and from a specific mating site is combined with the energy expenditure needed for effective foraging, the spawning site has the additional requirement of being proximate to productive foraging habitat. In the case of the spotted seatrout, this essential productive habitat is the estuarine seagrass meadow (Gilmore,1987; McMichael and Peters,1989).

If seatrout are territorial within seagrass systems of the estuary, then individuals from a large nocturnal spawning aggregation will need to migrate further away from diurnal feeding sites, over larger distances, to reach the spawning site. This will use more energy than if seatrout were not territorial and formed schooling aggregations during the diurnal foraging period. The diel migration between foraging and spawning sites is particularly disadvantageous to males, as they may use more energy than females due to daily choral activity. If spawners remain in the vicinity of a spawning site, food resources near this site may be significantly depleted if the site is not highly productive. The energy required for calling and migrating to effective spawning sites could mean that the location, quantity, and quality of seatrout forage resources will limit spotted seatrout populations.

As further research is obtained on seatrout physiology, ecology, behavior, and predator–prey relationships, as well as on early life histories relative to spawning activities, it will be possible to develop an evolutionary stable strategy model for the species. With this more holistic approach, we may begin to fully understand which abiotic and biotic factors, including human activities, have the greatest influence on spotted seatrout population dynamics and spawning behaviors.

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12 Diseases and Parasites of the Spotted Seatrout

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CONTENTS

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ABSTRACT

At least 7 protozoan, 62 metazoan, and various microbial disease agents infect the spotted seatrout, *Cynoscion nebulosus*. Typical life cycle patterns represent the major taxonomic groups for members infecting the seatrout; for each group, recommendations are included for treatment of disease outbreaks in closed systems. Noninfectious diseases and disorders of the seatrout are associated with environmental, nutritional, and congenital factors. Insofar as possible, examples of how patterns in the occurrence of agents elucidate host biology or environmental conditions. Where appropriate, reports of parasites and diseases in other sciaenids, most notably the sand seatrout (*Cynoscion arenarius*), illustrate additional infections and conditions that could affect *C. nebulosus*.

INTRODUCTION

Diseases and parasites are inherent parts of the life histories of all organisms. Hosts and disease organisms have coexisted for millennia and have evolved in response to one another (McIntyre and Amend, 1978; Ewald, 1994; Reno, 1998). Indeed, diseases may limit or regulate host populations (Scott and Dobson, 1989). Historically, diseases in fish have been viewed as the result of interaction of pathogen, host, and environment under limited circumstances. Hedrick (1998) pointed out that this view, unfortunately, may have placed too much focus on "stress" as the facilitator of disease (particularly in the culture environment). Hedrick further indicated that this view has contributed to the misperception that disease is unusual under normal circumstances. Such a perception may only broadly apply to overt disease, particularly if the statement is made in the context of the traditional paradigm that a good parasite does not kill or harm its host. It is noteworthy that, at least under normal circumstances in wild fish populations, diseased individuals are rarely seen. However, no empirical evidence suggests that diseases do not regularly kill wild fish.

A perhaps more important, and only recently appreciated, point is that subclinical effects of disease organisms in both wild and cultured populations may be more important manifestations than clinical ones. Small changes may have major impacts on survival. The concept of disease, therefore, must be broad enough to include *any* impairment that modifies normal functions (Wobeser, 1981). Thus, for purposes of this chapter, we adopt Wobeser's and Hedrick's views that toxicants, climate, nutrition, infectious agents, and congenital defects may directly produce disease or interact to modify normal function and produce disease.

Diseases and disease-causing organisms may also provide nonclinical information about fish and fish populations. Because such organisms, particularly parasites, are often dependent on other hosts or on specific environmental conditions for transmission, host movement or environmental conditions can be inferred based on patterns in the occurrence of these organisms. Williams et al. (1992) reviewed the use of parasites as indicators of the population biology, migration, and diet of fishes. Overstreet (1993, 1997) reviewed the use of parasitological data as monitors of environmental health.

Overstreet (1983b) summarized the knowledge of seatrout diseases, listing in his extensive review approximately 60 species of parasites representing virtually every group of parasitic organisms. In addition, Overstreet noted a viral disease, several common species of bacteria associated with spotted seatrout, and an algal agent. He also reported occasional congenital abnormalities, noninfectious disorders, environmentally induced mortalities, and potential public health threats related to the parasites and diseases of seatrout. Since Overstreet's paper was published, additional information has been sporadic. Riekerk (1992) examined a sample of spotted seatrout from Charleston, South Carolina, found two parasite species not on Overstreet's list, and listed 21 unidentified "taxa," some of which may be additions to the list.

In this chapter, we add additional records and review the protozoan, metazoan, and microbial disease agents reported from spotted seatrout. We review reports of noninfectious diseases and disorders associated with environmental, nutritional, and congenital factors as well as, insofar as possible, examples of how patterns in the occurrence of agents can elucidate host biology or environmental conditions. We include, where appropriate and illustrative, reports of parasites and diseases in other sciaenids, most notably the sand seatrout (*Cynoscion arenarius*). Our focus will be to update and expand upon the disease section of Overstreet's (1983b) paper.

MICROBIAL AGENTS

BACTERIA

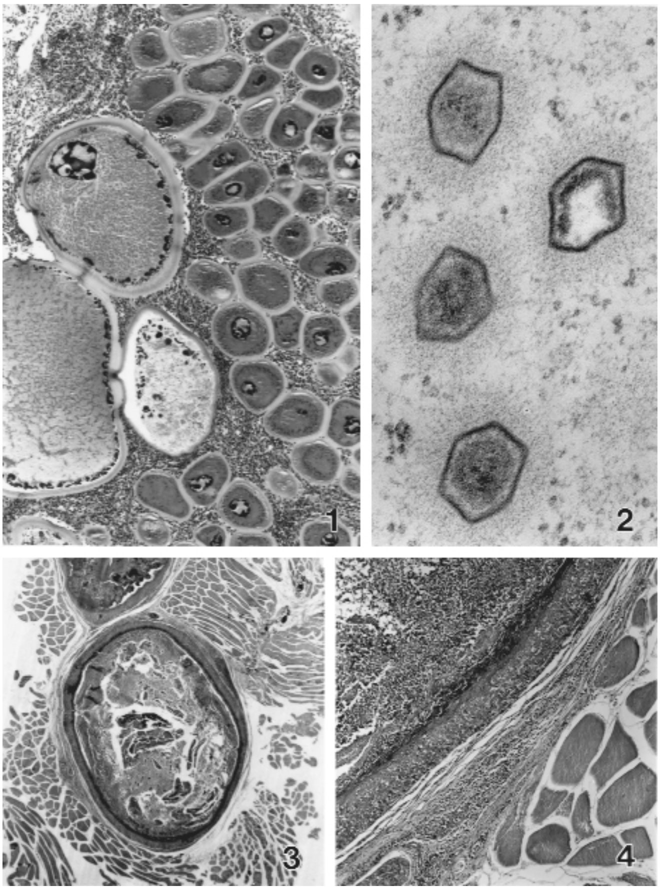
Bacteria are common components of the normal marine and estuarine environment. Many species of pathogenic bacteria are normally harmless microbial symbionts that become pathogenic and epizootic only under certain conditions. Such conditions include, but are not limited to, environmental (e.g., unionized ammonia, pesticides, heavy metals, rapidly changing or extremes in pH or water temperature, low oxygen concentrations, and high carbon dioxide [Plumb, 1994]) or nutritional stress, crowding, lesions created by ectoparasites, and mechanical damage due to handling or encounters with foreign objects. Cook and Lofton (cited in Overstreet and Howse, 1977) routinely found pseudomonads, aeromonads, and vibrios in blood, liver, and other internal tissues.

In some cases, nonpathogenic bacteria have invaded wounds or otherwise compromised fish and produced serious disease; the spotted seatrout appears to be particularly susceptible to "fin rot." Overstreet and Howse (1977) reported pseudomonads, vibrios, and aeromonads in fishes, including spotted seatrout, with lesions in the fins and elsewhere in the skin. Adkins et al. (1979) reported bacteria in lesions on seatrout that died in association with cold temperatures. We (unpublished data) found several vibrios infecting lesions on the opercula and tails of sand seatrout. There was little histopathological complication with experimentally tagged spotted seatrout when compared with secondary infections associated with tagged specimens of the spot, *Leiostomus xanthurus*. Vogelbein and Overstreet (1987) demonstrated relatively few granulomas and melanomacrophage aggregates associated with the tags in the seatrout. Only a single fish had a recognizable bacterial infection, early during the healing process.

Acute epizootics resulting from primary bacterial infections in estuarine or marine fishes are infrequent and usually attributable to *Vibrio anguillarum*, even though several strains of about ten species of *Vibrio* have been implicated in fish diseases (e.g., Plumb, 1994). An acute to chronic fish kill in Alabama and nearby Florida attributed to a nonhemolytic, group B, type I_b *Streptococcus* involved *Cynoscion nothus* as well as a few other fishes (Plumb et al., 1974). Cook and Lofton (1975) confirmed that the same bacterium, but not other tested isolates of *Streptococcus* spp., produced mortality of tested fishes when injected in doses of less than 10^6 cells per fish.

VIRUSES

We are aware of only one reported viral disease in spotted seatrout. Overstreet (1983b) reported lymphocystis (Figure 12.1) in spotted seatrout and sand seatrout from Mississippi. Infections of this iridovirid (*Cystivirus* sp.) are seen rather commonly every few years. More than one strain occurs, even in sciaenids, but infections in seatrouts occur at least from Texas (Johnson, 1978) to Georgia (Smith, 1970). This viral agent (Figure 12.2) infects connective tissue cells, causing hypertrophy that results in visible masses of hyaline-encapsulated cells. Middlebrooks et al. (1979, 1981) developed fish cell lines from *C. nebulosus* and *C. arenarius*, respectively, that supported replication of at least one sciaenid lymphocystis strain. Certainly, other viruses probably occur or could occur in seatrout, but these have not yet been detected. Some of these probably cause disease, and seatrout also may be a carrier for viruses that cause disease in other animals.



FIGURES 12.1 THROUGH 12.4 1. Lymphocystis in skin, low-power view with light microscopy showing considerable hypertrophy of infected host fibroblasts. The two size groups of hypertrophied cells surrounded by a thick hyaline capsule contrast conspicuously with the relatively small size of the basophilic nuclei of inflammatory cells in the background. 2. Transmission electron microscopic view of the icosahedral-shaped virions in an experimental infection in the spotted seatrout. 3. Unidentified algal infection in muscle tissue. 4. Close-up of margin showing relatively small amount of host inflammatory response, which is confined to area next to alga (Figures 12.3, 12.4 modified from Overstreet, *Gulf Res. Rep.*, Suppl., 1: 1–43,1983b).

FUNGI

Fungal infections in fish have long been a concern, particularly in cultured or tank-held fishes. Species of *Ichthyophonus* (now classified as a protist), *Saprolegnia*, *Aphanomyces* (water mold — now classified as a protist), and various deuteromycetes have been reported to cause disease in wild and cultured fishes (Bruno, 1989; Bruno and Wood, 1999; Lehmann et al., 1999; McVicar, 1999; Blaylock et al., 2001). In many cases, however, the disease associated with the fungus is assumed to be secondary to an injury or another compromising factor (Blaylock et al., 2001). That assumption may be valid in many cases, particularly in salmonids; however, Noga et al. (1988) and Dykstra and Kane (2000) show how *Aphanomyces* sp. produces primary disease in an estuarine fish sympatric with seatrout. Fungi have not been reported from the spotted seatrout, even though we have seen but not identified fungal organisms in spotted seatrout from Mississippi.

ALGAE

Most infective algae associated with fishes are opportunistic organisms that secondarily invade tissue and occasionally produce clinical disease (see review by Edwards, 1978). Overstreet (1983b) reported a single case of a unicellular alga infecting a spotted seatrout (Figures 12.3, 12.4). That infection, however, did appear to be systemic, though it may very well have begun as a secondary infection.

PROTOCTISTS

DINOFLAGELLATES

Amyloodinium ocellatum is the only dinoflagellate reported from the spotted seatrout (Table 12.1). This gill- and skin-dwelling organism can harm seatrout, especially in culture. The readily identifiable trophont stage feeds on skin and gill epithelium (Figure 12.5). After feeding, the trophont drops off, forms reproductive cysts (tomonts), undergoes repeated asexual divisions (Figure 12.6), and eventually releases flagellated dinospores that are infective to other hosts. Lawler (1980) demonstrated that most estuarine fishes from Mississippi, including the spotted seatrout, are susceptible to and can be killed by *A. ocellatum*. Wild-caught seatrout are infested at a relatively low level that probably does not harm the host in the wild. However, populations of the parasite can build to dangerous levels if a fish experiences a stress event, which can stimulate the trophonts to drop off and produce the dinospores. This is particularly important for tank-held fishes because the tank concentrates the infective dinospores in proximity to the fish hosts. We have seen mortalities in tank-held spotted and sand seatrout due to extremely heavy infestations with the parasite.

Treatment typically entails low doses of copper sulfate maintained for 2 to 3 weeks. However, copper sulfate kills only the infectious stage of the parasite. New outbreaks may occur in previously treated systems, even though hosts can acquire a protective immune response directed against the trophont (Cobb et al., 1998). In systems containing valuable specimens, we have maintained the therapeutic level of copper (0.15 to 0.20 mg/l) for several months with no evident ill effect on the fish.

Recently, *Pfiesteria piscicida* has received much attention. *Pfiesteria piscicida* and *Pfiesteria*-like organisms are unusual dinoflagellates capable of sensing, stunning, and devouring prey, including fishes. These organisms are reported to display at least 24 morphological forms but basically alternate between zoospores and zygotes in the water column (where they attack food) and amoebae and cysts in the sediments (where they digest, reproduce, and encyst). The complex of organisms is widespread in temperate–subtropical regions including the southeastern U.S. and the Gulf of Mexico, though they have been directly linked to fish kills only in North Carolina and Maryland (Burkholder and Glasgow, 1997; Burkholder, 1999). Mortalities of the spotted seatrout in its natural habitat caused by *P. piscicida* or another agent in that complex were reported from North Carolina by Burkholder and Glasgow (1997). The disease was originally noted in aquaria (Burkholder, 1999), emphasizing that captive marine and estuarine fishes are at risk. There is no known treatment.

APICOMPLEXANS

Coccidians are relatively common parasites in the intestinal tracts of fishes, but no coccidian has been reported from seatrouts, most likely because few biologists have looked critically for them. One hemogregarine has been reported from the blood of the spotted seatrout (Table 12.1). Hemogregarines constitute a group of poorly understood parasites in which, at least in the case of species infecting fishes, gamonts are produced in the fish blood cells and taken up by leeches, gnathiid isopods, or argulids, where they undergo sexual development into infective sporozoites. The effects of hemogregarines on the health of fishes are mostly unknown. Treatments for hemogregarines are unknown.

Table 12.1
Parasites of the Seatrouts *Cynoscion nebulosus* (Cn), *C. arenarius* (Ca), and *C. nothus* (Cno)

Parasite	Cn	Ca	Cno	Site	Geographic locality	Reference
Sarcomastigophora						
Dinoflagellida						
Amyloodinium ocellatum (Brown, 1931)	X	X		Gills, skin	MS, LA	Lawler (1980), Overstreet (1983b), this study
Apicomplexa						
Haemogregarinidae						
Haemogregarina sp.	X			Leukocytes	FL (west coast)	Saunders (1954)
Microspora						
Pleistophora sp.	X	X		Liver	MS	Overstreet (1983b)
Myxozoa						
Kudoa sp.		X		Muscle	MS	Overstreet (1983b)
Henneguya sp.	X	X		Dorsal, caudal fins	MS	Overstreet (1978a, 1983b)
Myxidium sp.	X			Gall bladder	MS, LA	This study
Ciliophora						
Trichodinidae						
Trichodina sp.	X	X		Gills	MS, LA	Overstreet (1983b), this study
Cestoidea						
Tetraphyllidea						
Scolex polymorphus	X	X		Cystic duct, intestine	NC, MS, LA	Linton (1905), Overstreet (1983b), this study
Scolex sp. (small)	X	X		Intestine, rectum	MS, LA, SC	Overstreet (1983b), Riekerk (1992), this study
Scolex sp. (large)	X	X		Pyloric ceca, intestine, rectum	MS, LA, SC	Overstreet (1983b), Riekerk (1992), this study
Rhinebothrium sp.		X		Intestine	MS	Overstreet (1983b)
Tetrarhynchea						
Poecilancistrium caryophyllum (Diesing,1850) metacestode (as *P. robustum* in some reports)	X	X		Muscle, body cavity	TX, LA, MS, FL, SC	Chandler (1935), Schlicht and Mc Farland (1967), Hutton and Sogandares-Bernal (1960), Goldstein (1963), Hutton (1964), Boertje (1976), Adkins et al. (1979), Overstreet (1977, 1978a, 1978b), Riekerk (1992), this study
Kotorella pronosoma (Stossich, 1901) (as *Nybelinia* sp. metacestode)	X	X		Stomach wall	MS	Overstreet (1983b), Palm and Overstreet (2000b)

Nybelinia bisulcata (Linton, 1889) (as *Tetrarhynchus b.*) metacestode (*K. pronosoma* ?)	X			Stomach wall	NC	Linton (1905)
Otobothrium crenacolle (Linton, 1890) probably junior synonym of *O. cysticum* [Mayer, 1842])	X	X		Stomach submucosa, mesentery	NC, MS	Linton (1905), Overstreet (1983b)
Rhynchobothrium sp.	X			Viscera	NC	Linton (1905)
Tetrarhynchea sp. abothriate metacestode	X			Muscle	MS, LA	Overstreet (1977)
Monogenea						
Diclidophoridae						
Neoheterobothrium cynoscioni (MacCallum, 1917) (as *Choriocotyle reynoldsi* or *C. cynoscioni*)	X	X	X	Gills	VA, FL (west coast), LA, MS, SC	Frayne (1943), Hargis (1955b), Thatcher (1959), Overstreet (1983b), Riekerk (1992), this study
Cyclocotyla louisianensis (Hargis, 1955)	X			Buccal cavity	LA, MS	This study
Diplectanidae						
Diplectanum bilobatum Hargis, 1955	X			Gills	FL (west coast), LA, MS, SC	Hargis (1955a), Thatcher (1959), Overstreet (1983b), Riekerk (1992), this study
Microcotylidae						
Cynoscionicola heteracantha (Manter, 1938) (some reports as *Microcotyle h.*)	X			Gills	NC, FL (west coast), LA, MS, SC	Linton (1905), Manter (1938), Hargis (1956), Thatcher (1959), Overstreet (1983b), Riekerk (1992), this study
Udonellidae						
Udonella caligorum (Johnston, 1835)	X			Mouth, gills (on *Caligus praetextus*)	MS	Overstreet (1983b)
Digenea						
Acanthocolpidae						
Stephanostomum interruptum (Sparks and Thatcher, 1958)	X	X		Intestine, rectum	TX, LA, MS, FL (west coast)	Sparks (1958), Sparks and Thatcher (1958), Overstreet (1983b), Nahhas and Short (1965)
Stephanostomum imparispine (Linton, 1905)	X				SC ?	Lawler (1978)
"Stephanostomum tenue"	X				NC	Linton (1905)
Stephanostomum sp., metacercaria (as *S.valde-inflatum*)	X			Cysts on viscera	NC	Linton (1905)
Lepocreadiidae						
Lepocreadium setiferoides (Miller and Northup, 1926)	X			Pyloric ceca	SC	Riekerk (1992)
Sanguinicolidae						
Cardicola laruei (Short, 1953)	X	X		Heart	FL (west coast)	Short (1953), Nahhas and Short (1965)

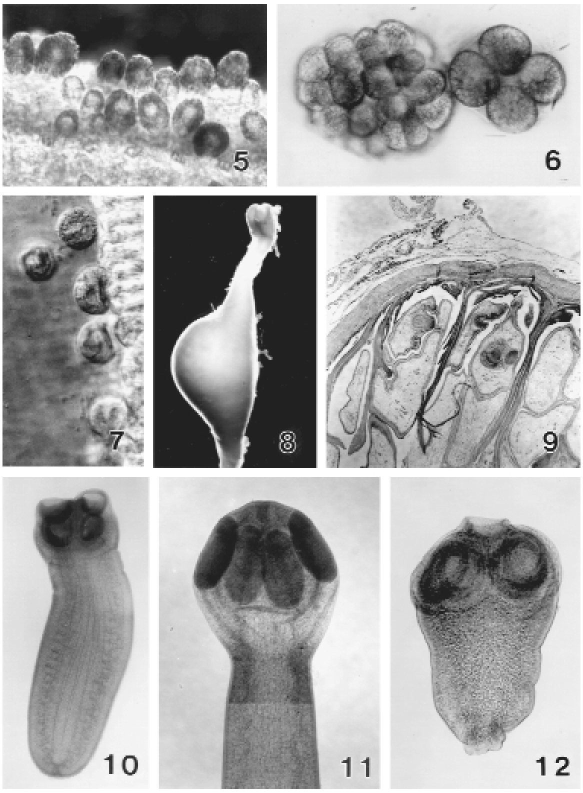
Table 12.1 (continued)

Parasite	Cn	Ca	Cno	Site	Geographic locality	Reference
Bucephalidae						
Bucephalus cynoscion (Hopkins, 1956)	X	X		Pyloric ceca, intestine, rectum	LA, MS	Corkum (1967), Overstreet (1983b)
Prosorhynchoides caecorum (Hopkins, 1956) n. comb.	X	X		Pyloric ceca, intestine	LA, TX, MS	Hopkins (1956), Sparks (1958), Corkum (1968), Sparks (1960), Overstreet (1983b)
Rhipidocotyle sp., metacercaria	X			Cornea, vitreous humor, anal and caudal fins	LA, MS	This study
Cryptogonimidae						
Metadena spectanda (Travassos, Freitas, and Bührnheim, 1967), metacercaria		X		Fins, flesh	MS	Overstreet (1983b)
Metadena sp.	X			Intestine	MS	This study
Didymozoidae						
Metacercaria	X	X		Stomach	MS	Overstreet (1983b)
Diplostomidae						
Posthodiplostomum minimum (MacCallum, 1921), metacercaria		X			LA	Arnold et al. (1967)
Gorgoderidae						
Phyllodistomum sp.		X		Urinary bladder	MS	Overstreet (1983b)
Hemiuridae						
"Lecithochirium monticellii"	X			Intestine	NC	Linton (1905)
Lecithochirium sp.	X	X		Stomach	MS	Overstreet (1983b)
Parahemiurus merus (Linton, 1910)	X			Stomach	FL	Nahhas and Short (1965)
Stomachicola rubea (Linton, 1910)	X				GA	Sinclair, Smith, and Sullivan (1972)
Stomachicola magna (Manter, 1931) (as *Tubulovesicula* sp.)	X	X		Stomach, air bladder, ovarian membrane, muscles, body cavity, stomach wall	NC, FL (west coast), MS	Manter (1931), Loftin (1960), Nahhas and Short (1965), Overstreet (1983b)
Immature hemiurids	X				LA	Sparks (1958)
Hirudinellidae						
Hirudinella ventricosa (Pallas 1774), metacercaria		X		Body cavity	MS	Overstreet (1983b)

Pleorchiidae						
*Pleorchis americanus (*Lühe, 1906)	X	X		Intestine, pyloric ceca	FL (west coast), LA, MS	Sogandares-Bernal and Hutton (1959), Hutton and Sogandares-Bernal (1960), Loftin (1960), Hutton (1964), Nahhas and Short (1965), Nahhas and Powell (1971), Sparks (1958), Overstreet (1983b)
Nematoda						
Anisakidae						
Hysterothylacium reliquens (Norris and Overstreet, 1975) juvenile	X	X		Mesentery	MS	Deardorff and Overstreet (1981)
Hysterothylacium type MB larva	X			Mesentery	MS	Deardorff and Overstreet (1981)
Ascaris sp. larva (*Hysterothylacium reliquens*?)	X			On viscera, mesentery	NC	Linton (1905)
Camallanidae						
*Spirocamallanus cricotus (*Fusco and Overstreet, 1978)	X	X		Intestine	MS	Overstreet (1983b)
Philometridae						
Margolisianum sp.	X			Mouth	MS, LA	Overstreet (1983b), this study
Incertae sedis – *Agamonema* sp.		X			LA	Arnold et al. (1967)
Acanthocephala						
Palaeacanthocephala						
Dollfusentis chandleri (Golvan, 1969)	X			Rectum	SC, LA, MS	Riekerk (1992), this study
Pomphorynchus rocci (Cordonnier and Ward,1967)	X			Intestine	SC	Riekerk (1992)
Annelida						
Hirudinea						
Malmiana philotherma (Sawyer, Lawler, and Overstreet, 1975)			X	Gills	MS	Overstreet (1983b)
*Myzobdella lugubris (*Leidy, 1851)	X			Skin, buccal cavity	LA	This study
Copepoda						
Lernanthropidae						
Lernanthropus gisleri (van Beneden, 1852)	X			Gills	LA, TX, Mexico, FL (west coast)	Causey (1953a, 1953b), Bere (1936), Pearse (1952)
Lernanthropus pomatomi (Rathbun, 1887)	X			Gills	TX	Causey (1953b)
	X			Gills	TX	Causey (1953b)
Lernanthropus sp. A	X			Gills	SC	Riekerk (1992)
Lernanthropus sp. B	X			Gills	SC	Riekerk (1992)
Caligidae						
Caligus bonito (Wilson, 1905)	X				TX	Simmons (1957)

Table 12.1 (continued)

Parasite	Cn	Ca	Cno	Site	Geographic locality	Reference
Caligus praetextus (Bere, 1936)	X			Gills	TX, MS	Causey (1953b), Overstreet (1983b)
Caligus rapax (Edwards, 1840) (as *C. repax*)	X	X		Gills	TX	Simmons (1957)
Caligus sciaenops (Pearse, 1952)	X			Roof of mouth	TX	Pearse (1952)
Caligus sp. larva	X			Usually dorsum	FL (laboratory)	Houde (1972)
Pseudocynidae						
Cybicola elongata (Pearse, 1951)	X				TX	Pearse (1952)
Branchiura						
Argulus alosae (Gould, 1841)	X			Mouth, gills	MS, LA	Cressey (1978), Overstreet (1983b), this study
Isopoda	X		X	Inside mouth, gill arches	LA, TX	Comeaux (1942), Kensley and Schotte (1989)
Cymothoidae						
Cymothoa excisa (Perty, 1833)						
Cymothoa exigua (Schioedte and Meinert, 1910)	X			Gill arches	LA	Comeaux (1942)
Nerocila acuminata (Schioedte and Meinert, 1910)	X			Near base of fins	MS	Overstreet (1983b)
Lironeca ovalis (Say, 1818)	X		X	Gills	TX, MS, SC	Pearson (1929), Overstreet (1983b), Riekerk (1992), this study
Acarina						
Unidentified mite	X			Pericardium	MS	This study



FIGURES 12.5 THROUGH 12.12 5. Heavy infestation of the parasitic dinoflagellate *Amyloodinium ocellatum* attached on gills, which are exhibiting hyperplasia and fusion. Light infestations often occur on skin of heavily infested individuals. 6. Dividing cells of *A. ocellatum*, occurring on substratum rather than on fish. From one feeding trophont on host, an ultimate 256 dinoflagellate infective swarming individuals, referred to as dinospores, are produced. Each of the dinospores can infest the seatrout or most other marine fishes and develop into a trophont. Heavy infestations typically are restricted to fish in a confined culture condition. (Figures 12.5 and 12.6 from Overstreet, Mississippi-Alabama Sea Grant Consortium, Ocean Springs, MS, MASGP-78–021, 1978a). 7. Infestation of the ciliophoran *Trichodina* sp. on gill filaments of red drum but also on seatrouts. (From Overstreet, *Gulf Res. Rep.* Suppl. 1:45–68, 1983c). 8. Cystic duct expanded with heavy infection of plerocercoid of tetraphyllidean cestode “Scolex polymorphus.” 9. Histological section of cystic duct, showing a few of the many plerocercoids shown in Figure 12.8. (Figures 12.8 and 12.9 from Overstreet, *Gulf Res. Rep.* Suppl., 1:1–43, 1983b). 10. Wholemount of 1.5-mm individual of same agent. 11. Wholemount of scolex, or attaching portion, of an individual over 4 mm of Scolex sp. large type plerocercoid (small) from pyloric cecum. 12. Scolex sp. small type plerocercoid (370 μm long) from intestine. Species in Figures 12.11 and 12.12 occur in both *Cynoscion nebulosus* and *C. arenarius.* (From Overstreet, *Gulf Res. Rep.* Suppl., 1:1–43, 1983b).

MICROSPORIDIANS

The only seatrout microsporidian recovered to date is a species of Pleistophora isolated from the liver of spotted seatrout and sand seatrout. More often, members of this phylum are considered parasites of invertebrates; however, they are distributed widely in fishes. These are small, single-celled, intracellular parasites characterized by spores containing a sporoplasm that extrudes through an everted polar tube into a host cell. Development of the spores of some species, such as those of *Pleistophora*, occurs in groups within a sporophorous vesicle. Also, a host “cyst,” making an infection apparent to the naked eye, encapsulates large numbers of spores. Spores of some species are directly infective.

Dyková (1995) believed that the greatest impact of piscine microsporidians involves young fish. This is probably especially true for cultured fish but primarily hypothesized for wild ones. The species from the seatrout requires investigation. We did not observe microsporidians in any of the young-of-the-year fish we examined, but we have observed then in other sciaenids. Prevention through proper sanitation and quarantine constitutes the best general method of control in culture facilities. Toltrazuril has been used with some success against vegetative stages of microsporidians in fishes (Dyková, 1995).

MYXOSPOREANS

Myxosporeans are pluricellular, spore-producing organisms that parasitize primarily teleosts and usually oligochaetes, polychaetes, or a few other invertebrates in the alternate, or actinosporean, phase of the life cycle. The parasites can be either histozoic or coelozoic in a variety of tissues; they develop in a variety of patterns, often occurring in "cysts" containing many spores or packets of spores that are infective to the alternate host. Myxosporeans are among the most important fish pathogens contributing significantly to morbidity and mortality in cultured and wild fishes.

Three species of myxosporeans belonging to three distinct genera have been reported from spotted and sand seatrout (Table 12.1). *Kudoa* sp. typically infects somatic muscle, *Henneguya* sp. infects the skin, and *Myxidium* sp. typically infects the gall bladder. Myxosporeans, like microsporidians, are difficult to identify to species; therefore, none of the myxosporeans from seatrout has yet been identified to species, but we are in the process of describing them. Classification is based on the structure of the spores. Coelozoic forms such as members of *Myxidium* are sometimes less pathogenic than the histozoic ones. Sanitation and quarantine are the best methods of control. Ultraviolet radiation can be effective against spores in the water supply. Lom and Dyková (1995) found promise in preventing infections by using fumagillin-medicated feed.

CILIATES

The cosmopolitan genus *Trichodina* contains the only ciliate species reported from the seatrout (Table 12.1). Members of *Trichodina* are difficult to identify to species; therefore, several species may be involved in the infestations. The gills and skin of spotted and sand seatrout are commonly infested in Mississippi and Louisiana. Strictly speaking, the organisms are commensals in the wild and use the fish only as a means to anchor or as a source to accumulate detritus or bacteria on which to feed. They are host specific and are passed directly from fish to fish. No mortality linked to trichodiniasis in wild fishes has been reported; however, species of *Trichodina* commonly cause disease under stressful conditions. In debilitated fish or in confined spaces, large numbers of the organisms can accumulate and irritate the skin at their attachment sites and by grazing (Figure 12.7). Treatment is difficult, but NaCl, formalin, malachite green, and potassium permanganate have been effective to some degree. Lom (1995) reviewed treatments for trichodiniasis.

Other ciliates that pose potential problems to cultured seatrout include the freshwater *Ichthyophthirius multifiliis*, the causative agent of "ich," and its marine counterpart *Cryptocaryon irritans*. These organisms alternate between fish-free, encysted tomonts, which produce theronts that infect fishes and become the feeding trophonts that inhabit the basal layer of the epithelial cells on the skin and gills. These parasites are extremely difficult, if not impossible, to treat, due in large part to the parasite's presence in the basal layer of the epithelium shielding it from most treatments. Serial transfers of infected fish (every 5 to 7 days for ich and every 3 to 5 days for *Cryptocaryon*) to clean water, salt, formalin (ich), malachite green (ich), copper sulfate, and quinine derivatives have been used with varying levels of success. As with treatments for *A. ocellatum*, most of those act on the free-swimming infective stage. Dickerson and Dawe (1995) reviewed treatment regimes for these ciliates.

PLATYHELMINTHS

CESTODES

Cestodes, or tapeworms, are perhaps the most well-known parasites of seatrout. These flatworms, typically segmented as adults, generally live in the intestinal tracts of a wide variety of animals, including fishes. The life cycle involves several hosts. Eggs of aquatic species develop into stages infective to invertebrates; infected invertebrates are consumed by fishes, in which the parasites can either develop into adults or encyst as metacestodes. These fishes transmit the parasite to other fishes, birds, or mammals. In many cases involving fish tapeworms, the metacestode stage can be transferred from host to host many times before it develops further or enters the definitive host (paratenesis).

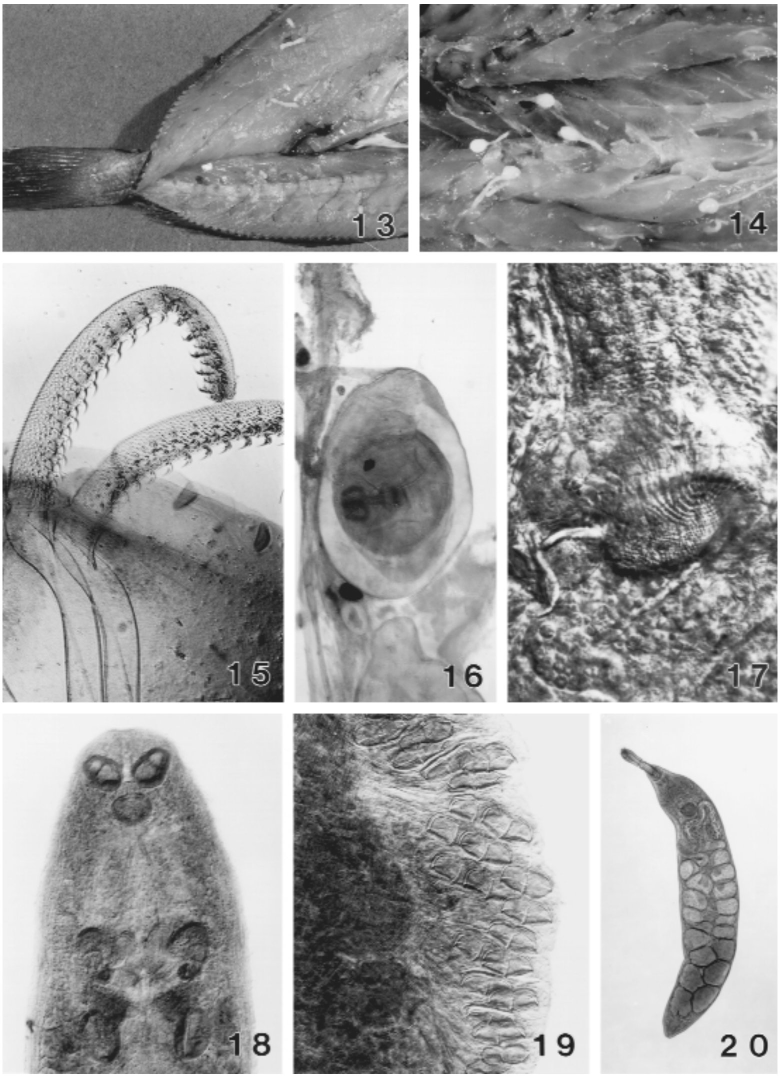
As is generally the case with most marine teleosts, seatrouts do not serve as a definitive host for tapeworms. However, they act as intermediate or paratenic hosts for several cestodes that mature in elasmobranchs. Among the most common cestodes found in seatrouts is the ubiquitous "Scolex polymorphus (Table 12.1)." Juvenile tetraphyllideans inhabiting the cystic duct (Figures 12.8 to 12.10) and intestinal tract (Figures 12.11 and 12.12) comprise several species that belong in a group collectively termed "Scolex polymorphus." Species are difficult to identify because the scolex, the prime taxonomic character, differs in juvenile and adult stages, changing considerably as the worm develops. The metacestode from the cystic duct of seatrout in the Woods Hole region of Massachusetts apparently develops into an adult identified as *Phoreiobothrium triloculatum* in the sand shark (Curtis, 1911). Typically, metacestodes are broadly categorized by site of infection and size and shape of the scolex. Four kinds of tetraphyllidean metacestodes have been reported in local seatrouts. These include *Rhinebothrium* sp. from a sand seatrout; that genus can be identified by the scolex.

Other cestodes from seatrout include at least five trypanorhynchean metacestodes. Trypanorhynchs are typically found encapsulated in the flesh (Figures 12.13 to 12.15) or viscera (Figure 12.16) and are characterized by four eversible, hook-bearing tentacles. The metacestodes of species of *Otobothrium* and the *Kotorella–Nybelinia* complex are relatively widespread in fishes and apparently cause little harm. The species reported from the seatrouts require some taxonomic attention. Palm and Overstreet (2000a) considered *O. crenacolle* a synonym of *O. cysticum* on the basis of the hook pattern, but the status of *O. cysticum* should be determined with molecular data.

Probably the most well-known cestode in seatrout is the trypanorhynch *Poecilancistrium caryophyllum*. This larval tapeworm appears as a chalky, opaque, worm-like object twisted within the flesh, typically in the middle of the fillet adjacent to the vertebral column (Overstreet, 1977). Overstreet (1977) demonstrated that small fish were not infected and that prevalence of infection increased with fish size. He indicated that explanations for the pattern could be that small fish are killed by the parasite or that small fish usually do not come into contact with the prey intermediate host. Overstreet also suggested that parasite intensities were maintained due to an immune response that prevented subsequent infection. Because the parasite is not infective to humans, the greatest problem related to it is an aesthetic issue (Overstreet, 1983b); the presence of plerocercoids in the flesh makes the fillets unsightly. Although most cestode infections rarely harm the host or seafood consumers, control is difficult. Prevention through quarantine and elimination of additional hosts is the first line of defense. Commercial anthelmintics are probably effective (Stoskopf, 1993) but usually only for the adult stages.

MONOGENEANS

Monogeneans commonly occur as ectoparasites on the gills and body surfaces of fishes. The different species attach by means of a variety of hooks, anchors, suckers, and clamps located on a posteriorly located haptor (Figures 12.17 to 12.19). The life cycles of these parasites are typically direct; some species lay eggs, but others bear live young. Eggs hatch into infective oncomiracidia that invade the same or another individual of the host species. Some oncomiracidia are free swimming and some crawl. Viviparous species produce well-developed embryos that directly infest the host but can be passed on to other individuals.



FIGURES 12.13 THROUGH 12.20 13. Filleted seatrout showing cut portions of two plerocercoid individuals of the tetrarhynchean cestode *Poecilancistrium caryophyllum* that causes "wormy trout" (From Overstreet, *Gulf Res. Rep*., Suppl., 1:1–43, 1983b). 14. Close-up of five individuals, each showing long tubes and bulbous portion containing scolex (From Overstreet, *J. Parasitol*., 63:780–789, 1977). 15. Close-up of two of the four hooked tentacles extruded from the scolex, which also contains small dark sensory papillae (From Overstreet, Mississippi–Alabama Sea Grant Consortium, Ocean Springs, MS, MASGP-78-021, 1978a). 16. Metacestode of much smaller tetrarhynchean from mesentery. A 0.5-mm individual of what is probably *Otobothrium cysticum* within a 1.0-mm cyst. 17. Relatively small, < 1.0-mm-long tissue-feeding diplectanid, *Diplectanum bilobatum*, showing one of the two characteristic squamodiscs and anchors on the opisthaptor used for attaching to gills. 18. Anterior end of the much larger (6.9-mm individual) microcotylid blood-feeding monogenean *Cynoscionicola heteracantha*, showing two small buccal suckers, a pharynx, and a complicated genital atrium armed with a spiny coronet associated with two pairs of multichambered suckers. 19. Some of the 200-plus clamps on the haptor of the same individual used for attachment to the gills rather than anchors or other structures, as used by members of other groups of monogeneans. 20. Metacercaria of digenean in the family Didymozoidae, free in stomach of spotted seatrout; such small individuals often also occur freely in the tissues of several species of fish (From Overstreet, *Gulf Res. Rep*., Suppl., 1:1–43, 1983b).

Monogeneans are of two general types: sanguiniferous polyopisthocotyleans, usually with multiple attachment structures in the haptor, and tissue-grazing monopisthocotyleans, usually with one or two relatively large pairs of anchors and very small marginal hooks in the haptor. Because of the direct life cycle, populations of monogeneans can build rapidly, producing detrimental effects particularly when the host occurs in confined areas. Cone (1995) suggested that the polyopisthocotyleans cause little host damage, but the monopisthocotyleans cause significant damage. Some polyopisthocotyleans infecting teleosts and elasmobranchs, however, can cause severe lesions and mortalities, especially in culture conditions (e.g., Paperna et al., 1984).

Five species of monogeneans belonging to four families infest spotted seatrout (Table 12.1). None of the species has been reported to occur in harmful numbers. Three are polyopisthocotyleans, and *Cynoscionicola heteracantha*, which is a relatively large worm (Figures 12.18 and 12.19), infests wild fingerling seatrout in rather large numbers suggesting a potential threat in culture conditions. The single monopisthocotylean, *Diplectanum bilobatum* is typically low in prevalence and intensity in wild fish (Figure 12.17) but also is likely to be a threat to cultured seatrout. Overstreet (1983b) also reported *Udonella caligorum* in association with spotted seatrout; however, this parasite, although it can be found on the fish itself, is more directly a hyperparasite of a parasitic copepod (in this case, *Caligus praetextus*) than of the seatrout.

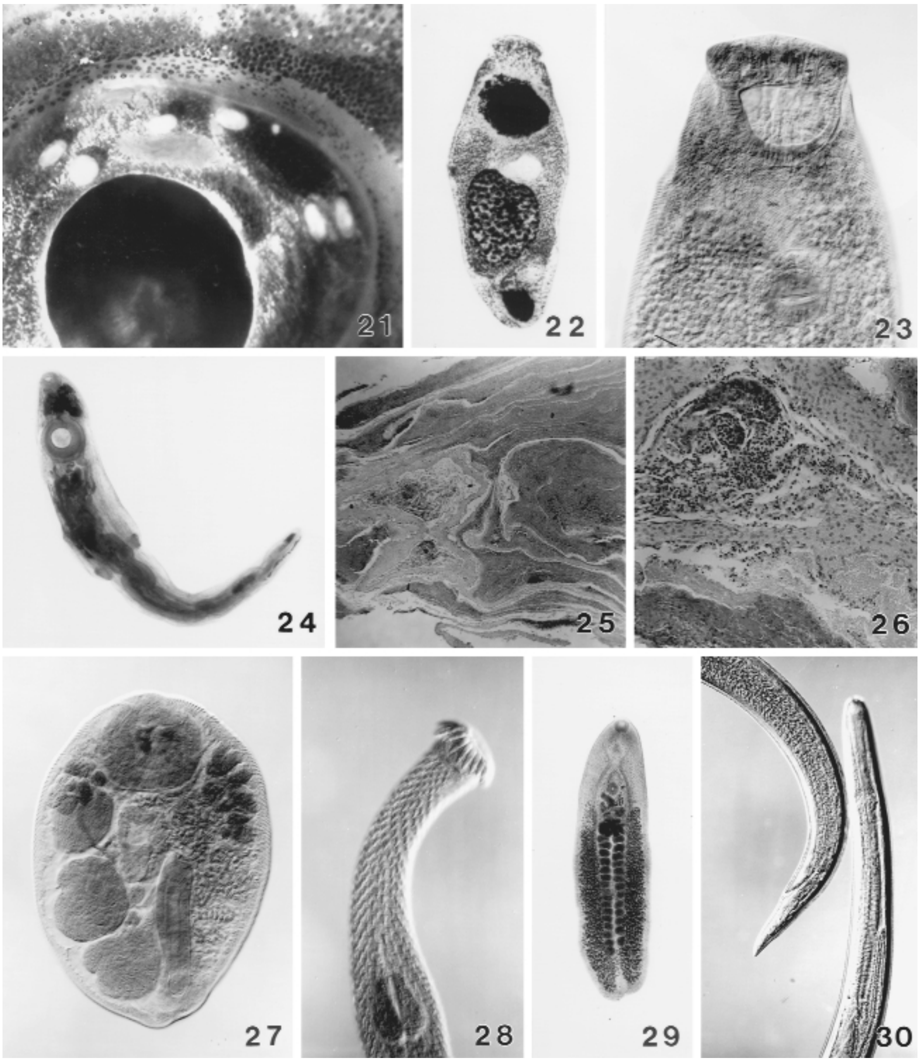
As noted, monogeneans can present significant problems for confined fishes. Treatment for adults is relatively easy and efficacious. Dips in fresh water for saltwater fishes (and vice versa) can be effective, as can treatment with several compounds such as Dylox, praziquantel, and formalin. The difficulty comes in ridding the tank system of the agent, because worm eggs containing the infective stages are often resistant to treatment. Ideally, fish should be moved to clean facilities after treatment; in any case, repeated treatments are required. Cone (1995) reviewed treatments.

DIGENEANS

Digeneans in seatrouts, as in most other marine fishes, are the most abundant metazoans, both in numbers of species and individuals. These parasites are among the most complex of parasitic organisms, requiring multiple hosts to complete their life cycles. Typically, eggs produce miracidia that enter mollusks where they, in turn, produce a sporocyst or, in some cases, a redia. After what can be several asexual generations in the mollusk, each sporocyst or redia produces many cercaria, which leave the mollusk, infect a second intermediate host, and often encyst as a metacercaria. Metacercariae, encysted, encapsulated, or free, are infective to appropriate definitive hosts.

Seatrout can act as both intermediate and definitive hosts for digeneans. Approximately 20 species representing ten families have been reported from seatrout (Figures 12.20 to 12.29; Table 12.1). Five of these species are juvenile forms whose adults live in fishes or birds. The acanthocolpids, represented by perhaps four species, can infect seatrout as both metacercariae and adults. The most conspicuous trematodes in seatrouts belong to Hemiuridae. These worms, of which as many as six species have been reported, typically inhabit the digestive tract and can be quite large and visible to the naked eye. One species, *Stomachicola magna*, can be found encapsulated or migrating within the viscera or flesh (Figures 12.24 to 12.26).

Cryptogonimids, didymozoids, and diplostomes are represented as metacercariae. Although digenean infections rarely harm the host (at least as adults), control is difficult. Some examples, such as diplostome metacercariae, when present in high-enough numbers, are known to impair or kill freshwater catfish in farms (e.g., Coblentz, 2000). Prevention through quarantine and elimination of intermediate or final hosts is the first line of defense. Commercial anthelmintics are probably effective (see Stoskopf, 1993; Paperna, 1995) but are typically used for the adult stages only.



FIGURES 12.21 THROUGH 12.30 21. Encysted metacercariae of the bucephalid digenean *Rhipidocotyle* sp. in the cornea of the eye. Individuals also occur in the vitreous humor of the eye and in the anal and caudal fins. 22. Live excysted metacercarial individual. 23. Anterior end of fixed and stained 1.2-mm-long excysted individual. The anterior sucker, in this species with a hood, is not associated with a mouth as in other groups of digeneans. Mouth can be seen associated with muscular pharynx more posteriorly. 24. The metacercaria of *Stomachicola magna*, a much larger, 7.5-mm-long hemiurid species that occurs unencysted in the flesh as well as in the mesentery, air bladder, and other tissues where the pinkish-colored worm can be easily seen by those cleaning seatrout or purchasing fillets. 25. Low-power view of section of degenerating specimen of *S. magna* in flesh. 26. Higher-power view showing host inflammatory response (Figures 12.25 and 12.26 from Overstreet, *Gulf Res. Rep.*, Suppl., 1:1–43, 1983b). 27. Adult specimen of different and smaller (629-μm-long) species of bucephalid than those shown in Figures 12.21 through 12.23, *Bucephalus cynoscion* from intestine, but infections also occur in pyloric ceca and rectum. 28. Anterior end showing spiny oral sucker area (about 675 μm of 3.00-mm-long specimen) of much larger and relatively narrow adult acanthocolpid digenean, *Stephanostomum interruptum*, from intestine. 29. A 5.3-mm-long adult specimen of the pleorchiid digenean *Pleorchis americanus* from intestine. 30. Specimen of single-coiled juvenile ascaridoid nematode *Hysterothylacium reliquens*, from a host encapsulation in the mesentery, showing anterior and posterior ends. The seatrout can serve as a paratenic (transfer) host for this common nematode.

NEMATODES

Seatrout host relatively few species of nematodes, and most of the individuals are juveniles (Figure 12.30; Table 12.1). Nematodes can be found in the intestinal tract (Figures 12.31 and 12.32), viscera, mesentery, and tissues (Figure 12.30). Seatrout acquire the worms, depending on the species, by consumption of eggs, juveniles, or the intermediate host, often a copepod intermediate host. Some species can be acquired from a paratenic host, that is, one in which development of the parasite does not occur. Seatrout also serve as a paratenic host for the juvenile stage of some species. After one or two molts in the definitive host, nematodes mature and produce eggs or larvae that are, in turn, shed from the definitive host to infect the appropriate intermediate host, where another series of molts occurs. Nematodes are typically dioecious and often markedly sexually dimorphic. In many species, including those in seatrout, females often constitute the majority of worms observed.

Some nematodes certainly cause pathology (e.g., abdominal adhesions in salmonids caused by species of *Philonema*), but few cause overt disease in either wild or cultured fish. Some obvious exceptions result from infections in abnormal hosts, such as the case of the introduction of the eel nematode, *Anguillicola crassus,* into the U.S. This nematode from East Asia is relatively nonpathogenic in native eels. When introduced, first into Europe and now into the U.S. (Fries et al., 1996), it is pathogenic and causes mortalities in the different eel species. Heavy infections of other nematodes may affect fish condition or behavior. Even if they do not, large numbers, especially in the flesh, can affect the marketability of fish.

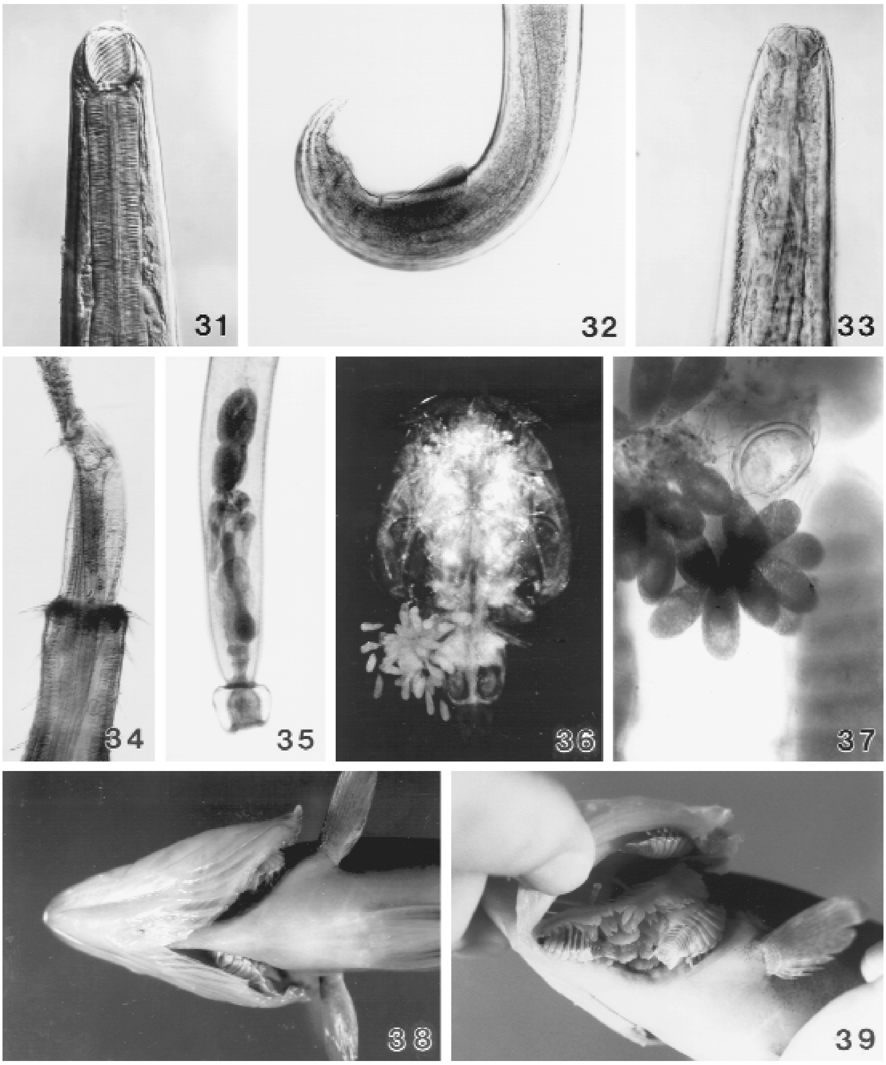
Five species of nematodes have been reported from seatrout in the southeastern U.S. Three of these species are juveniles of one or more species of *Hysterothylacium* that ultimately mature in other fishes. A species of *Margolisianum*, an adult philometrid probably acquired through consumption of the copepod intermediate host, has been reported inhabiting tissues of the mouth (Figure 12.33). Grossly visible philometrids are always females; males of this group are typically very small and often inhabit a totally different site in the host. The camallanid *Spirocamallanus cricotus* is the only adult nematode to inhabit the intestinal tract (Figures 12.31 and 12.32). Females of the philometrid and camallanid release free-living larvae that are eaten by their copepod intermediate hosts.

Control of these and other nematodes is best accomplished through prevention. Proper quarantine procedures reduce the risk of introduction. Water can be filtered to remove intermediate hosts; however, large-scale systems can develop their own fauna of agents and hosts, which interact with outside fauna such as birds. Because birds act as definitive hosts for some nematodes parasitizing fish, infective stages may be introduced. However, no such avian nematode has yet been reported from a seatrout. Postinfection treatments with standard anthelmintics are possible but unreliable, both in terms of efficacy and side effects. Reviews of anthelmintics are included in Stoskopf's (1993) review of fish chemotherapeutants.

ACANTHOCEPHALANS

Acanthocephalans, also known as spiny-headed worms, are a small, unique group of parasites related to rotifers (Dunagan and Miller, 1986). Acanthocephalans inhabit either the intestine as adults or the body cavity or tissues as juveniles and typically have simple life cycles involving two hosts: a vertebrate and an "arthropod." Shell-encased embryos (acanthors) are released from adult worms and passed in the vertebrate definitive host's feces. In species infecting an aquatic vertebrate, a specific crustacean then consumes the acanthor, which develops into a juvenile in the crustacean. Definitive hosts are infected either by consumption of the arthropod intermediate host or, in cases of some species, by a vertebrate or invertebrate paratenic host.

Fish may serve as paratenic or definitive hosts. Epizootics of acanthocephalans are known from hatcheries (Bullock, 1963) and wild populations (Schmidt et al., 1974), but they are unusual. The two species of acanthocephalans reported from seatrout are both adults, but the spotted seatrout does not serve



FIGURES 12.31 THROUGH 12.39 31. Anterior end showing sclerotized spiraled bands of buccal capsule of an adult specimen of the camallanid nematode *Spirocamallanus cricotus* from the intestine. 32. Posterior end of same male specimen, showing caudal alae with associated papillae. 33. Anterior end of a 10-mm-long adult female philometrid nematode *Margolisianum* sp. from tissues in mouth. 34. Anterior end of palaeacanthocephalan acanthocephalan *Dollfusentis chandleri* from rectum, showing hooks, including large basal ones on everted proboscis, relatively long neck, and anterior portion of trunk that contains spines. 35. Posterior end of 6.5-mm-long male individual of same species showing testes, cement glands, cement reservoir, Saefftigen's pouch, and everted copulatory bursa. 36. Caligid copepod *Caligus praetextus* from gills, showing eggs of udonellid monogenean *Udonella caligorum* (from Overstreet, R.M., Metazoan symbionts of crustaceans, in Provenzano, A.J., ed., *The Biology of Crustacea: Pathobiology*, Vol. 6, Academic Press, Inc., New York, 1983a). 37. Close-up of eggs of the monogenean as well as egg sacs of the copepod (From Overstreet, R.M., Mississippi–Alabama Sea Grant Consortium, Ocean Springs, MS, MASGP-78-021, 1978a). 38. Ventral view of year-old juvenile spotted seatrout from Mississippi in May showing opercula flared because of infestation by six individuals of the cymothoid isopod *Lironeca ovalis* on gills, with individuals obvious on both sides. 39. Opened operculum showing three specimens destroying gill filaments on one side. Usually, there is only one isopod per side.

as the typical definitive host for either (Table 12.1). *Dollfusentis chandleri*, a parasite common in other sciaenids, occurred as only single specimens (Figures 12.34 and 12.35) from two spotted seatrout in Louisiana and Mississippi.

Prevention of acanthocephalans through quarantine and limiting exposure to intermediate hosts is the best method of control. Nickol (1995) reported that loperamide was efficacious in treating an acanthocephalan outbreak in rainbow trout.

CRUSTACEANS

COPEPODS

Copepods are crustacean parasites that typically infest the skin, fins, gill filaments, gill rakers, and mouth and are among the most grossly noticeable of all fish parasites. Life cycles are generally direct and involve various numbers of molts, progressing from nauplius to copepodid, chalimus, preadult, and adult stages. Nine species of copepods belonging to three families have been identified from the spotted seatrout (Table 12.1). Three species plus two unidentified species are lernanthropids, which attach to the gill filaments and feed on blood, mucus, and epithelium and are among the most common of parasitic copepods. The taxonomy of this group requires attention. Surprisingly, this group of copepods also has received relatively little attention with respect to potential health effects. As with most copepods, there is great sexual dimorphism, and the majority of observed specimens are female. By extension from knowledge about other copepods that behave similarly, they can cause extensive gill damage, severe hemorrhage, and inflammation resulting in blockage of filaments and associated vessels, loss of gill surface area, hyperplasia of epithelium, and infiltration with various immune cells.

Caligid copepods, of which there are five species reported from spotted seatrout, are among the most well known of the copepods. Caligids live on the skin of many fish species, where they feed on the epithelium and mucus, often producing large skin lesions that contribute to massive mortalities of cultured fish such as pen-reared salmonids; however, they also affect wild stocks (Johnson et al., 1996). Members of *Caligus*, which includes species reported from spotted seatrout (Figures 12.36 and 12.37), are also known for their destructive nature. Overstreet (1983b) noted that larval seatrout can be infested, and a single *Caligus* individual can kill a small fish.

Pseudocynid copepods, of which one species is reported from the spotted seatrout, attach to the gill arches and feed on host epithelium and mucus. Major damage can result from host reaction at the attachment site; however, many individual copepods are probably necessary to cause serious harm to a host unless the host is a juvenile or otherwise compromised.

Treatment of copepod infections is possible but risky to the health of the host. As always, the best method of treatment is prevention through sanitation and quarantine. Filtering water supplies can eliminate infective stages. Organochlorine insecticides are generally effective, but most are toxic to fishes, sometimes at doses only marginally higher than those toxic to the copepods, and they can contaminate the environment. Cleaner fishes have been used in net pens to eat the copepods off host fish with some success. Lester and Roubal (1995) summarized treatments for copepod infections.

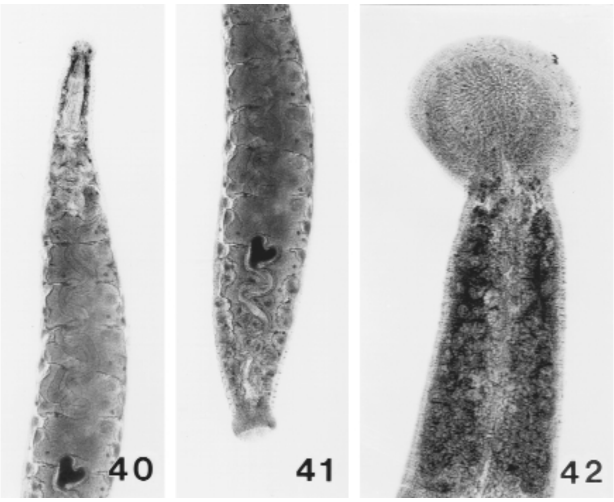
BRANCHIURANS

Species of *Argulus*, commonly known as fish lice, and related branchiuran genera, constitute this distinct group of parasitic crustaceans. These organisms do not use an intermediate host; eggs are typically deposited on a hard substratum and can survive a considerable length of time, even in harsh conditions. A copepodid-like stage emerges from the egg and is immediately infective to the host, usually the same species on which it will mature. Once on the host, the parasite undergoes a series of molts into the adult stage (Lester and Roubal, 1995). Argulids feed through a tubular mouth equipped with a stylet that everts and pierces the host (Overstreet et al., 1992). The combination of the rapid multiple penetrations of the stylet and the products released, at least some of which are hemorrhagic, can result in severe pathological changes in the host. Thus, heavy infections with an argulid can decimate hosts and stocks, particularly in confined areas (Lester and Roubal, 1995). One species of *Argulus* has been reported from the spotted seatrout (Table 12.1). Treatment is the same as for copepods.

ISOPODS

Isopods belong to a third group of crustaceans with representatives parasitic on fishes. Little is known concerning the complete life histories of parasitic forms. Of those isopods parasitizing fishes, about half belong to Cymothoidae, of which four species in three genera infect spotted seatrout (Table 12.1). Another, *Aegothoa oculata*, has also been mentioned (Pertuit, unpublished data) as infesting *C. nothus*; this isopod is actually the young developing stage of an undetermined cymothoid. Other species infect other seatrouts; for example, *Cymothoa oestrum* infests *Cynoscion* sp. off eastern Panama (Kensley and Schotte, 1989), and *Nerocila californica* infests *Cynoscion macdonaldi* in the upper Gulf of California (Brusca, 1978).

Cymothoids typically attach to the mouth, in the branchial area, or near the base of the fins with their claw-like legs. With these and their piercing or sucking mouthparts, some are capable of producing severe lesions, destroying gill filaments (Figures 12.38 and 12.39), causing anemia, and serving as vectors for other infectious organisms such as viruses. Leeches (Figures 12.40 to 12.42) also feed on blood and can transmit protozoan, bacterial, and viral infections. Some isopods harm their hosts simply because of their size. The pathogenic species *Lironeca ovalis* is reasonably common on the gills of juvenile spotted seatrout in Mississippi (Figures 12.38 and 12.39) and elsewhere in the Gulf of Mexico, as well as on *C. regalis* along the Atlantic coast and on the red drum (Overstreet, 1983c) and other fishes. Pearson (1929) and Overstreet (1983b) both suggested that the isopod might contribute to significant morbidity and mortality among the juvenile spotted seatrout through destruction of gill filaments. *Cymothoa excisa* also causes loss of gill filaments. Treatment is the same as for copepods.



FIGURES 12.40 THROUGH 12.42 40. Anterior end of young 5.0-mm-long clitellid hirudinean *Myzobdella lugubris* that had been feeding on the blood from the skin of a fish from moderate salinity. 41. Posterior end of same individual. 42. Anterior end of 15-mm-long specimen of *Malmiana philotherma* on the gills of a seatrout from high salinity, showing conspicuous sucker.

NONINFECTIOUS DISEASES

Noninfectious diseases also affect seatrouts. These diseases can result from deficiencies in diet, environmental influences, genetics, or combinations thereof. Occasional abnormalities in spotted seatrout have been reported. Rumbold and Snedaker (1999) reported a typical 15% prevalence of abnormalities such as lordosis, scoliosis, and failure to develop at 48 h post-hatch. However, as discussed earlier, the impact of these diseases on wild fish is hard to assess because it is likely that debilitated seatrout in the wild quickly become prey. Perhaps a more important aspect of some noninfectious diseases is that they may affect the incidence of parasitic diseases by making hosts susceptible to parasites that otherwise would not cause harm.

ABNORMALITIES

Rose and Harris (1968) and Hein and Shepard (1980) reported two spotted seatrout with pug heads. Burgess and Schwartz (1975) reported specimens with lordosis. Overstreet (1983b) reported internal abnormalities of unknown etiology but noted that the lesions may have been related to predator attacks, inadequate diets, or congenital problems. He also noted that the degeneration of parasites, particularly the cestode *P. caryophyllum*, might result in lesions. Neoplasms are not common. Couch (1985) tentatively diagnosed a tumor in a single specimen of *C. nebulosus* from Pensacola Bay in northwest Florida as a fibrolipoma, which was probably similar to another tumor reported in the weakfish *Cynoscion regalis* from Virginia by Tubiash and Hendricks (1973). A different tumor collected from *C. regalis* in Virginia by Zwerner, Ruddell, and Wilburn was diagnosed as a ganglioneuroma by John Harshbarger (Registry of Tumors in Lower Animals [RTLA] No. 1605). Other non-neoplastic cases from the same species have been deposited in the RTLA: infectious granuloma (RTLA 1724) and panopthalmitis and retrobulbar granuloma (RTLA 1986) from North Carolina and chronic inflammation (RTLA 4441) "fin rot" (RTLA 4466) from New Jersey. Similar cases occur in the spotted seatrout in Mississippi. Fournie et al. (1996) reported less than 1% of the weakfish in Virginia and fewer than 1% of the sand seatrout *C. arenarius* in Louisiana with gross pathologic signs.

ENVIRONMENTAL ISSUES

Abiotic Factors

Most nonparasitic diseases are caused by environmental influences, including pollution. Temperature and salinity changes can have a major influence on seatrout. Several instances of seatrout mortality and morbidity associated with cold-weather events have been reported (Gunter, 1952; Tabb, 1958; Moore, 1976; Adkins et al., 1979). In Fort Bayou and other recreational fishing sites near Ocean Springs, Mississippi, when temperatures rapidly drop toward or below freezing over a 1- to 2-day period, a large number of spotted seatrout become stunned. When this condition happens every few years, many of the local residents collect the stunned seatrout to fill their freezers for future eating.

Generally, temperatures below 7°C cause morbidity of local fishes. Individuals can recover from short-term exposures to 7°C, but a 24-hour exposure has been shown to be lethal. Tabb (1958) considered 7 to 10°C "adverse" for the spotted seatrout. A more important factor, however, may be the rate of the temperature change. Rapid changes (in either direction) are more likely to be detrimental. Vetter (1982) suggested that *C. nebulosus* was able to adapt better to temperature changes than was *C. arenarius* or *C. nothus*.

Salinity concentration is also important. Temperature-sensitive species such as *C. nebulosus* and *Mugil cephalus* tolerated some freezing conditions when salinity values, and presumably high calcium levels, were relatively high. In Mississippi, those species survived freezing conditions in 8.0-ppt salinity and 138-ppm calcium, while mullets and other fishes in water with lower values died (Overstreet, 1974). Given that the spotted seatrout is an estuarine species, some tolerance to a range of salinities can be expected. Serafy et al. (1997), however, found that the spotted seatrout was among the least tolerant (out of ten species) of drastic salinity changes. Wakeman and Wohlschlag (1977) reported 20 ppt as the optimal salinity for metabolic processes at 28°C. Drastic or rapid temperature changes affect the ability of a fish to osmoregulate and, therefore, to tolerate salinity changes (Overstreet, 1974).

Wild fish, of course, can migrate to mitigate environmental changes. The health and survival of tank-held fish, on the other hand, are dependent on an understanding of these tolerances. Larvae may be especially sensitive to temperature and salinity changes. Banks et al. (1991) demonstrated that salinity tolerance of spotted seatrout was at its minimum in 3-day-old larvae. They also suggested that exposure to changing salinity early in development was related to an increased ability to tolerate changes later in life.

Ammonia and nitrite levels may also be important in tank-held fishes. Daniels et al. (1987) found that larval spotted seatrout were more sensitive to changes than eggs and that tolerance for unionized ammonia increased with age through 4 months. Both eggs and larvae were extremely tolerant of nitrite, probably due to the high chlorine and calcium ion levels in seawater. Once again, the rate of change may be a significant factor in determining toxicity. Johnson et al. (1977) found that chlorinated effluents caused considerable larval mortality.

Biotic Factors

Toxic materials may influence the health of spotted seatrout. Such toxins may be either naturally occurring or related to pollution events. Naturally occurring toxins include those produced by algae or dinoflagellates during so-called harmful algal blooms (HABs) and compounds such as hydrogen sulfide. Mortality events associated with HABs in the Gulf of Mexico and along the Atlantic coast involve many fish species and are well documented. In these events, mortalities can be caused by neurotoxins released from the algae or by the combination of neurotoxins and depleted oxygen levels due to decomposition of the algae. Rumbold and Snedaker (1999) demonstrated that brevetoxin, the toxic component of some red tides, is toxic to spotted seatrout eggs and embryos. Burkholder (1999) reviewed the toxicity of *Pfiesteria*.

Hydrogen sulfide can accumulate in bottom sediments as a result of the normal decomposition process; events such as high winds or thermoclines can result in release of the compound. As a result, oxygen levels decrease and mortalities occur. Also, unusual combinations of water conditions involving more than oxygen concentration along the eastern shore of Mobile, Alabama, and the Mississippi coast occasionally result in an event locally referred to as a "jubilee." Fish become stunned or die when trapped in relatively fresh river water overlaid by saltwater, allowing the local residents to fill their freezers with spotted seatrout and other fishes (e.g., Overstreet, 1978a).

Pollution

Organic materials from agricultural run-off can contribute to oxygen depletion by using available oxygen for degradation. Organics can stimulate primary productivity that eventually requires oxygen for degradation. Organochlorine pesticides can accumulate in the tissues of seatrout. Kennish and Ruppel (1996, 1998) showed that chlordane, polychlorinated biphenyls (PCBs), and DDT continued to accumulate in the flesh of *C. regalis* long after some governments restricted the use of those pesticides. Butler (1969) and Butler et al. (1970) showed that seatrout with DDT residues as high as 8 ppm in the gonads failed to breed for as long as 2 years. Meyers and Hendricks (1982) summarized the effects of chlordane, DDT, and PCB on aquatic animals, noting liver, gill, spleen, intestine, kidney, skin, gonad, and brain abnormalities. One of the studies summarized by Myers and Hendricks was performed on spot (*Leiostomus xanthurus*), another sciaenid, and showed liver abnormalities after exposure to PCBs.

Petroleum hydrocarbon residues that may result from oil spills or street run-off are known to be toxic. Paperna and Overstreet (1981) cited work showing that mullet (Mugilidae) exposed to oil lost weight, showed decreased condition, and became disoriented. Previously stressed fish died quickly after exposure to the oil. Solangi and Overstreet (1982) demonstrated histopathological alterations in fishes exposed to crude oil fractions. Khan (1990) demonstrated that exposure to water-soluble fractions of crude oil increased the prevalence and the intensity of trichodinid infestations. The spotted seatrout is susceptible to all these situations.

INDICATORS

Given knowledge of the life histories of disease organisms and how the various components of ecosystems interact, patterns in infection, changes in those patterns, or comparative patterns can provide insight into host biology or environmental conditions. The most well-known examples are the use of patterns in parasite infections to distinguish stocks of fishes (e.g., Margolis, 1963; Lester et al., 1988; Lester, 1990; Arthur and Albert, 1993). However, increasing concern over the fate and effects of environmental contaminants also has resulted in interest in parasites and diseases as indicators of environmental health. Overstreet (1993, 1997) summarized the relationship between parasitic diseases in fish and toxicants and other environmental factors. Overstreet et al. (1996) showed how the western mosquitofish could be used to assess the influence of pulp and paper mill effluent on the environment. Kloepper-Sams et al. (1991) and Hinton et al. (1992) also showed how fish biomarkers can be used to assess environmental health.

The environment can be evaluated using the presence, absence, or intensity of parasites or diseases. Environmental effects can be assessed through an evaluation of lethal or sublethal changes in tissue, growth, or reproduction (Overstreet, 1997). The parasites and lesions of seatrout probably could be developed to serve as a general indicator of inshore environmental health and host biology.

With respect to seatrout, several diseases and parasites have the potential to serve as indicators. Because the spotted seatrout is an almost entirely estuarine species and perhaps limited in movement among estuaries, it may be possible to differentiate fish from different estuaries based on their parasites. Typically, long-lived parasites found in relatively high abundance in at least one locality and with no multiplication in the host are used in stock discrimination (Arthur and Albert, 1993). Myxozoans, microsporans, helminth intermediate stages, and nematode juveniles broadly fit those requirements. Other parasites of seatrout, including bacteria and ectoparasites, may serve as monitors of environmental health because many bacterial diseases are related to environmental conditions.

Many species of bacteria, including but not limited to those in the genera *Vibrio, Aeromonas, Pasteurella*, and *Mycobacterium*, are common and normal components of the estuarine environment. Abnormal temperature and poor water quality can select for virulent bacterial strains or cause fish to be stressed and susceptible to disease caused by bacteria that would otherwise be harmless (Actis et al., 1999). Ciliates, monogeneans, dinoflagellates, copepods, leeches, branchiurans, and perhaps isopods may directly indicate the status of the surrounding environment. The internal helminths and other parasites with more than one host may indirectly indicate it. Crowding of fish in confined areas, perhaps in combination with the stress related to poor water quality, changing salinity, extreme temperatures, or low oxygen levels could result in increases or decreases in intensity of some of these parasites. Sand seatrout have been identified as part of a wild fish kill related to *Amyloodinium ocellatum* and low oxygen concentration (Overstreet, 1993). Trichodinids are known to respond to temperature changes (Lom, 1995). Flagellate infections have been linked to mortalities in summer flounders exposed to unusually cold water (Burreson and Zwerner, 1984). Copepods are known to kill salmon held in net pens or confined to areas of high temperature (Wootten et al., 1982; Johnson et al., 1996).

Digeneans, cestodes, nematodes, and acanthocephalans can serve as indicators, as well; however, because these organisms are internal parasites, they are usually indirect indicators. As a general rule, organisms in this group have more complex life cycles than the organisms in the previous group;

therefore, patterns must be interpreted carefully. Because these parasites are usually acquired through consumption of intermediate hosts, they provide a record of what the host has eaten. Thus, given knowledge of the distribution of the intermediate hosts, inferences can be made about where fish have been. For example, MacKenzie (1988) used the presence of certain digeneans to identify the summer feeding grounds of herring in the North Sea. These types of parasites also serve as good indicators of diet. Möller (1984) used differences in parasites of flounders to conclude that the fish were specializing on different prey items in different areas. Blaylock et al. (1998) showed that the parasite fauna of Pacific halibut changed as the fish grew, thus reflecting, among other things, ontogenetic niche shifts.

PUBLIC HEALTH ISSUES

Seatrout harbor relatively few parasites or diseases with the potential to harm humans. The bacterium *Vibrio parahaemolyticus* and other microbial organisms can cause disease in humans if contaminated fish are not adequately prepared. Romero-Ayulo et al. (1994) isolated *Escherichia coli* and *Staphylococcus aureus* (some of which were enterotoxigenic strains) in samples of the related *Cynoscion leiarchus* in Brazil. Toxic heavy metals and organic pollutants concentrated in fish tissue can pose public health risks if the concentration is high enough or the exposure is long term. Therefore, eating fish from heavily polluted environments could constitute a public health risk. At least one nematode from seatrout, *Hysterothylacium* type MB larvae, can cause mucosal hemorrhaging and focal eosinophilia in the rhesus monkey, white mouse, and probably humans (Overstreet and Meyer, 1981). Although it is incapable of infecting humans, the most conspicuous parasite in seatrout and the parasite that generates the largest number of public inquiries is the metacestode *P. caryophyllum* (see Overstreet, 1983b). In all cases, no parasite infecting properly prepared seatrout can harm humans.

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13 Management of Spotted Seatrout and Fishery Participants in the U.S.

Steven J. VanderKooy and Robert G. Muller

CONTENTS

ABSTRACT

The management of spotted seatrout is multifaceted. Managers must take into consideration the biological requirements of fish, as well as the impact on and response of participants to major changes in the fishery. Management no longer consists of estimating catch and effort and assigning ages to landed fish; management now requires an understanding of ex-vessel values, angler satisfaction, and socioeconomic impacts to communities before regulatory or legislative actions can occur. Management goals will continue to be reevaluated as the expectations of the fishing communities infringe upon the biological requirements of the resource. Although spotted seatrout are a natural resource owned by all, many anglers and fishermen avoid facing the fact that they are a finite resource and therefore must be managed with the best science available to ensure persistence of the fishery and prevent another "tragedy of the commons."

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INTRODUCTION

Spotted seatrout is an important recreational and commercial species taken almost exclusively within state jurisdictions due to its close association with marsh and estuarine habitats. Spotted seatrout management and allocation issues have precipitated controversy over harvest limits and gears within and between fishing groups. While the increase in participation in recreational fishing is a more recent trend, commercial catch records of spotted seatrout date back as far as 1887 in Louisiana, when an estimated 237.6 metric tons (mt) were caught in a single year. Despite the popularity of the fish, the commercial market for spotted seatrout is small in comparison to other species, in part due to the public's preference for seatrout as a fresh-caught fish. Limited commercial harvest is conducted mainly with inshore gill nets, trammel nets, haul seines, otter trawls, and hook and line, ensuring quick return to market.

The Magnuson Fishery Conservation and Management Act of 1976 (the Magnuson Act) mandates preparation of fishery management plans for important fishery resources within the exclusive economic zone (EEZ), the 370-km area off U.S. coasts in which foreign fishing is prohibited. The Magnuson Act set seven national standards to be met when managing a species in the EEZ, which include the prevention of overfishing, conservation based on science, and fair and equitable allocation. The 1996 reauthorization of the Magnuson Act established three additional national standards for fishery conservation and management that included requirements for the description of essential fish habitat (EFH) and new definitions of overfishing.

Since implementation of the Magnuson Act, there have been heightened awareness and recognition of the economic importance and impacts of recreational and commercial fishing in the marine environment. In addition, the movement of the human population to coastal areas has resulted in an increase in the number of participants in recreational marine fisheries. Both trends have led to major changes in the philosophy of fisheries management in the late 1970s and early 1980s.

In response to increased user group demands throughout the 1970s, a spotted seatrout profile for the Gulf of Mexico was developed by the Gulf States Marine Fisheries Commission (Perret et al., 1980) and a regional management plan for the Gulf of Mexico was completed in 2001 (VanderKooy, 2001). Similarly, the Atlantic States Marine Fisheries Commission developed a fishery management plan for spotted seatrout in 1984 through their Interstate Fisheries Management Program (Mercer, 1984). These management plans provide the most current biological information available for the species, address its management by each state partner, and develop a regional perspective for future management of the species in the two respective regions.

In this chapter, we will focus on the management history of spotted seatrout fisheries and responses to management measures. In addition, we will include available information on the social and economic changes that have occurred over the last 20 to 30 years and discuss their relevance to past and present management regimes.

THE RECREATIONAL FISHERY

Spotted seatrout have long been a targeted recreational species for most saltwater anglers and are considered one of the preferred recreational species on both the south Atlantic and Gulf coasts (Tabb, 1960; Perret et al., 1980; Brown, 1981; Rutherford, 1982; Ditton et al., 1990). They are easily accessible throughout their range from boat or shore, making them highly sought by anglers who use techniques ranging from jigs and artificial plugs to live bait with great success. In Virginia and North Carolina, Brown (1981) reported that the largest spotted seatrout were captured by consistently fishing with stingray grubs, bucktails, and Mirrolures®, while live peeler crabs (*Callinectes* spp.) and spot (*Leiostomus xanthurus*) were the highest-producing natural baits. C. Wenner (SCDNR, personal communication) suggests that quartered peeler crabs are the preferred bait by most anglers fishing over grass beds in Virginia. In Florida, live pigfish (*Orthopristis chrysoptera*), mullet (*Mugil* spp.), and shrimp (*Penaeus* spp.) are the preferred live bait of most recreational anglers.

A myriad of artificial baits too numerous to list are also popular throughout the Gulf of Mexico. In recent years, Atlantic croaker (*Micropogonias undulatus*) has become a very popular spotted seatrout bait with Texas anglers. The demand for live Atlantic croaker has become so great that some anglers believe that the recreational fishery may have adverse effects on spawning and recruitment of croaker in Texas, although no biological evidence of adverse impacts to date exists (VanderKooy, 2001). However, as the recreational effort increases, some anglers are shifting toward more conservation-responsible philosophies, such as catch-and-release, and more specialty fishing, such as fly fishing and trophy fishing. Guide services for catch-and-release fishing are apparently increasing on both coasts, although the actual number of these services is presently unknown.

With the advent of handheld GPS receivers (global positioning systems), satellite imagery, laptop computers, fishing sonars, and echo sounders, as well as advances in tackle in general, today's fishery participants are more efficient in their ability to impact fish populations. As the affordability and rapid evolution of new technology allow almost anyone to possess and use it (Simpson, 1998), an increasing number of fishermen armed with these new high-tech "weapons" makes the management of spotted seatrout more difficult.

Despite the high participation of anglers in the recreational spotted seatrout fishery, this sector has been poorly chronicled. Other than anecdotal reports, little historical information exists regarding the recreational sector prior to the mid-1970s and early 1980s. Archaeological sites in Florida have revealed that hook-and-line fishing and net fishing occurred among coastal inhabitants long before Europeans arrived in Florida (Russo, 1990). In Texas, Colura and Vickers (1998) identified 492 spotted seatrout otoliths dating from 1200 A.D. to 3000 B.C., found in Native American middens from the Corpus Christi Bay and upper Laguna Madre estuarine systems.

Prior to 1981, general information on recreational angler participation, effort, and catch was unavailable except as entries in local rodeos and fishing tournaments like the Grand Isle Tarpon Rodeo, founded in 1928. Guest and Gunter (1958) indirectly addressed the lack of recreational data in the northern Gulf of Mexico when they indicated that the recreational or sport catch "undoubtedly exceeds the yearly commercial catch," referring to the almost 2300 mt marketed commercially in 1954. Only recently have some states imposed regulations on the recreational sector that allow accurate assessment of recreational contribution.

The National Marine Fisheries Service (NMFS) Marine Recreational Fisheries Statistics Survey (MRFSS) and the Texas Parks and Wildlife Department (TPWD) Marine Sport-Harvest Monitoring Program provide the most current recreational fishing information available. The Texas monitoring program has been in place since 1974 and the MRFSS has existed since 1979. Together they provide the best estimates of landings and effort by recreational anglers in each state. The trend to include economic questions in the surveys facilitates the acquisition of socioeconomic information on the recreational sector. In recent years, MRFSS and the Texas monitoring program have increased sampling efforts, leading to more reliable estimates of the recreational contribution to the spotted seatrout fishery.

In 1998, the total recreational landings for spotted seatrout in the U.S. was 5400 mt, of which roughly 87% was landed by Florida (both coasts), Louisiana, and Texas (Table 13.1). Although the percent contribution each state makes to the total recreational harvest has varied, these three states have historically been the primary production areas for the species and will be the focus of this section. North Carolina, Mississippi, Georgia, and South Carolina contribute roughly 11%, while Alabama, New Jersey, Delaware, Maryland, and Virginia contribute approximately 2% annually to the total U.S. recreational harvest.

Changes in human population demographics suggest the potential for increased fishing pressure in coastal areas. Nearly half the U.S. population currently lives within 45 km of a coast, and recent studies have shown that coastal populations are growing faster than other populations (Culliton et al., 1990; Cohen et al., 1997). Nearly 50 million people were projected to live along the Atlantic coast from Maine to Virginia by 2000, constituting almost a quarter of the total U.S. population, while 16 million people were projected to live along the coastline of the Gulf of Mexico (Culliton et

TABLE 13.1
Annual Recreational Landings Estimates of Spotted Seatrout in the U.S. by Weight (Metric Tons) from 1981 to 2000

	State												Total US
Year	NJ	DE	MD	VA	NC	SC	GA	FL	AL	MS	LA	TX	Landings
1981	0.0	0.0	0.0	0.0	28.6	6.7	62.9	1,416.5	4.0	67.9	1,060.7	1,190.5	3,739.6
1982	0.0	0.0	0.0	0.0	54.5	267.2	80.7	1,822.4	148.3	177.3	3,340.8	1,110.3	6,599.2
1983	0.0	0.0	0.0	0.0	43.7	62.8	146.9	2,213.1	124.0	268.1	2,813.5	1,417.5	6,836.2
1984	0.0	0.0	0.0	0.0	18.1	52.7	64.1	3,171.9	23.9	27.4	1,073.6	378.3	4,675.1
1985	0.0	0.0	0.0	0.0	130.7	231.1	106.5	1,883.2	32.3	48.6	1,439.4	703.9	4,107.4
1986	0.0	0.0	2.3	29.2	149.0	266.5	199.9	3,530.4	66.3	284.3	4,130.0	893.6	8,904.7
1987	0.0	0.0	10.2	17.5	166.2	268.8	222.9	2,103.5	53.9	225.3	3,399.9	916.0	6,698.6
1988	0.0	0.0	16.6	208.8	177.3	203.4	243.6	2,837.1	65.9	171.1	2,851.1	944.2	6,869.4
1989	0.0	0.0	83.6	51.0	117.8	125.9	275.8	3,231.1	38.8	97.3	2,587.0	704.9	6,659.2
1990	0.0	0.0	17.7	54.9	128.3	79.3	192.2	1,096.9	18.6	83.2	1,215.3	304.7	2,718.6
1991	0.0	0.4	15.8	55.2	214.3	284.9	657.6	2,075.1	41.8	167.7	3,424.4	626.2	6,335.2
1992	0.0	0.0	3.5	25.7	230.8	103.1	195.5	1,526.8	30.7	123.8	2,895.0	1,096.8	5,673.1
1993	0.0	0.0	5.8	91.4	139.3	121.6	266.0	1,161.0	75.6	146.8	2,557.4	1,023.5	4,964.3
1994	0.0	0.1	12.1	79.5	308.4	83.2	187.1	1,254.4	11.2	92.4	3,041.8	1,023.0	5,422.8
1995	0.0	0.0	14.3	67.4	217.1	112.5	302.7	1,387.9	49.5	164.9	3,435.7	991.3	6,029.3
1996	0.0	0.0	0.0	35.0	89.5	77.9	89.1	918.1	40.4	170.6	3,444.9	998.5	5,572.6
1997	1.8	0.3	15.0	118.8	141.5	74.3	110.0	1,009.8	29.2	214.8	3,273.8	1,206.4	5,734.1
1998	0.0	0.1	16.9	28.1	201.6	68.8	119.2	1,167.8	61.0	200.7	2,465.1	1,148.1	5,042.7
1999	0.0	0.0	0.0	131.9	313.3	66.4	415.9	1,345.1	94.9	239.5	3,539.2	NA	NA
2000	0.0	0.0	1.3	86.4	164.7	116.5	247.2	1,456.1	125.1	153.6	5,024.8	NA	NA

Notes: (NMFS, personal communication from the National Marine Fisheries Service, Fisheries Statistics and Economics Division, Silver Spring, MD; TPWD unpublished data.) Estimates from the Northeastern Atlantic states in the early 1980s may be a result of low encounter rates with the target species by MRFSS samplers and may not reflect actual landings. (NA = data not available.)

al., 1990). Coastal population growth, coupled with increased numbers of tourists and vacationers, has increased demands on aquatic habitats and fishery resources. For the years between 1990 and 2025 in Texas alone, the projected rates of growth in the number of saltwater anglers (60%) will trail population growth (66%) but will far exceed the rate of growth among freshwater anglers (42%). This will place additional pressure on all saltwater fisheries, including those for spotted seatrout (Murdock et al., 1992).

FLORIDA

Klima and Tabb (1959) described the recreational fishery in northwest Florida as anglers coming to fish camps to launch or rent boats and hire guides to fish using cane poles, rod and reels, or spinning gear. While some anglers used artificial lures, the most popular baits were whole or cut pinfish, *Lagodon rhomboides*, with the largest catches of spotted seatrout caught in the winter (Klima and Tabb, 1959). Some anglers sold all or some of their catches to local fish houses. The only statewide regulation on spotted seatrout was a statewide minimum size of 30.7 cm total length (TL), except in Franklin and Wakulla counties in northwest Florida, which remained exempt from size restrictions. Tabb (1960) indicated that spotted seatrout were in the top three most-sought-after species by recreational anglers because they readily took a lure or bait and could be caught at nearly any time of day in most seasons. In the Indian River, live bait was more successful than artificial and the most skilled anglers caught the largest fish.

Today, recreational catch methods are similar except that anglers have more reliable boats, an increased ability to locate good fishing sites, and gear made from more durable materials. Skill, however, still increases an angler's probability of success. The size of spotted seatrout caught today by unskilled anglers is about the same (25.6 to 33.3 cm) as what Tabb (1960) reported more than 40 years ago.

In 1998, it was estimated that 2.3 million residents participated in saltwater fishing in Florida, landing 1179 mt of spotted seatrout and contributing 27% of the total reported recreational landings in the U.S. for the species (NMFS, personal communication from the National Marine Fisheries Service, Fisheries Statistics and Economics Division). From 1989 (when the state began requiring a recreational fishing license) through 1998, license sales rose from 420,000 to 560,000. Florida exempts residents under 16 or over 65 years of age and any resident fishing in saltwater from land or a structure fixed to land. Florida anglers made approximately 22.3 million fishing trips in 1998, with spotted seatrout contributing 2.7% by number and 4.4% by weight of the total catch for all species harvested recreationally in Florida (NMFS, personal communication from the National Marine Fisheries Service, Fisheries Statistics and Economics Division).

Recreational spotted seatrout landings in Florida have varied greatly since 1981, primarily because of regulatory changes (Figure 13.1). In November 1989, the Florida Marine Fisheries Commission (now the Florida Fish and Wildlife Conservation Commission) imposed stricter regulations on the recreational spotted seatrout fishery by implementing a statewide minimum size of 35.9 cm TL, an allowance for only one fish of more than 61.5 cm TL, and a ten-fish-per-day bag limit with a 2-day possession limit. As expected, recreational landings dropped in response to these regulations, resulting in a population with more age classes and higher spawning biomass (Murphy et al., 1999). In 1996, Florida changed the recreational size limits to a slot limit of 38.5 to 51.3 cm TL, except for the northwest region, which had a 38.5 to 61.5 cm TL slot limit. Florida closed the recreational fishery during November and December on the east and southwest coasts and only during February for the northwest region; however, east coast anglers reduced the effect of the closure by increasing their activities during September and October (Murphy et al., 1999). Lastly, the daily bag limit was lowered from ten fish per day to five fish per day, except in the northwest region which had a seven-fish daily bag limit.

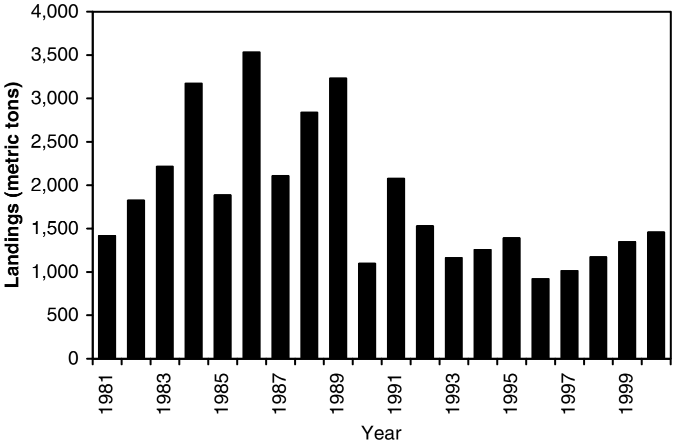

FIGURE 13.1 Florida recreational landings (mt) of spotted seatrout from 1981 to 2000 (NMFS, personal communication).

LOUISIANA

Spotted seatrout has consistently been reported as one of the primary target species by recreational anglers in Louisiana, constituting 52% by number and 30% by weight of the total recreational catch in Louisiana for 1998 (NMFS, personal communication from the National Marine Fisheries Service, Fisheries Statistics and Economics Division). Prior to 1976, the spotted seatrout fishery in Louisiana was unregulated; estimates of recreational landings before 1981 do not exist other than in anecdotal accounts, historical publications such as newspapers and magazines, or events such as rodeos and tournaments. In a survey by Adkins et al. (1990), 63.8% of interviewed Louisiana anglers preferred spotted seatrout to all other species.

An estimated 475,000 Louisiana residents participated in marine recreational fishing and made 2.7 million trips in 1998 (NMFS, personal communication from the National Marine Fisheries Service, Fisheries Statistics and Economics Division). A total of 5.0 million spotted seatrout weighing 2449 mt were taken in 1998 by recreational anglers in Louisiana waters alone (NMFS, personal communication from the National Marine Fisheries Service, Fisheries Statistics and Economics Division). This constituted approximately 49% of the total landings by weight of spotted seatrout in the U.S. Although fluctuating greatly, landings in Louisiana since 1981 have generally increased (Figure 13.2). The declines in 1984, 1985, and 1990 were related to widespread mortality due to extremely cold temperatures that seriously impacted the adult spotted seatrout population. The Louisiana Department of Wildlife and Fisheries implemented a recreational minimum size of 30.8 cm TL in 1987, and the daily bag limit was lowered from 50 to 25 fish in 1988. In addition to increased landings, resident recreational saltwater license sales in Louisiana increased substantially after they were introduced in 1984, from approximately 83,500 to almost 300,000 in 1998. Resident anglers under 17 and over 60 years of age are not required to purchase a saltwater license in Louisiana.

TEXAS

Spotted seatrout in Texas are caught recreationally from private boats, charter boats, head boats, lighted piers, jetties, and the shoreline. The fishery occurs along the entire Texas coast, with Galveston Bay generally reporting the highest landings annually. The 1998 estimate indicated that

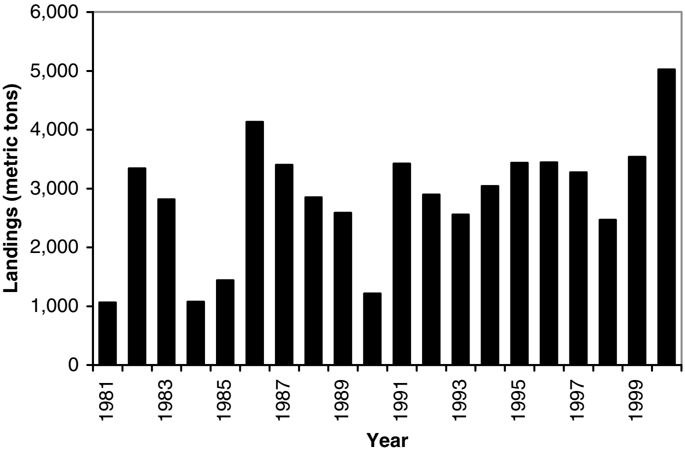

FIGURE 13.2 Louisiana recreational landings (mt) of spotted seatrout from 1981 to 2000 (NMFS, personal communication).

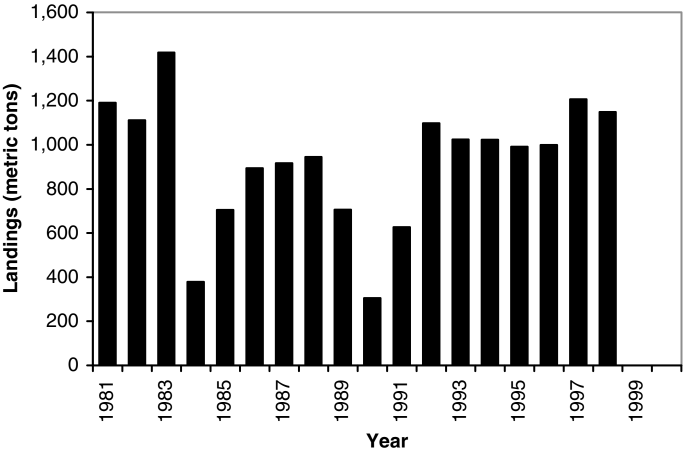

FIGURE 13.3 Texas recreational landings (mt) of spotted seatrout from 1981 to 2000 (NMFS, personal communication).

913,000 residents and nonresidents fished in Texas waters and landed 1133 mt of spotted seatrout with hook and line (Figure 13.3). The ban on commercial sales of spotted seatrout and effective elimination of the commercial harvest were expected to result in higher recreational landings; in fact, landings have remained relatively stable since 1981. In 1984, managers raised the minimum size to 35.9 cm TL and lowered the recreational bag limit to ten fish, which resulted in a reduction in the total landings from over 2 million in 1983 to just over 500,000 in 1984 (TPWD, unpublished data). The low landings in 1990 and 1991 were attributed to mortalities associated with a severe cold spell in December 1989 and January 1990.

Murdock et al. (1992) predicted that most of the anticipated change in the rate of participation in saltwater fishing in Texas from 2000 to 2025 will result from an increase in the average age of the human population and growth of coastal cities — not from overall population growth. The proportion of minority group members participating in saltwater fishing in Texas is also expected to increase to 56% by 2025 (Murdock et al., 1992). Species and management preferences, fishing motivations, and determinants of satisfaction for minority group members have not been studied to any great extent by any state bordering the U.S. Gulf of Mexico.

THE COMMERCIAL FISHERY

In contrast to the limited information on the recreational fishery, records of commercial catches of spotted seatrout date back as far as 1887 in the Gulf of Mexico and 1923 in the Atlantic (Mercer, 1984). The commercial market for spotted seatrout is smaller than for other species because the delicate flavor is preferred by consumers as a fresh product rather than a frozen one. The commercial fishery traditionally used inshore gill nets, trammel nets, haul seines, and otter trawls, although other harvest techniques included hand lines, trot lines, splatter poles, and, more recently, rod and reel. The splatter pole is basically a fixed length of line connected to a long pole or rod in which a live bait, typically a pigfish (*Orthopristis chrysoptera*), is swung out to a school of spotted seatrout. The noisy bait produces a feeding response in the school, allowing the fisherman to effectively yank a hooked trout out of the water before it can alarm the rest of the school. The method is very effective. Splatter pole fishing for spotted seatrout is still practiced in a few areas in Florida, although it is primarily associated with the Atlantic coast and the Indian River Lagoon.

Several states have eliminated commercial fisheries by designating spotted seatrout as a gamefish. In 1981, the Texas legislature banned the sale of native spotted seatrout, eliminating any commercial harvest in Texas waters. At its height, the commercial fishery in Texas rivaled the east coast of Florida and Louisiana in annual weight landed, between 771.0 and 977.5 mt from the late 1960s to the 1973 to 1975 period. While South Carolina, Georgia, and Florida primarily contribute to the recreational landings for spotted seatrout, North Carolina has the only substantial commercial fishery of all the Atlantic Coast states and accounted for roughly half the total U.S. commercial landings in 1998. Excluding North Carolina, Florida, and Louisiana, the remaining Gulf and Atlantic states contributed on the order of 10 to 15% of the total annual commercial harvest at this time (Table 13.2). Although many of the Gulf states have banned or restricted the use of nets, the remnant gill-net fishery in Louisiana, Mississippi, and Alabama still contributes to the total landings for spotted seatrout, drum, mullet, and flounder.

FLORIDA

Florida's commercial fishery began in the 19th century using nets and hook-and-line gear; more recent gears include haul seines and trammel nets. The recreational and commercial landings were not clearly separated until 1983, when the legislature required both sectors to have saltwater products licenses to sell their catch. Historically, recreational anglers were a major source of spotted seatrout for fish houses. Parsons (1984) interviewed 66 wholesale dealers and 30 fishermen and reported that gill nets were the main gear, accounting for 30% of the catch, with recreational hook-and-line anglers accounting for 25%. At that time, dealers considered fishermen who made less than 50% of their income from selling their catch recreational anglers. Tabb (1960) tells how experienced anglers were able to select the size of seatrout for marketing by their bait selection. Recreational anglers who had bought saltwater products licenses were displaced from the fishery when Florida declared spotted seatrout a restricted species: spotted seatrout could not be sold unless the license holder had a restricted species endorsement on the saltwater products license. To qualify for the endorsement, fishermen had to derive more than 50% of their income, or $2500, from selling fish.

Recorded landings were spotty prior to 1950, when the University of Miami's Marine Laboratory began collecting harvest data for the Florida State Board of Conservation (Tabb, 1960). Overall, commercial landings of spotted seatrout have declined over the past 70 years. Landings averaged 1905 mt statewide from 1939 until 1952 and then dropped to an average of 1542 mt until 1970. Another drop to 1179 mt ensued until 1983, followed by a general decline after the elimination

TABLE 13.2
Annual Commercial Landings Estimates of Spotted Seatrout in the U.S. by Weight (Metric Tons) from 1950 to 1999

	State										
Year	**MD**	**VA**	**NC**	**SC**	**GE**	**FL**	**AL[a]**	**MS**	**LA**	**TX**	**Total US Landings**
1950	0.0	42.5	218.6	11.6	15.4	2,037.1	28.4	27.9	305.2	NA	NA
1951	0.5	29.7	121.3	54.0	14.1	1,892.1	31.2	64.5	246.4	NA	NA
1952	0.0	32.8	291.8	39.1	10.7	2,156.4	46.3	571.4	259.5	NA	NA
1953	0.0	38.7	286.5	22.8	7.7	1,686.6	44.2	92.0	227.0	NA	NA
1954	0.0	47.0	299.3	11.6	9.1	1,565.2	26.1	63.4	184.3	NA	NA
1955	0.0	46.5	200.8	63.0	19.6	1,327.5	36.8	75.6	222.2	NA	NA
1956	0.0	89.2	176.6	101.2	5.2	1,402.6	1.4	97.0	259.9	NA	NA
1957	0.0	54.4	262.3	25.4	2.4	1,543.9	27.6	95.6	259.7	NA	NA
1958	0.0	27.4	80.4	9.3	1.2	1,674.0	23.7	128.5	271.2	NA	NA
1959	0.0	63.5	176.4	16.6	0.1	1,605.5	31.9	115.2	284.2	NA	NA
1960	0.0	24.9	77.7	24.0	0.5	1,657.6	16.8	52.8	189.4	NA	NA
1961	0.0	33.5	94.8	25.4	0.8	1,419.9	37.2	77.9	243.6	NA	NA
1962	0.0	12.9	92.9	12.3	0.5	1,534.7	17.4	50.6	140.1	539.9	1,861.3
1963	0.0	11.7	105.4	21.7	2.3	1,529.8	24.3	36.4	172.5	443.5	1,904.2
1964	0.0	10.6	92.9	27.0	0.9	1,616.5	29.3	67.2	131.8	533.5	1,976.2
1965	0.0	18.3	79.4	15.9	4.0	1,837.9	24.4	67.4	180.6	684.2	2,228.0
1966	0.0	5.4	52.6	11.1	1.5	1,768.0	21.5	65.6	293.3	689.9	2,219.0
1967	0.0	1.7	55.6	0.7	3.1	1,467.8	41.2	77.7	281.5	848.8	1,929.3
1968	0.0	2.6	44.1	5.4	0.8	1,679.9	45.7	121.8	280.8	532.0	2,181.0
1969	0.0	8.8	85.8	3.8	1.2	1,405.4	44.6	100.2	326.4	524.7	1,976.1
1970	0.0	29.9	183.5	4.1	4.5	1,521.4	38.3	115.6	356.7	674.7	2,254.1
1971	0.0	20.1	153.1	11.0	7.1	1,114.0	62.3	178.4	509.0	680.1	2,055.1
1972	0.0	5.8	228.1	8.2	11.9	1,258.4	99.8	115.5	770.9	890.4	2,498.5
1973	0.0	4.3	277.2	2.6	12.2	1,311.8	159.4	166.0	1,146.5	905.4	3,080.0
1974	0.0	11.9	304.0	4.0	7.3	1,323.8	164.9	133.7	963.9	537.2	2,913.5
1975	0.0	32.9	286.9	7.8	14.0	1,226.8	47.3	119.2	860.4	802.2	2,595.2
1976	0.0	17.7	289.2	2.6	13.6	1,276.4	19.5	80.5	730.8	610.9	2,430.4
1977	0.0	1.7	146.7	0.3	7.3	1,100.3	9.8	66.7	491.9	527.1	1,824.7
1978	0.0	2.8	44.1	0.1	1.1	1,097.0	14.4	47.8	309.4	467.3	1,516.7
1979	0.0	1.6	47.6	1.4	2.3	1,161.9	33.6	49.7	362.1	443.6	1,660.2
1980	0.0	0.5	77.7	3.7	1.9	1,140.6	11.8	12.4	274.1	292.9	1,522.6
1981	0.0	1.8	51.4	0.9	0.3	1,228.6	121.2	4.1	266.2	—	1,565.4
1982	0.0	1.5	38.0	2.0	2.3	1,243.6	283.9	7.6	330.0	—	1,653.5
1983	0.0	2.0	75.0	1.1	2.6	1,066.8	270.1	24.5	608.1	—	1,807.1
1984	0.0	1.4	69.4	0.8	2.0	870.2	93.0	24.9	441.5	—	1,419.4
1985	0.0	3.8	49.5	5.5	3.2	680.8	1.8	21.5	526.9	—	1,293.1
1986	0.0	8.4	86.9	5.4	3.9	711.2	1.5	17.3	897.2	—	1,731.8
1987	0.0	6.0	143.1	0.2	4.9	754.4	1.2	26.0	817.3	—	1,753.1
1988	0.0	7.0	134.5	0.0	4.1	761.9	0.4	29.7	650.2	—	1,587.9
1989	0.0	8.4	205.0	0.5	4.8	618.8	2.3	35.2	675.4	—	1,550.4
1990	0.0	9.7	113.7	0.0	2.7	455.8	—	13.8	294.2	—	890.0
1991	0.0	9.6	299.7	—	3.3	477.1	—	14.2	553.5	—	1,357.4
1992	0.2	4.7	238.7	—	5.1	408.6	—	14.3	440.7	—	1,112.3
1993	0.0	17.3	204.1	—	3.9	348.3	0.3	23.3	516.2	—	1,113.0
1994	0.0	20.2	187.1	—	2.3	403.2	—	33.1	464.3	—	1,110.4
1995	0.1	13.0	260.5	—	3.8	242.9	—	32.7	298.5	—	851.6
1996	6.8	2.0	102.8	—	3.4	32.2	—	19.8	351.3	—	518.3
1997	7.1	5.3	105.5	—	3.5	40.7	—	18.8	249.3	—	430.1
1998	9.0	9.9	139.6	—	1.3	37.3	—	19.3	50.8	—	267.2
1999	16.5	17.5	247.5	—	1.5	38.0	—	22.9	31.2	—	375.0

[a] Commercial sale of spotted seatrout was eliminated in 1985 with the designation to sportfish status; however, some fish were still encountered by samplers after 1985. (M. VanHoose, ADCNR, personal communication.)

Notes: NMFS, personal communication from the National Marine Fisheries Service, Fisheries Statistics and Economics Division, Silver Spring, MD, TPWD, unpublished data. NA = data not available; — indicates no commercial fishery.)

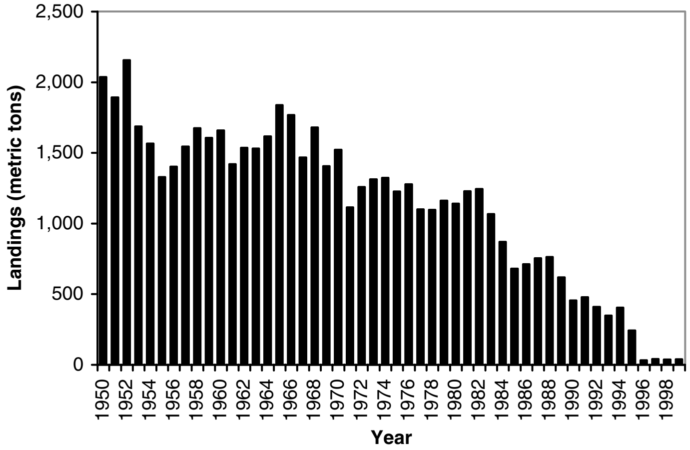

FIGURE 13.4 Florida commercial spotted seatrout landings (mt) from 1950 to 1999 (NMFS, personal communication).

of entangling gear in 1995 (Figure 13.4). A variety of explanations has been put forth to explain the 1980s and 1990s decreasing trend, and Tabb (1960) attributed the decline after 1952 to low mullet prices reducing the incidental catch of spotted seatrout by mullet fishermen.

Recent spotted seatrout landings have declined in response to regulations. In 1989, the Marine Fisheries Commission divided Florida into three regions for management purposes: east coast, southwest, and northwest; commercial quotas were established for each region. The size limits were the same as for the recreational fishery (a 35.9 to 61.5 cm TL slot limit with allowance for one fish more than 61.5 cm). When the red drum (*Sciaenops ocellatus*) fishery was closed in 1986, effort for spotted seatrout was also reduced in the southwest. Because the quotas were based on landings prior to and during the closure, the southwest region's allocation was never achieved, although the quotas in the northwest and east coast regions were filled. After entangling gear was eliminated through a constitutional amendment in 1995, and with the establishment of a restricted June through August commercial fishing season, commercial landings in Florida have averaged fewer than than 45 mt.

LOUISIANA

The commercial harvest of spotted seatrout in Louisiana was initially a bycatch fishery. In the 1880s and early 1900s, the fishery was based largely on shrimp-seine bycatch or on a secondary hook-and-line effort. The adoption of the shrimp trawl around 1920 and the resulting decrease in use of shrimp seines led to the introduction of trammel nets and resulted in a directed winter fishery conducted between shrimp seasons from December to April or May. The spotted seatrout fishery developed into a year-round fishery when gill nets were introduced in the 1960s. Although many commercial fishermen preferred the hook-and-line method (Pesson, 1974), by the mid-1970s gill nets were the primary method of harvest, followed by seines and trammel nets (Bowman et al., 1977). Monofilament gill nets, an improvement over the older twine nets, were introduced in 1971 (Bowman et al., 1977). After the monofilament gill-net ban in 1977, the use of webbing composed of three or more twisted strands of monofilament became widespread. Gill nets remained the primary method of harvest, and trammel nets displaced seines as the second-most-popular gear type through the 1980s and early 1990s. Since March 1, 1997, only hook and line may be used to harvest spotted seatrout commercially in Louisiana waters. This has resulted in a sharp decline in landings since 1997 (Figure 13.5).

Louisiana's landings increased from fewer than 1 million lbs in the late 1800s to a high of 1134 mt in 1973. Reported annual landings in Louisiana have averaged approximately 386 mt since 1887

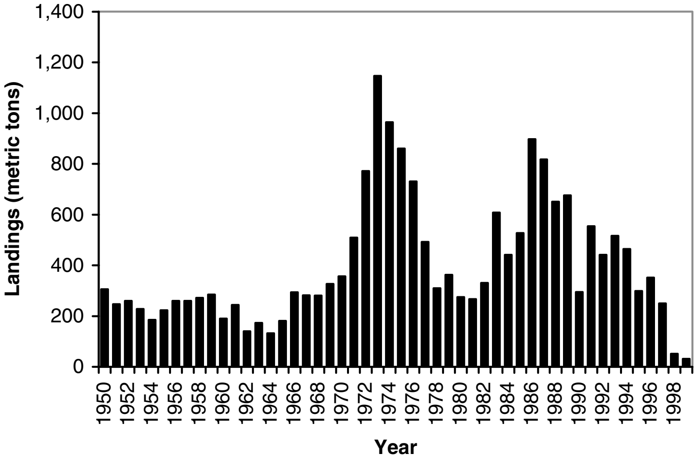

FIGURE 13.5 Louisiana commercial spotted seatrout landings (mt) from 1950 to 1999 (NMFS, personal communication).

and seldom exceeded 454 mt prior to 1971. Landings increased steadily through the early 1970s and peaked at 1134 mt in 1973. Commercial harvest quotas were established in 1987, and a season was set between September 15 and May 1 in 1992. Since the fishing year does not coincide with the calendar year, there is more variation in harvest by calendar year than by fishing year. In 1995, the harvest season was modified to operate from the third Monday in November until May 1.

NORTH CAROLINA

The recreational spotted seatrout fishery in North Carolina has been historically small in comparison to the commercial fishery. Prior to the net bans in Florida and Texas, the commercial fishery in North Carolina ranked third in landings among the Atlantic and Gulf Coast states. With the reduction in commercial fisheries elsewhere, North Carolina maintained its landings and has become the largest commercial producer of spotted seatrout in the U.S., landing 247 mt in 1999 (Table 13.2).

The North Carolina gill-net fishery had its origins in Hatteras around the 1920s (Ross, 1989). Traditionally, the nets were set and retrieved by hand. Today, many of the nets are set and retrieved using hydraulic winches. Gill nets have accounted for the majority of the commercial landings, with long-haul seines and trawls contributing around 3% (Zhao and Burns, in preparation), although Mercer (1984) indicated in trawl studies that incidental catch of spotted seatrout from North Carolina, South Carolina, Georgia, and Florida was minimal.

North Carolina's commercial fishermen participate year round in the inshore gill-net fishery, with peaks of activity in the spring, late summer, and fall (Wilson, 1997). The largest catches of spotted seatrout are made from October through December (Mercer, 1984). Set nets (sinking and floating gill nets) constitute about 93% of the total trips annually in the inshore fishery. The remaining 7% is made up of runaround nets (gill nets set around a visible school and then closed to encircle the school) and drift nets (similar to set nets but not anchored).

Commercial landings of spotted seatrout in North Carolina have fluctuated greatly since 1950 (Figure 13.6), but the average for the last 10 years has been 190 mt annually. The highest commercial landings recorded by NMFS for North Carolina was in 1974, at just over 304 mt and valued at $207,000 (Table 13.2). This was roughly 10% of the total U.S. landings that year. The cause of the decline in landings in the late 1950s and early 1960s is unknown; however, the large decline from 1976 to 1978 (289 to 44 mt) resulted from high mortalities caused by extremely cold winter temperatures in 1976 and 1977 (Merriner, 1980).

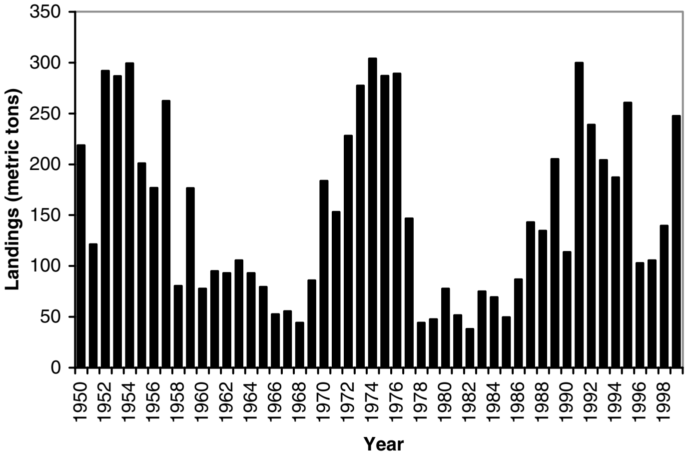

FIGURE 13.6 North Carolina commercial spotted seatrout landings (mt) from 1950 to 1999 (NMFS, personal communication).

TABLE 13.3
Number of Recreational For-Hire Vessels Licensed by the Gulf States

Fiscal Year	State					Gulf Total
	FL[a]	AL[a]	MS[a]	LA[b]	TX[c]	
89/90	2049	—	80	—	360	2489
90/91	1888	—	46	—	391	2325
91/92	1836	—	41	—	411	2288
92/93	1877	68	42	—	428	2415
93/94	1930	80	70	—	484	2564
94/95	2196	88	83	68	573	3008
95/96	2057	89	89	226	656	3117
96/97	2085	99	95	281	659	3219
97/98	2605	98	90	321	669	3783
98/99	2726	109	89	406	686	4016
99/00	2947	131	124	476	715	4393

[a] Listed as charter boats.

[b] License issued to persons, not vessels.

[c] For coastal counties only; listed as guide boats.

Note: — indicates no license available. (*Source:* state fishery directors (FFWCC, ADCNR, MDMR, LDWF, TPWD). Modified from GMFMC, 2001.

SOCIOECONOMICS OF THE FISHERY

Changes in marine fisheries regulations and policy may be associated with financial strains and difficult psychological and social adjustments by commercial fishermen and their families. While much greater effort has been given in recent years to collecting economic data, social science issues, although not necessarily ignored, suffer from a lack of appropriate research on social and cultural aspects of marine fishery regulations. Methodologies to address this aspect of management are currently being developed for the recreational and commercial fisheries through socioeconomic add-ons in the MFRSS program and commercial trip ticket systems.

RECREATIONAL COMPONENT

Spotted seatrout are an important species for the nearshore saltwater sportfishing industry in the Gulf of Mexico and on the Atlantic Coast. Assigning an economic value to the recreational harvest of this species is difficult. Several studies have attempted to measure expenditures, preferences, or amount of targeted effort in the recreational fishery for spotted seatrout at local or state levels. These studies offer some insight into the popularity and economic importance of the recreational spotted seatrout fishery.

Ditton and Hunt (1996) found that 18% of the marine recreational anglers in Texas directed their effort at spotted seatrout. An earlier survey of spotted seatrout anglers in Texas found that 265,000 anglers targeted spotted seatrout and spent, on average, $132 while on a typical trip (Ditton, 1993). In an earlier study, Ditton et al. (1990) found similar levels of spotted seatrout preference by Texas marine recreational anglers. The significance of this species to recreational anglers is demonstrated by spotted seatrout constituting the largest percentage volume of all species caught recreationally within the coast-wide bay and pass regions of Texas (Warren et al., 1994).

Spotted seatrout is an important recreational species in Louisiana (Bourgeois et al., 1996). Adkins et al. (1990) reported that spotted seatrout was the preferred species of approximately 64% of Louisiana saltwater anglers in a 1984 survey. They found a seasonal preference: most Louisiana anglers targeted spotted seatrout from May through August and then changed to red drum in all other months. Wieting (1989) found that up to 25% of the saltwater recreational catch in Louisiana is composed of spotted seatrout, and Kelso et al. (1991) estimated that 56% of Louisiana saltwater anglers consider spotted seatrout the species of highest preference. Bertrand (1984) found that Louisiana anglers averaged almost $30 in expenditures per saltwater fishing trip; the majority of these anglers targeted spotted seatrout.

The economic activities associated with saltwater angler expenditures in the U.S. have been estimated by Maharaj and Carpenter (1997). Initial expenditures by anglers initiated a series of inputs in local economies that resulted in economic output and products, secondary purchases of goods and services by associated businesses, generation of wages and salaries, and creation of jobs. True economic impact occurs when these consequences are associated with expenditures by nonresident anglers. Maharaj and Carpenter (1997) found that the economic activities associated with saltwater angling were substantial. The economic outputs associated with saltwater angling expenditures in the Gulf (excluding Florida) and the south Atlantic Coast (including Florida) were $2.9 and $7.04 billion, respectively. This generated $2.72 billion in total annual wages and salaries, as well as 136,000 jobs. Estimates are not currently available, however, for a state-by-state perspective on the total expenditures, economic output, wages and salaries, and jobs related to recreational fishing specifically for spotted seatrout.

A "typical" spotted seatrout angler is difficult to characterize because the recreational sector represents a true cross section of American culture. All educational, income, age, and ethnic groups participate in recreational fishing in the U.S. Because spotted seatrout are accessible from shore, dock, or boat, there is virtually no limit to their access by the recreational fishing public.

Socioeconomic data in the MRFSS found that the majority of participants in marine recreational fishing in the southeast region of the U.S. (North Carolina to Louisiana; notably, Texas anglers were not included) were white, averaging 90.4% of the total fishing population, whereas 7.5% were black (Milon, 2000). Of all those surveyed (white, black, Asian, and other), 4.5% claimed to be of Spanish or Hispanic origin, with the highest numbers (5.8%) from Florida (again, noting that Texas anglers were not surveyed by MRFSS). Approximately 60% of the marine recreational fishing participants have annual household incomes between $25,000 and $60,000, and most are male (72.8%).

Ditton et al. (1990) surveyed the Texas saltwater fishing community in 1986 and determined that the majority of individuals participating in saltwater fishing were middle-class males between the ages of 20 to 49, from urban areas along the Texas coast, and that 80% of the respondents were male. In 1996, Ditton and Hunt (1996) collected data on race and ethnicity and reported that most participants (89%) were white or Anglo, 5% were African–American, and 6% were Asian–American, Native American, or other. When asked about their ethnic origin, 10% of Texas anglers indicated that they were of Spanish or Hispanic origin.

COMMERCIAL COMPONENT

The commercial spotted seatrout fishery in the U.S. can be evaluated utilizing dockside value, which represents the total amount paid by the first handler to the harvester during the initial off-loading of the fish. Dockside value does not include the price markups at subsequent market levels. Information on prices and dockside value provides some basic insight into the economic importance and performance of the commercial spotted seatrout harvest sector.

The real dockside values (adjusted for inflation) for spotted seatrout in the Gulf of Mexico increased throughout the 1970s but have steadily declined since the mid-1980s (Figure 13.7). This decline in value reflects the decline in commercial landings Gulf-wide (Table 13.2). Declining total commercial values are directly related to policy and regulatory changes that have limited availability of the resource to the commercial sector throughout the Gulf. Dockside values for the Atlantic Coast during the same period have remained relatively stable, at around $700,000, driven primarily by North Carolina's sustained commercial landings.

Since the 1970s, Vietnamese–American fishermen have constituted a large portion of the commercial fishing sector in the northern Gulf (Starr, 1981; Osburn et al., 1990; Moberg and Thomas, 1993; Durrenberger, 1994). In a description of the shrimp-trawl fishery in the Gulf, Starr (1981) noted that several groups (including individuals of Laotian and Cambodian descent) have been lumped into the Vietnamese category for simplicity. Frequently, clashes occurred between ethnic groups during the resettlement of the first Vietnamese to U.S. coastal areas in the mid-1970s because of cultural differences, language barriers, and misunderstanding of unwritten local fishing rules and customs (Starr, 1981; Osburn et al., 1990).

Other regions of the Gulf are composed of various ethnic groups and are frequently localized such that ethnic stratification can occur. For example, prior to the net ban and designation of spotted seatrout as a gamefish, the ethnic makeup of the commercial fishing communities in Texas varied regionally. Overall, commercial fishing in the upper Laguna Madre was dominated by Anglo fishermen, with a few Hispanics; the lower Laguna Madre was dominated by Hispanic fishermen (90%). In the upper (Galveston Bay) and middle coasts of Texas, transgenerational Anglos and Asians are the predominant ethnic groups in the black drum trotline fishery (R.P. Campbell and L. Robinson, TPWD, personal communication).

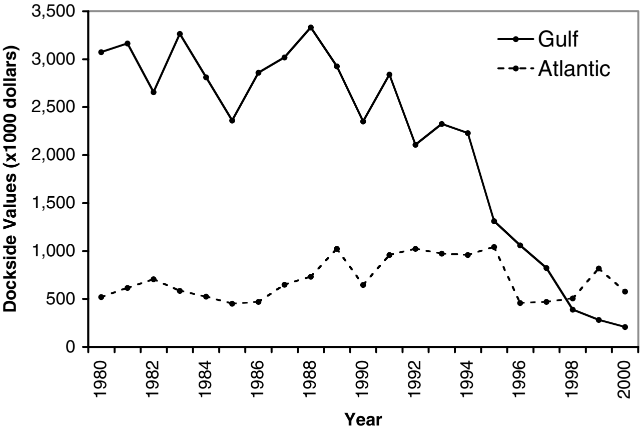

FIGURE 13.7 Real (adjusted for inflation) dockside values of commercial spotted seatrout landings for the Atlantic and the Gulf from 1980 to 1999 (NMFS, personal communication).

Many Vietnamese settlers in the Florida Panhandle initially entered the Gulf fishery as gill-net fishermen (Starr, 1981). In 1978, net boats captained by recently immigrated Vietnamese constituted one-eighth of the gill-net fleet in Pensacola Bay. American net fishermen protested the use of nontraditional lengths of net, the failure to properly mark nets, and the extended duration of net sets practiced by Vietnamese fishermen. Through legislation and regulations, the recent immigrants were forced to comply with local standards (Starr, 1981).

The ethnic makeup of the participants in the commercial fishery is less well documented. Johnson and Orbach (1996), in their socioeconomic profile of the commercial fishery of North Carolina, noted that, although almost 22,000 vessels were commercially licensed in 1994 and 1995, most licenses were not active in the commercial fishery. The survey also documented that commercial fishermen in this region seasonally switch between fisheries, in gear and in species. A single fishermen might actively fish two or three species in a year using gill nets and also set crab traps or drag trawls when the preferred species is less readily available.

In North Carolina, the majority of fishermen surveyed (96.8%) considered themselves white or Caucasian, while the remainder were black (2.7%) or other (0.4%); none were Asian or Hispanic (Johnson and Orbach, 1996). Approximately 80% of part-time and full-time commercial fishermen were married, and roughly 25% had spouses or children involved in fishing. Respondents indicated that some part-time commercial fishermen were reasonably well educated and held down other full-time jobs (Johnson and Orbach, 1996). These results typify a few participants in North Carolina and cannot be taken to represent the entire Atlantic Coast commercial fishery.

SHIFTING MANAGEMENT PHILOSOPHIES

The traditional view of marine fisheries management has changed considerably over the last 30 years. The large-scale migration of the human population to coastal communities and the increased participation in saltwater recreational fishing have required managers to spend as much time managing fishermen as they do managing fish. Along with biological data, state marine agencies spend considerable time, effort, and money collecting user-group data. Economists and sociologists are now employed or under contract with the state marine resource agencies to report on the saltwater-angling population and their impact in volume and value on the fishery. The recreational and commercial fishing public now participates in the management of their respective fisheries directly through state fish commissions, task forces, shareholder meetings and indirectly through well-organized advocacy groups and other nonprofit fishing organizations. These organizations, as well as a changing public opinion on how best to allocate a limited resource between commercial and recreational users, have led to the perception of unfair reallocations and quotas.

This shift in management philosophy was most evident in Texas with the 1981 designation of red drum and spotted seatrout as gamefish, effectively eliminating any commercial sale in that state. Alabama and South Carolina, likewise, gave spotted seatrout gamefish status in 1985 and 1986, respectively, only allowing the sale of "imported" fish from states with a legal commercial harvest. Opponents of the gamefish designation have suggested that subsequent legislation in 1988 banning all nets from Texas waters pushed the management of the spotted seatrout and red drum fisheries further into the economic and political arenas.

Two groups participate in the spotted seatrout fishery at this time: a few commercial fishermen, using limited gear in only a few states, and recreational anglers. A fine line separates commercial and recreational spotted seatrout fisheries, especially since the significant reduction in the use of nets. While the general public easily recognizes the traditional net fishermen as commercial, very few in the charter and guide industry acknowledge their commercial role in the fishery. Since 1990, the number of charter boats in the Gulf of Mexico has nearly doubled from 2489 to 4393 (Table 13.3).

As a result of these philosophical shifts in management approaches to fisheries in general and spotted seatrout fisheries specifically, management goals for each state have been redefined by biological needs and public satisfaction with the fishing experience. Therefore, evaluating the status of the regional spotted seatrout stock is problematic because different states use different conservation standards or conservation thresholds. For example, Louisiana has adopted a spawning potential ratio (SPR) value of 18% as their conservation standard. The SPR is defined as the number of eggs that could be produced by an average recruit in a fished stock, divided by the number of eggs that could be produced by an average recruit in an unfished stock (Goodyear, 1980). Louisiana's SPR in 1996 was 22%; therefore, the state does not consider the population to be overfished.

In contrast, Florida's management objective is a transitional SPR value of 35%, so the state currently considers its spotted seatrout to be overfished (22% in the northwest region and 25% in the southwest region). While Louisiana's standard was chosen to produce more fish, Florida's conservation standard was chosen to increase the number of large, older fish in the spawning stock. Both standards are ultimately based on angler satisfaction.

Texas determined spotted seatrout were overfished and began rebuilding the stocks long before SPR came into vogue. Goodyear first described the concept of SPR in 1980, the same year House Bill 1000, making spotted seatrout a gamefish in Texas, was passed into law. Therefore, Texas does not use a conservation threshold associated with any one stock measure to guide management of the spotted seatrout fishery. Rather, a broad-based, more holistic approach is used. The state's management objectives are 1) to allow fish to spawn at least once before entering the fishery, 2) to prevent growth overfishing, and 3) to provide for a quality trophy fishery.

On the Atlantic Coast, recent work done by Zhao et al. (in preparation) estimates that Georgia's SPR for spotted seatrout is just below 20% and the population may be growth overfished. Since Georgia has a substantial recreational fishery and only a minor commercial component, it has been recommended that the state adopt a SPR similar to Florida's threshold of 35% (Muller, 1997). North Carolina estimated that an SPR for its spotted seatrout is roughly 20% (Zhao and Burns, in preparation). While South Carolina has not had a commercial fishery since 1986, it may also be experiencing growth overfishing at a 20% SPR. Based on these data, all three states anticipate a reevaluation of their management goal for the spotted seatrout fishery (C. Wenner, SCDNR, personal communication).

CONCLUSIONS

Fish stocks are finite, and spotted seatrout are no exception. Unlimited take of spotted seatrout by all fishing sectors is no more possible than with any other exploitable fish species. The desire by the public to continue participating in the spotted seatrout fishery and the continued demand for fresh fish in markets further complicates the "balancing act" of fisheries management.

In addition to the biological needs of the fishery, managers must also deal with resource allocation and resolve nonfishery user group conflicts. As fishing grounds and coastal waters in general become increasingly crowded with boaters, personal watercraft, recreational and commercial harvesters, and other user-groups, competition for additional limited resources such as space, quality of experience, and solitude will intensify. As all the coastal states report increased recreational effort toward inshore fish species, particularly spotted seatrout, and projected changes in human demographics suggest the potential for increased fishing pressure along these coastal areas, the task of fisheries management in the future will become increasingly complicated. Such is the "balancing act" of fisheries management.

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14 Modeling the Distribution and Abundance of Spotted Seatrout: Integration of Ecology and GIS Technology to Support Management Needs

Randall D. Clark, Wendy Morrison, John D. Christensen, Mark E. Monaco, and Michael S. Coyne

CONTENTS

ABSTRACT

The spotted seatrout, *Cynoscion nebulosus*, is one of the most preferred recreational sport fish in northern Gulf of Mexico estuaries. Management of most recreational and commercial species has been based on stock surplus or recruitment models. Recent advances in the integration of ecological modeling and geographic information system (GIS) technology promote the ability to predict seatrout relative abundance and distribution based on their habitat affinities and encourage an ecosystem approach to resource management. The integration of ecological models and GIS technology provides a "seascape" view (maps) of habitat suitability in geographic space through time.

Modeling approaches vary based on data availability. A continuum of approaches has been developed to evaluate the efficacy of suitability index derivation. The continuum was based along a progression of data type, requirement, availability, reliability, and robustness. The range of approaches includes reliance on qualitative literature review and the use of quantitative analysis of fisheries' independent monitoring data. Managers can choose the approach that adequately answers their management questions, based on data availability and resource constraints. This chapter will

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discuss a suite of research approaches and modeling techniques to predict spotted seatrout distribution. In addition, it will describe the concept of model transferability, in which models developed from robust monitoring programs can be applied to systems lacking biological information.

INTRODUCTION

The spotted seatrout, *Cynoscion nebulosus,* is one of the most important recreational and commercial fishes in the northern Gulf of Mexico and off the southeast coast of the U.S. Approximately 68% of recreational anglers in the Gulf Coast region target spotted seatrout as their fish of choice (LDWF, 2000). Over the past 15 years, commercial and recreational landings throughout Gulf Coast estuaries were high, especially in Florida and Louisiana (Murphy et al., 1999). Spotted seatrout life history typically occurs within the fishes' natal estuary (Moffett, 1961; Ingle et al., 1962; Iversen and Moffett, 1962; Topp, 1963; Beaumariage, 1964; Tabb, 1966; Overstreet, 1983; Chester and Thayer, 1990; Baker and Matlock, 1993). Therefore, spotted seatrout populations are almost exclusively affected by local fishing pressures and severe environmental events such as freezes (Murphy and Taylor, 1994).

Today, managers are increasingly faced with declining stocks and increasing pressure for management policy. Traditional management approaches tend to concentrate on surplus-production, yield-per-recruit, and stock-recruitment models. However, the existing approaches and available data do not adequately support the policy-making process. A key to developing a robust approach is to address increased understanding of biological systems nested within and driven by physical processes (Rothschild and Ault, 1992). Without an understanding of fishery habitats, communities, species interactions, and anthropogenic impacts, today's management strategies are basically reactive rather than preventive (Rubec and McMichael, 1996).

Recent advances in technology, combined with increasing awareness of data needs, have promoted an ecosystem approach for fisheries management. Many scientific disciplines have been using geographic information systems (GISs) for years. Only recently has this technology become attractive to fisheries researchers and managers. A GIS is a data management and information analysis system that is able to capture, synthesize, generate, retrieve, analyze, and output spatial information (Haddad et al., 1996). A GIS is often perceived as a reflection of its products, such as computer-generated maps. A GIS is a computer system that can store and link nongraphic attributes or geographically referenced data with map features; this allows information processing, such as modeling (Antenucci et al., 1991).

The Center for Coastal Monitoring and Assessment Biogeography Program (CCMA/BP) has been developing habitat suitability models (HSMs) using GISs to provide estuarine and marine resource managers a habitat assessment capability. This approach has been designed to produce a "seascape" representation of habitat suitability in space through time. A specific type of HSM is the habitat suitability index model (HSI). HSI models are simple mathematical expressions for calculating a unitless index of habitat quality as a function of one or more environmental variables that define habitat quality for a particular species or life history stage (Brown et al., 1997). The underlying modeling approach was introduced by the U.S. Fish and Wildlife Service's (USFWS) Habitat Evaluation Procedures Program, whereby models resulted in a numerical index of habitat suitability ranging from 0.0 to 1.0. Models were based on the assumption that a positive relationship exists between the index and a habitat's carrying capacity for a given species (Schamberger, 1982).

Our techniques have taken a considerable departure from USFWS methods by incorporating a GIS spatial component, which allows the visualization of environmental or biological data in geographic time and space. In addition, the BP has developed a continuum of approaches to define species suitability index (SI) values that, when combined with GIS, constitute the HSI output (Figure 14.1). This continuum portrays the progression of approaches related to data type, requirement, availability, reliability, and robustness (Coyne and Christensen, 1997). The simplest approach, which relies on scientific literature and expert knowledge, can be used to develop broad spatial and

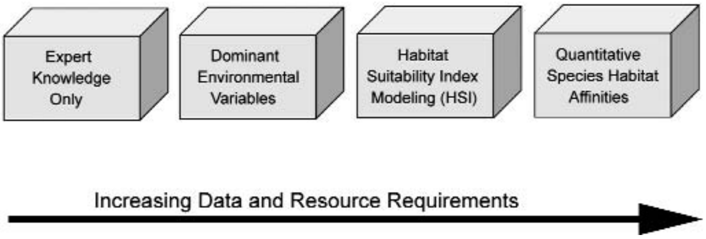

FIGURE 14.1 Continuum of approaches to evaluate the efficacy of SI derivation.

temporal species distribution maps or atlases (SAB, 1986). With sufficient habitat or environmental data, maps can be developed to portray species distributions in an environmental spatial framework. For example, the BP's estuarine living marine resources (ELMR) database contains monthly relative abundance information within a salinity zone framework for 153 species in 122 estuaries throughout the contiguous U.S. (Nelson and Monaco, 2000).

If numerous environmental frameworks can be developed for a known area, HSI modeling can provide a more spatially explicit view of habitat quality (Brown et al., 2000). Spatially and temporally robust FIM data provide the necessary information to develop sophisticated modeling methods (e.g., multivariate, logistic regression) that can be used to quantify species habitat affinities (Rubec et al., 1999; Livingston et al., 2000; Clark et al., in review).

This chapter presents the methodology and results of two different approaches that examined habitat suitability for spotted seatrout in northern Gulf of Mexico estuaries. A qualitative habitat assessment was designed to investigate the feasibility of developing meaningful habitat suitability models in Pensacola Bay, Florida, where limited scientific data that would support more rigorous statistical models are available. Suitability indices were developed based on existing scientific literature and expert knowledge. In contrast, a quantitative assessment was designed for Charlotte Harbor, Florida, that examined three modeling methodologies. In addition, the concept of model transferability across Gulf of Mexico estuaries with similar geomorphologic and hydrological characteristics was addressed.

PENSACOLA BAY

HSI models were developed in Pensacola Bay, Florida, to examine the relationships between spotted seatrout distribution and hydrological and biological parameters. The intent was to produce a simple qualitative spatial model that could provide a habitat assessment capability that could be applied to a wide range of estuarine systems. Pensacola Bay was chosen as the test area because its hydrographic conditions were considered representative for most Gulf-wide estuaries. For a more complete description of this study, see Christensen et al. (1997).

MODEL DEVELOPMENT

The first step in developing the HSI model was to conduct a comprehensive data and literature search. This was combined with an expert review process to identify the critical set of biological and environmental variables to include in the model. Salinity, water temperature, dissolved oxygen content, bathymetry, substrate type, and the presence or absence of submerged aquatic vegetation (SAV) and emergent wetland macrophytes (EV) were selected to model seatrout habitat suitability.

A species occurrence matrix (presence/absence) was developed in one-unit increments for each environmental parameter: salinity (ppt), water temperature (°C), dissolved oxygen content (mg/l), depth (m), presence of SAV (i.e., *Halodule wrightii*), and presence of EV (i.e., *Spartina alterniflora*).

These matrices enabled identification of critical values for suitability index (SI) values, which were derived under the assumption that all other parameters were held constant, at or near their optimum. Although interactions commonly occur, environmental parameters were classified independently. Under these assumptions, complete absence indicated zero suitability, and SI coefficients were set to zero.

Juvenile and adult spotted seatrout SI values were generated through an extensive literature search for documented tolerances to, and affinities along, each biological and environmental gradient (Reid, 1954; Stewart, 1961; Tabb, 1966; Copeland and Bechtel, 1974; Taniguchi, 1980; Peebles and Tolley, 1982; Lassuy, 1983; Kosteki, 1984; Johnson and Seaman, 1986; Van Hoose, 1987; Bryan et al., 1989; McMichael and Peters, 1989; Patillo et al., 1997). SI values previously developed by the U.S. Fish and Wildlife Service (USFWS, 1984) were used as baseline, where appropriate. Assigning SIs involved considerable expert knowledge and judgment; values may also require adjustments based on biogeographic differences. Due to the lack of density data for SAV and EV, SI values were assigned based on the presence or absence of these habitats. Table 14.1 displays adult and juvenile SI values for the selected environmental variables.

Because the relationship between environmental and biological gradients and species distributions is inappropriate to quantify without a robust data set, variables were not weighted in a conventional manner; they were categorized as either critical or noncritical, based on their potential effect on seatrout distribution. A critical variable was defined as one exhibiting the potential to exclude a population if physiological tolerances are exceeded, e.g., salinity, water temperature, dissolved oxygen, and bathymetry. Critical variables were scaled from 0 to 1.0, and for any variable that scored a 0, the model would predict complete exclusion. Noncritical variables were defined as those that have an effect on species distributions; however, they are not independently limiting. Substrate type and the presence or absence of SAV (Submerged Aquatic Vegetation) and EV (Emergent Vegetation) were considered noncritical for this study. These variables were scaled from 0.2 to 1.0 and, by scaling the SIs in this manner, we were able to weight the variables without using statistical methods to quantify the relationships.

Once SI values were developed, environmental GIS data grids were constructed to represent a spatial view of the environmental variables. Continuous data that vary along a gradient, such as bathymetry, dissolved oxygen, salinity, and temperature, were acquired from the Florida Department of Natural Resources and the Environmental Protection Agency's EMAP Program (FLDNR, 1991; USEPA, 1996). These data were then independently mapped by georeferenced (latitude and longitude) sampling stations. The point data, measured from irregularly spaced locations, were converted into continuous, contoured surfaces using an inverse distance weighting (IDW) method and then rasterized into a grid format (ESRI, 1996). A conceptual view of GIS grid development is shown in Figure 14.2.

Each grid was created with the same coordinate system, and cells among grids were aligned in geographic space to facilitate intergrid processing. All grids had the same cell size of 1000 m^2. At this resolution, each environmental grid map in Pensacola Bay consisted of approximately 37,000 cells. Each grid was then categorized: salinity (Figure 14.3a) was mapped in 5-ppt increments (Orlando et al., 1993), water temperature (Figure 14.3b) in 2°C isotherms (SAB, 1986), and dissolved oxygen in 1-mg/l increments (SEA, unpublished data). Substrate was categorized using a modified Shepard's classification scheme (Shepard, 1954) and classified as either sand, silt, or clay. The distribution of SAV and EV was documented by aerial photography and digitized by the USFWS (USFWS, 1985). SAV and EV grids were classified as either present or absent.

Models were run during four time periods to address seasonal fluctuations in seatrout distribution. Representative periods for the Pensacola Bay HSI model were determined by characterizing salinity conditions in the estuary. Seasonal depth-averaged salinity was modeled from a subset of field salinity data collected between 1970 and 1994 (Orlando et al., 1993). Consequently, salinity seasons consisted of four 3-month periods: high salinity (September to November), low salinity (February to April), increasing salinity (May to August), and decreasing salinity (December to January). These periods represent the typical salinity conditions experienced under average seasonal

TABLE 14.1
Suitability Index (SI) Values for Spotted Seatrout in Pensacola Bay, FL

HABITAT VARIABLE	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
SALINITY (PPT)																																																			
adult	▦	▦	▦	▦	▦	▦	▤	▤	▤	▤	▓	▓	▓	▓	▓	▓	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓	▓
juvenile	▦	▦	▦	░	░	░	░	░	■	■	■	■	■	■	■	■	■	■	■	■	■	▓	▓	▓	▓	▓	░	░	░	░	░	░	░	░	░	░	▤	▤	▤	▤	▤	▤	▤	▤	▤	▤	▤	▤	▤	▤	▤
TEMPERATURE (C)																																																			
adult	□	□	□	□	□	□	▦	▦	▦	▦	▦	▦	▦	▦	▦	░	░	░	░	░	▓	▓	▓	▓	■	■	■	■	■	■	■	▓	▓	▓	▓	░	░	░	░	▤	▤	▤	▦	▦	▦	□	□	□	□	□	□
juvenile	□	□	□	□	□	□	▦	▦	▦	▤	▤	▤	▤	░	░	░	░	░	░	░	■	■	■	■	■	■	■	■	■	■	■	▓	▓	▓	▓	░	░	░	░	▤	▤	▤	▦	▦	▦	□	□	□	□	□	□
D.O. (mg/l)																																																			
adult	□	□	□	░	░	░	■	■	■	■	■	■	■	■	■																																				
juvenile	□	□	□	░	░	░	■	■	■	■	■	■	■	■	■																																				
DEPTH (m)																																																			
adult	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
juvenile	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x

SAV (pres/abs)	Presence	Absence
adult	■	▓
juvenile	■	░

Wetlands (pres/abs)	Presence	Absence
adult	■	■
juvenile	■	░

Substrate	Clay	Silt/Mud	Sand
adult	■	■	■
juvenile	■	■	■

■	SI = 1.0	▤	SI = 0.4
▓	SI = 0.8	▦	SI = 0.2
░	SI = 0.6	□	SI = 0.0

x SI = 1.0, parameter not pertinent

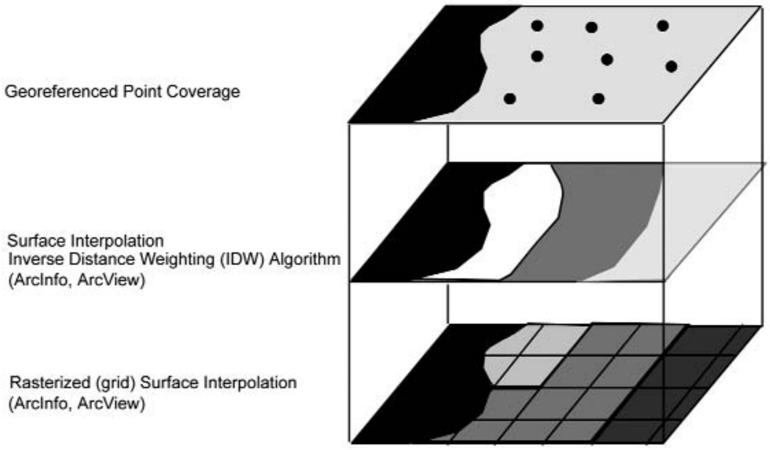

FIGURE 14.2 Conceptual model of grid map development.

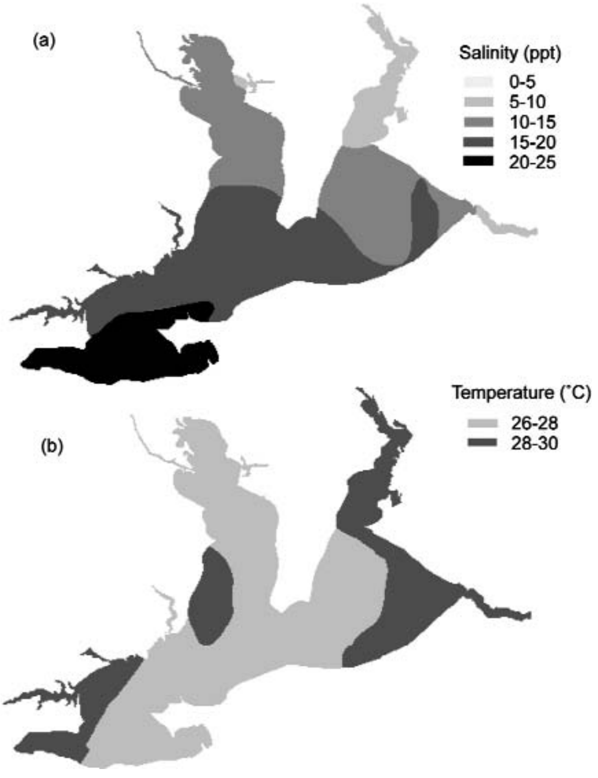

FIGURE 14.3 Salinity and temperature distribution during the increasing salinity time period (May to August) in Pensacola Bay, FL.

freshwater inflow conditions. Five-ppt isohalines were developed to represent the typical range of salinity conditions experienced under average seasonal freshwater inflow. The isohalines shift seasonally due to environmental factors such as freshwater inflow, tides, evaporation, and wind (Orlando et al., 1993). Water temperature was contoured for the same months as the salinity seasons to ensure temporal uniformity in the models.

Arc/Info 7.03 GRID© module was used to conduct the HSI modeling. GRID supports cartographic spatial analysis using a high-level computation language. Thus, processing between grids utilizes a simple and efficient map–algebra calculation of numeric cell values. HSI values were calculated using a geometric mean for each cell across all grids:

$$\mathrm{HSI} = [\overset{n}{\underset{i=1}{\pi}} (v_i)]\text{^}(1/n); \tag{14.1}$$

where v_i = environmental variable and n = number of variables in the model.

Optimum HSI values (1.0) are achieved if all environmental variable SIs within a cell are at optimum. Likewise, if any one variable SI is unsuitable (0.0) within a cell, the HSI model will indicate unsuitable habitat regardless of the SI value for all other variables. An example of the integration of SI values and grid maps to produce HSI models is shown in Figure 14.4. HSI values were categorized to simplify map interpretation: unsuitable = 0.00, low = 0.01 to 0.33, moderate = 0.34 to 0.66, high = 0.67 to 0.99, and optimum = 1.0.

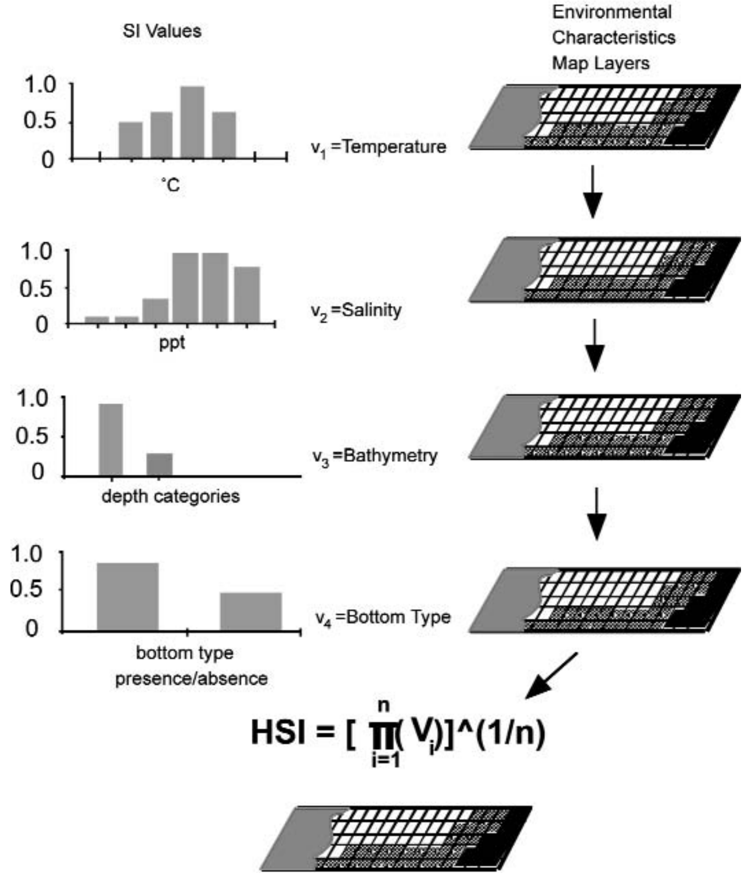

FIGURE 14.4 Conceptual view of HSI map development.

HSI MODEL RESULTS

Juvenile spotted seatrout HSI models exhibited great spatial and temporal sensitivity to fluctuating environmental parameters. Highest suitability values were observed in EV and SAV habitats during the increasing salinity season (May to August), when water temperatures were at an optimum level (Color Figure 14.5).* We assumed that growth of spotted seatrout is temperature dependent (Johnson and Seaman, 1986), with optimum temperatures for somatic growth and condition (K) consistently reported between 25 to 30°C (Tabb, 1958; Stewart, 1961; Taniguchi, 1980; Patillo et al., 1997). Juvenile spotted seatrout are abundant in vegetated habitats to avoid predation pressures (Johnson and Seaman, 1986; Chester and Thayer, 1990) and feed upon the copepods, mysid and caridean shrimp, and post-larval penaied shrimp typically abundant in these habitats (Moody, 1950; Darnell, 1958; Adams et al., 1973; Overstreet and Heard, 1982; Hettler, 1989; Minello, 1999). Suitability was moderate in the nonvegetated habitats throughout the rest of the bay.

Low suitability was observed throughout the bay during the decreasing-salinity time period (December to January), when temperatures declined to 10 to 14°C. This does not indicate that juvenile trout are leaving the estuary; rather, it is a comparison of suitabilities relative to the remaining salinity-defined seasons. Spotted seatrout have been observed to move to warmer waters of deep channels and depressions to avoid thermal stress in the winter (Moody, 1950; Tabb, 1966). Moderate HSI values were observed bay-wide during the low (February to April) and high (September to November) salinity time periods, as temperatures declined away from or increased toward the optimum.

Similar patterns were observed in adult seatrout HSI distribution. Optimum and high suitability was predicted for shallow, vegetated habitats during the increasing and high salinity time periods. Optimum and high-suitability zones were more extensive for adults compared to juveniles. Approximately 90% of the bay was considered high or optimum habitat for adult seatrout during these time periods (Color Figure 14.6).*

Cooler temperatures during the decreasing (December to January) and low (February to April) salinity time periods resulted in medium or low suitability throughout the unvegetated portions of

FIGURE 14.5 Juvenile spotted seatrout HSI map calculated during the increasing salinity time period (May to August).

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* Color insert figures follow page 242.

FIGURE 14.6 Adult spotted seatrout HSI map calculated during the increasing salinity time period (May to August).

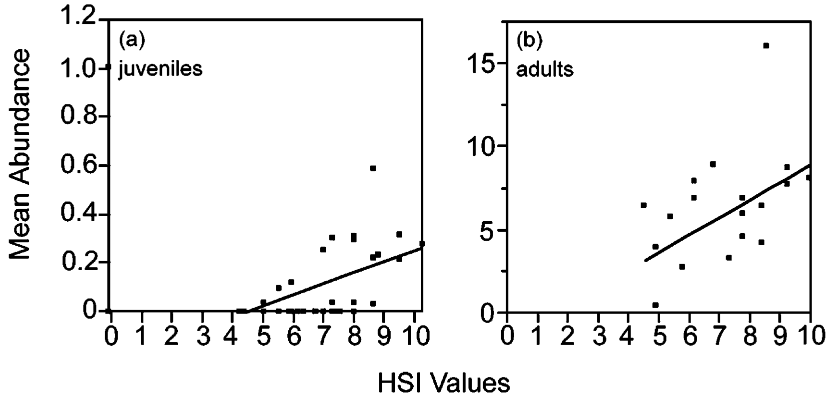
the bay. Vegetated habitats in the lower portion of the bay were ranked as highly suitable during the low salinity time period and medium during the decreasing salinity time period.

MODEL VALIDATION

Due to the lack of consistent and robust FIM data for spotted seatrout in Pensacola Bay, Christensen et al. (1997) conducted a qualitative assessment to validate the spotted seatrout models. Local fisheries biologists and commercial fishermen compared the seatrout HSI results to their collective expertise and concluded that the HSI maps were a reasonable depiction of the potential distribution of spotted seatrout in Pensacola Bay.

In order to test model performance and transferability, SI values developed in Pensacola Bay were applied to 10 years (1987 to 1996) of FIM data collected by the Texas Parks and Wildlife Department (TPWD) in Galveston Bay, Texas. Juvenile seatrout data from TPWD bag seine samples (N = 1808) were used to test juvenile HSI model performance, while gill net samples from 1994 to 1996 (N = 268) were used to assess the adult HSI model. The TPWD data did not include the presence or absence of EV or SAV in their samples; therefore, only SI values for dissolved oxygen content, salinity, and temperature were applied. Overall, 94% of the bag seine samples were classified as either optimum or high suitability and these constituted almost 98% of seatrout captured by this gear type. Moderate suitability was classified for 108 samples, and no samples were ranked as low suitability. Eight samples were classified as unsuitable.

Mean bag seine CPUEs were compared to mean HSI values to examine the efficacy of the model predictions. Linear regression and analysis of variance (ANOVA) results revealed a significant positive relationship between mean HSI value and mean bag seine CPUE (Figure 14.7a). Although vegetated habitat SI values were not applicable to the TPWD FIM data, the model performed adequately using the critical environmental variables in determining seatrout distribution in Galveston Bay. Minello (1999) determined that juvenile seatrout densities were greater in shallow, marsh-edge, and seagrass habitats in Texas and Louisiana estuaries. Numerous authors



Mean Abundance= -0.2047+0.0483 HSI	
Rsquare	0.27
Observations	1809
Prob>F	0.0011

Mean Abundance= -1.5755+1.0466 HSI	
Rsquare	0.35
Observations	268
Prob>F	0.0085

FIGURE 14.7 Performance of SI values derived for juvenile (a) and adult (b) spotted seatrout for Pensacola Bay and applied to Texas Parks and Wildlife fishery-independent monitoring data from Galveston Bay.

(Moody, 1950; Reid, 1954; Tabb, 1958; McMichael and Peters, 1989; Helser et al., 1993) also support these findings, thus emphasizing the importance of vegetated habitats as nursery grounds for juvenile spotted seatrout.

Adult SI values (dissolved oxygen, salinity, temperature) from Pensacola Bay were applied to the Galveston Bay gill net CPUE data. HSI values for these samples consisted of 20% moderate, 49% high, and 31% optimum. No samples were classified as either low or unsuitable, which may be a reflection of temporal bias. TPWD gill net monitoring occurred only during April to November; thus, lower HSI values might be expected in the cooler months as estimated from the literature (Table 14.1). Regression of mean gill net CPUEs and mean HSI values (Figure 14.7b) revealed similar results to those observed with juveniles — mean CPUE values were positively correlated with mean HSI values.

CHARLOTTE HARBOR AND TAMPA BAY

Fisheries scientists from Florida Department of Environmental Protection (FDEP) and CCMA/BP collaborated to develop quantitative HSI models for spotted seatrout in Charlotte Harbor and Tampa Bay, Florida. The objectives of this research were to explore and implement various HSI modeling techniques and to assess the transferability of models developed in one estuary and applied to adjacent estuarine systems. For a more detailed description, see Rubec et al. (1999).

In this study, Charlotte Harbor and Tampa Bay FIM data collected from 1989 to 1997 were used to develop spotted seatrout HSI models. Spotted seatrout CPUE data were collected by numerous gear types with various mesh sizes. Therefore, CPUEs were standardized across all gear types that exhibited high catch rates of juvenile seatrout ranging from 10 to 119 in mm standard length.

Coyne and Christensen (1997) described quantitative approaches to derive suitability functions from species abundance and habitat data. Three methodologies were used to develop seatrout suitability indices in Charlotte Harbor and Tampa Bay:

Cumulative frequency method — This method was used to determine biologically relevant environmental ranges for spotted seatrout HSI modeling. Catch data from the study areas were plotted in a frequency-of-occurrence histogram for each environmental variable and a frequency score was calculated for each variable increment (SAS, 1995). Each frequency scores was then plotted against its respective environmental variable (Figure 14.8a). Portions of the plot with the greatest slope represent greater frequency of occurrence, while slopes approaching zero represent lower frequency of occurrence. Straight lines were drawn through portions of the curve with linear relationships (Figure 14.8b) to identify biologically relevant ranges. The slope of each line was determined using linear regression, and suitability values were calculated by dividing each slope by the maximum slope observed and then scaled from 0 to 10 for each environmental data set.

Range-mean method — This method was similar to the cumulative frequency method; however, mean CPUE values were used to generate SI values for each biologically relevant range of the environmental variables. SIs were calculated by dividing the mean CPUE values by the maximum observed mean CPUE and scaling from 0 to 10 (Rubec et al., 1999).

Smooth-mean method — This method was a revision of the range-mean method in which mean CPUE values were calculated and plotted along an environmental variable gradient. A polynomial regression curve was then fit to the mean CPUE values using JMP software (SAS, 1995). Predicted CPUE values along the curve were divided by the maximum observed CPUE and scaled from 0 to 10 to generate SI values (Rubec et al., 1999).

These methods were used to generate SI values for bottom salinity, bottom temperature, and depth. Bottom type was a categorical variable (presence/absence), and SI values were determined by using the range-mean method.

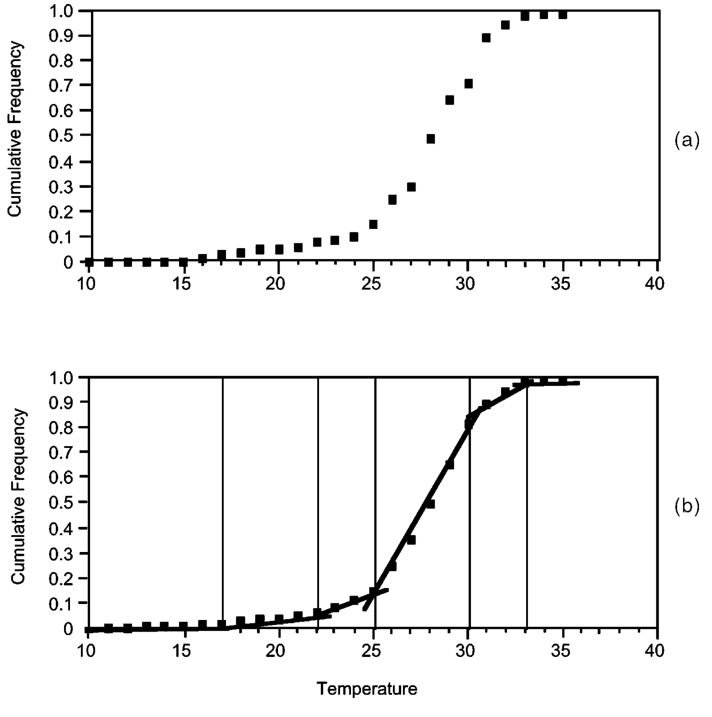


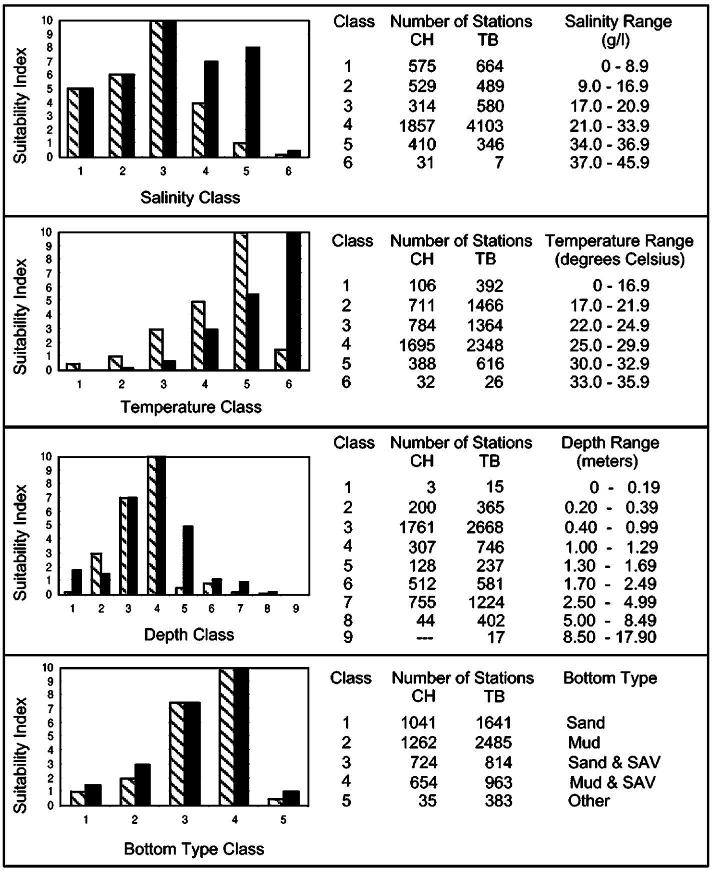
FIGURE 14.8 (a) Plot of cumulative frequency scores for spotted seatrout and salinity. (b) Linear relationships within the cumulative frequency score curve. Intersect points are used to delimit biologically relevant ranges.

ENVIRONMENTAL VARIABLES AND GIS LAYERS

Comparisons of the three suitability methods (cumulative frequency, range-mean, and smooth-mean) were made by plotting the suitability values across each variable gradient. The two CPUE methods yielded similar SI values for all environmental variables (salinity, temperature, depth), whereas SI values from the cumulative frequency method exhibited prominent differences. Consequently, habitat suitability maps were developed using the mean CPUE methods. Figure 14.9 displays the SI values for the range-mean method for Tampa Bay and Charlotte Harbor. Table 14.2 provides the smooth-mean polynomial regression SI equations for salinity, temperature, and depth for Tampa Bay and Charlotte Harbor.

Environmental data (salinity, water temperature, depth, and bottom type) taken concurrently with biological samples were used exclusively to develop suitability indices. These data were also used to create the habitat grids for use in the GIS modeling process.

Habitat-suitability maps were created for Charlotte Harbor during the fall season using salinity, temperature, depth, and bottom-type SI functions. Four maps were derived using the two mean CPUE methods, two using Charlotte Harbor SI functions and two using SI functions transferred from Tampa Bay. Habitat-suitability maps were computed in ArcView spatial analyst using the



Class	Number of Stations CH	Number of Stations TB	Salinity Range (g/l)
1	575	664	0 - 8.9
2	529	489	9.0 - 16.9
3	314	580	17.0 - 20.9
4	1857	4103	21.0 - 33.9
5	410	346	34.0 - 36.9
6	31	7	37.0 - 45.9

Class	Number of Stations CH	Number of Stations TB	Temperature Range (degrees Celsius)
1	106	392	0 - 16.9
2	711	1466	17.0 - 21.9
3	784	1364	22.0 - 24.9
4	1695	2348	25.0 - 29.9
5	388	616	30.0 - 32.9
6	32	26	33.0 - 35.9

Class	Number of Stations CH	Number of Stations TB	Depth Range (meters)
1	3	15	0 - 0.19
2	200	365	0.20 - 0.39
3	1761	2668	0.40 - 0.99
4	307	746	1.00 - 1.29
5	128	237	1.30 - 1.69
6	512	581	1.70 - 2.49
7	755	1224	2.50 - 4.99
8	44	402	5.00 - 8.49
9	---	17	8.50 - 17.90

Class	Number of Stations CH	Number of Stations TB	Bottom Type
1	1041	1641	Sand
2	1262	2485	Mud
3	724	814	Sand & SAV
4	654	963	Mud & SAV
5	35	383	Other

FIGURE 14.9 SI functions across biologically relevant gradients of salinity, temperature, depth, and bottom type for Charlotte Harbor and Tampa Bay using the range-mean method. (From Rubec et al., *Am. Fish. Soc. Symp.*, 22:108–133, 1999.)

TABLE 14.2
Polynomial Regression Suitability Index (SI) Equations for Charlotte Harbor and Tampa Bay Derived from Mean CPUEs across Gradients of Temperature, Salinity, and Depth

Location	Regression Equation	Coefficient
	Temperature ($i = 1$)	
CH	$S_1 = 0.0317758 - 0.00557T + 0.000298T^2 - 0.00000447T^3$	$r^2 = 0.582$
TB	$S_1 = 0.3478437 - 0.048949T + 0.0021345T^2 -0.000028T^3$	$r^2 = 0.602$
	Salinity ($i = 2$)	
CH	$S_2 = 0.0040184 - 0.000393G + 0.0001427G^2 + 0.00000654G^3 + 0.000000007896G^4$	$r^2 = 0.705$
TB	$S_2 = 0.0027424 + 0.0007294G + 0.000018G^2 - 0.000000903G^3$	$r^2 = 0.600$
	Depth ($i = 3$)	
CH	$S_3 = 0.00223614 + 0.0212379D - 0.019623D^2 + 0.0061119D^3 - 0.000792D^4 + 0.0000363D^5$	$r^2 = 0.604$
TB	$S_3 = 0.0041553 + 0.036787D - 0.035219D^2 + 0.0124316D^3 - 0.002082D^4 + 0.000167D^5 - 0.000005D^6$	$r^2 = 0.659$

Notes: CH = Charlotte Harbor, TB = Tampa Bay, T = temperature, G = salinity, D = depth. The coefficient of determination (r^2) is based on the fitted mean CPUEs. (From Rubec et al., *Am. Fish. Soc. Symp.*, 22:108–133, 1999.)

geometric-mean formula (Equation 14.1) for each cell across the environmental grids. Resultant grid-cell HSI values were categorized into four classes: low (0.0 to 1.9), moderate (2.0 to 3.9), high (4.0 to 5.9), and optimum (6.0 to 10.0). Model performance was tested by superimposing the point data from the FIM samples over the predicted range-mean and smooth-mean HSI maps. The points were then assigned an HSI value according to the zone in which they resided. Comparisons of mean CPUE and mean HSI value were then used to test the performance of the suitability functions.

HABITAT SUITABILITY RESULTS

The range-mean and smooth-mean models using Charlotte Harbor SI functions yielded similar patterns for the continuous habitat variables (depth, salinity, temperature). Highest juvenile spotted seatrout suitability indices occurred at mid-range salinities (15 to 25 ppt), high temperatures (> 26°C), and shallow depths (< 1.5 m). Optimum suitability was observed in the SAV bottom-type category (Color Figure 14.10).* Similar results occurred when the models developed from Tampa Bay FIM data were applied to the Charlotte Harbor environmental grids. SI functions were consistent between the two methods but differed in the areal extent of HSI zones.

Model performance of the Charlotte Harbor–derived SI functions and transferred SI functions from Tampa Bay revealed that the smooth-mean model performed as expected: increasing mean CPUE with increasing mean HSI value (Figure 14.11). The range-mean method did not exhibit a consistent positive correlation for either set of SI models.

Chi-square tests were used to compare the resultant HSI maps developed with SI functions from both estuaries. The range-mean model using Charlotte Harbor SI values estimated significantly different ($p < 0.001$) seatrout HSI zones than the model transferred from Tampa Bay. In contrast, estimated HSI zone areas developed from the smooth-mean models from both estuaries were not significantly different ($p > 0.05$).

In summary, the two HSI approaches based on different levels of available data agree with published literature describing juvenile spotted seatrout distribution (McMichael and Peters, 1989; Killam et al., 1992; Christensen et al., 1997; Patillo et al., 1997). Optimum- and high-suitability areas for juvenile and adult spotted seatrout were observed in shallow waters containing SAV. Predicted areas of high suitability for adult spotted seatrout extended into deeper waters compared

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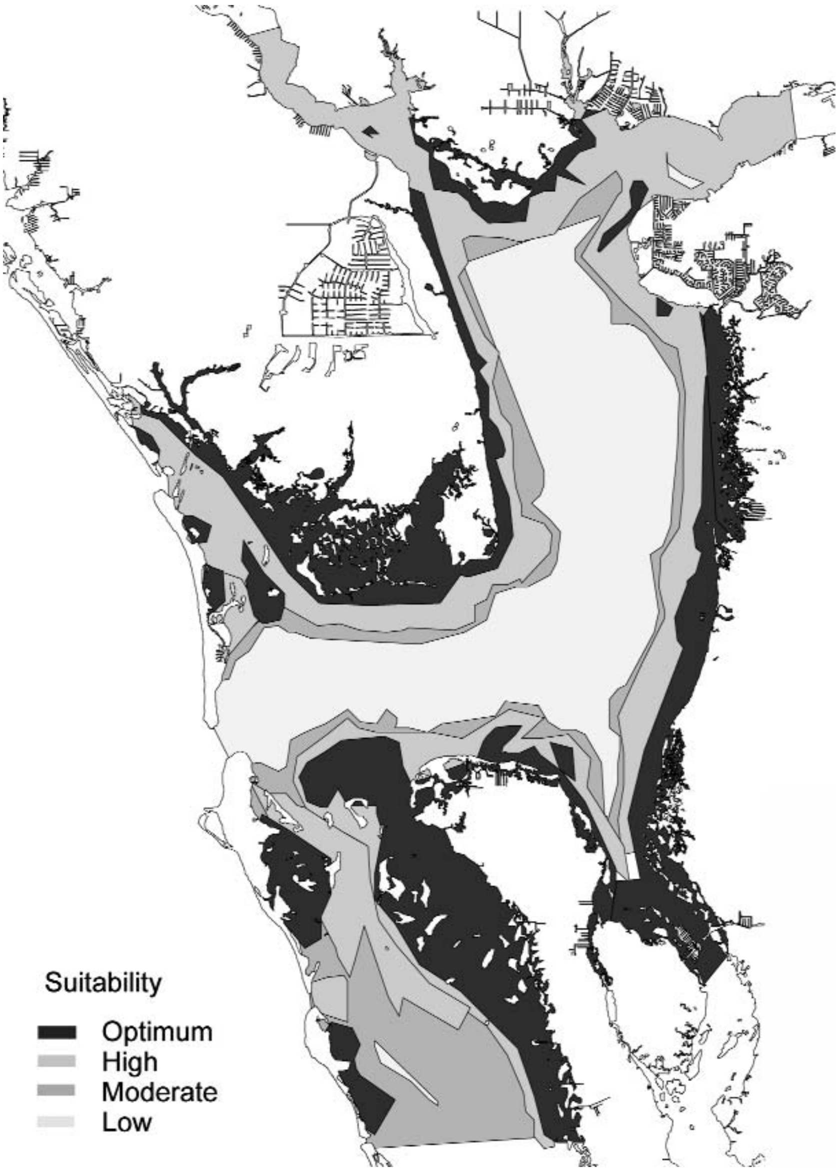

FIGURE 14.10 Juvenile spotted seatrout smooth-range HSI map using Charlotte Harbor FIM data. (From Rubec et al., *Am. Fish. Soc. Symp.*, 22:108–133, 1999.)

to those for juveniles. This result also agrees with the literature, as adult spotted seatrout are mid-water to surface piscivores and not as dependent on the shallow, vegetated habitats that juveniles utilize as nursery habitats (Darnell, 1958; Johnson and Seaman, 1986).

Depth was not considered in the modeling approach for adult and juvenile spotted seatrout in Pensacola Bay. This may be reasonable when considering adults, which are more solitary and mobile in nature; however, numerous authors have cited that juvenile spotted seatrout and other estuarine-dependent species concentrate in shallow, vegetated nursery areas that foster survival or growth (Lassuy, 1983; Boesch and Turner, 1984; Chester and Thayer, 1990; Minello, 1999). Rubec et al. (1999) calculated high juvenile seatrout SI values in shallow waters (0.4 to 1.6 m)

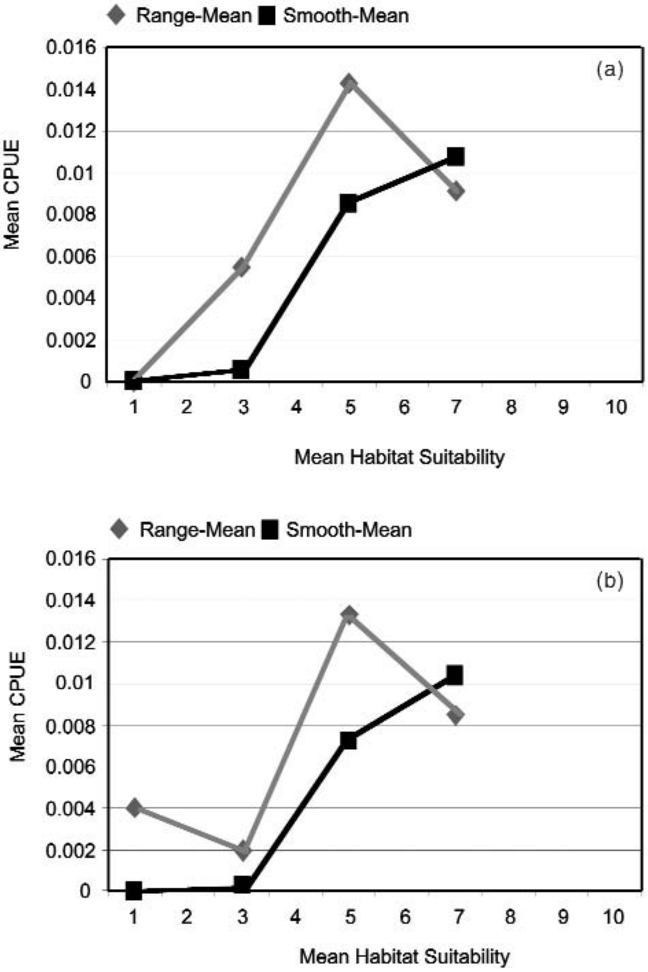

FIGURE 14.11 Comparison of mean CPUE values and mean HSI values by suitability zones using range-mean and smooth-mean SI functions from Charlotte Harbor (a) and Tampa Bay (b). (From Rubec et al., *Am. Fish. Soc. Symp.*, 22:108–133, 1999.)

based on Charlotte Harbor and Tampa Bay FIM data. Marsh and submerged aquatic vegetation are typically located in shallow depths throughout Gulf of Mexico estuaries and may act as a surrogate for depth in the models.

RECOMMENDATIONS FOR MANAGERS

The HSI modeling approach has been designed for simplicity and can be modified and applied with minimal resources (Rubec et al., 1999). SI continuum approaches can provide fisheries managers an assessment tool that focuses on habitat and ecosystem dynamics. Managers must determine what level of effort and resources is necessary to answer their management questions. Thus, a combination of methods along the continuum may be required, because most FIM datasets do not cover complete ranges of available habitats and exhibit disproportionate seasonal and spatial sampling effort.

The transferability of models from well-studied estuaries to those with little or no FIM data is of increasing concern. Fisheries monitoring programs are demanding on financial and personnel resources, and this approach will benefit those states with numerous estuarine systems, such as Florida and Texas. The results from the two HSI methods discussed in this chapter are promising, but more research is needed to understand biological and environmental limitations fully.

HSI maps can be used in a broad range of assessments requiring information on habitat distribution and quality. Individual species maps can be used to identify areas of varying habitat quality, as discussed in this chapter. This approach can identify habitats or species that may be sensitive or vulnerable to environmental or anthropogenic impacts. The models discussed in this chapter predicted optimum habitats to be those containing shallow waters and vegetation. These habitats constitute a very small proportion of the total available habitat in each system and should be considered important habitats for conservation.

Scenario analyses compare habitat suitability changes in response to changes in environmental conditions. For example, Christensen et al. (1997) examined potential changes of habitat suitability in Pensacola Bay by artificially altering freshwater-inflow patterns. Little change was observed for spotted seatrout, but significant changes in habitat suitability were observed for eastern oyster *(Crassostrea virginica*) and white shrimp (*Farfantepenaeus setiferus*). Livingston et al. (2000) estimated eastern oyster mortality in Appalachicola Bay, Florida, in response to changes in freshwater inflow. Oyster biological data were linked to a three-dimensional hydrodynamic circulation model in a GIS to depict the spatial range of oyster mortality in response to varying rates of freshwater inflow.

As GIS technology and modeling techniques advance, many more opportunities will evolve to enhance fisheries management. The current methods appear to be adequate to predict spatial distributions but cannot predict actual abundance (Rubec et al., 1999). Clark et al. (in review) have developed a multivariate habitat model that examines the relationship between brown shrimp (*Farfantepenaeus aztecus*) abundance and habitat. Results indicated that small brown shrimp (10 to 100 mm) were most abundant in marsh and submerged aquatic vegetation within mid- to high salinity (< 15 ppt) areas of Galveston Bay. These results could be incorporated into the spotted seatrout HSI models to investigate species interaction. Post-larval and juvenile brown shrimp are important dietary components for juvenile spotted seatrout. An approach for assessing brown shrimp–spotted seatrout interaction could be attempted by using the HSI models for spotted seatrout and adding a measure of prey availability (e.g., brown shrimp density estimates from Clark et al., in review). Deeper understanding of the abundance–habitat relation will allow more sophisticated models to be developed and further support fisheries management.

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15 A Spatial Ecosystem Model to Assess Spotted Seatrout Population Risks from Exploitation and Environmental Changes

Jerald S. Ault, Jiangang Luo, and John D. Wang

CONTENTS

ABSTRACT

Explosive regional human population growth, overfishing, and habitat degradation have stimulated system restoration projects that are redefining the quality and functioning of the south Florida coastal ecosystem. Because spotted seatrout are sensitive ecosystem indicators, we developed a spatial biophysical predator–prey model to assess seatrout population risks from exploitation and environmental changes. The model couples the production dynamics of a higher trophic level age-structured predator population (e.g., seatrout, *Cynoscion nebulosus*) to a key prey (e.g., pink shrimp, *Farfantepeneaus duorarum*) through a dynamic array of biophysical processes. This is done

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by mathematically linking bioenergetic principles of fish physiology, population ecology, fish–habitat relationships, and community trophodynamics to a regional hydrodynamic circulation and mass transport model.

We focused an important model application on the issue of expected ecosystem transitions from changes in freshwater discharges to "tide" under the comprehensive Everglades restoration plan. Specifically, we evaluated impacts to seatrout population productivity, fishery yields, and ecosystem performance resulting from two alternative water management scenarios associated with Everglades restoration; these scenarios are expected to affect the quantity, timing, and location of freshwater delivered to Biscayne Bay, Florida.

INTRODUCTION

The coastal marine environment of south Florida and the Florida Keys ecosystem currently supports a multibillion dollar annual fishing and tourism economy (Johns et al., 2001). However, rapidly growing regional human populations, serial overfishing, and habitat degradation, coupled with changes in regional water quality from a comprehensive Everglades restoration project, make the south Florida coastal region an "ecosystem at risk" — one of the nation's most significant, yet most stressed, marine resource regions under management of NOAA, the State of Florida, and the National Park Service (Bohnsack et al., 1994; Schmidt et al., 1999; Ault et al., 1997, 1998, 2001a, b; Harper et al., 2001). The networks of coastal bays and lagoons function as prime nursery and fishery production areas that provide critical ecosystem linkages between modulation of terrestrial freshwater outputs and the offshore Florida Keys coral reef system. The Comprehensive Everglades Restoration Plan (CERP) projects a 30-year implementation program to restore the terrestrial Everglades ecosystem while meeting south Florida coastal estuaries' requirements and remaining water needs for the next 50 years. This has resulted in hydrologic projects of historic proportions (www.evergladesplan.org). An important aspect of restoration is to provide guidance as to what ecosystem transitions can be expected.

Prior to the 20th century, the approximately 100,000 people who lived in south Florida were restricted to building on high ground near the coastal and central ridges, as it was simply too wet much of the time to live in the interior. Devastating hurricanes in the late 1920s and again in the 1940s resulted in cries for help from citizens and elected officials. The Central and South Florida Project (CS&F) authorized by Congress in 1948 instructed the U.S. Army Corps of Engineers (USACE) and the South Florida Water Management District (SFWMD) to begin construction of what was to become the most elaborate and effective water management system in the world.

Canals put in place before 1940 to provide drainage were subsequently added to and enhanced in order to serve the additional functions of flood and salinity intrusion control. Because of the naturally flat topography of adjacent wetlands and the shallow, free-surface aquifer, the management of the hydrologic system was constrained to a very narrow water table range and a small soil water storage capacity. These constraints necessitated alterations in the quantity and temporal distribution of freshwater runoff to the bays, which became more pulsed with larger peak discharges in the wet season, with substantial water quality impacts. During the dry season, less freshwater reached the bays because of the reduced terrestrial storage and lowered groundwater levels.

This network of canals has negatively affected not only the Everglades but also the downstream south Florida marine ecosystem by greatly altering the distribution of freshwater within the watershed, as well as the quantity, quality, and timing of freshwater discharges to coastal bay environments like Biscayne Bay, Florida Bay, Whitewater Bay, and Charlotte Harbor along the terrestrial–marine boundary of the south Florida ecosystem (see Davis and Ogden, 1994; Harwell et al., 1996; Wang et al., 2002).

The Biscayne Bay lagoonal system on the southeastern coast of Florida is connected to the Atlantic Ocean to the east and bordered by mangrove shorelines and the city of Miami to the west (Figure 15.1). Biscayne Bay is a unique tropical marine environment of national significance, renowned for its productive ecosystem, diverse and abundant natural resources, fantastic

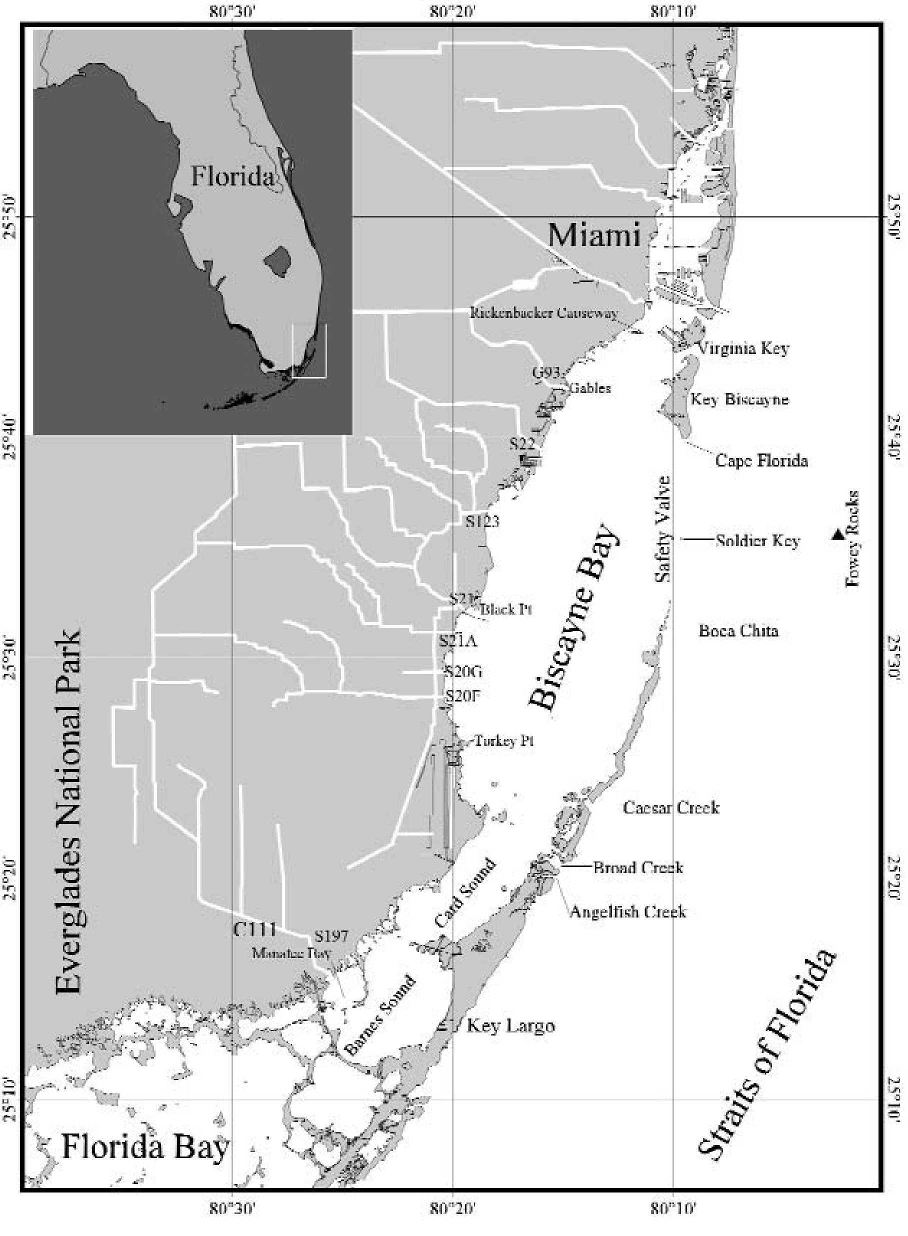

FIGURE 15.1 South Florida (inset) and Biscayne Bay lagoonal system. Canal structures are indicated by the white lines on land, and freshwater delivery points at the bay's western edge are indicated by the structure names.

sportfishing, and spectacular scenic beauty. As a downstream receptor of larvae and juveniles from offshore spawning adults, this bay plays a critical role in the greater Florida Keys coral reef ecosystem and provides critical functional support for dynamic coastal marine fisheries like seatrout, bonefish, tarpon, and permit. Biscayne Bay is a source point for adult productivity of groupers, snappers, pink shrimp, and lobsters that mature as juveniles in the bay and then migrate back to the coral reef tract (Bohnsack and Ault, 1996; Ault and Luo, 1998; Ault et al., 1999b; Lindeman et al., 1999, 2000).

At present, salinity variations in Biscayne Bay result primarily from canal discharges through gated control structures managed to meet the municipal water supply, agricultural, and flood control objectives (Wang et al., 2002). Additional, smaller freshwater exchanges in the bay are driven by overland runoff, rainfall, and evaporation. Timing (seasonality), intensity, and duration of precipitation events are critical to dynamics of the regional environment. Moreover, a population of more than 6 million people lives on a narrow ridge along the coast, so the hydrological cycle has tremendous societal implications, affecting issues of urban and agricultural water supply, flood protection, support for fisheries, tourism, as well as recreational and energy usages and patterns of urban development. Restoration of freshwater flows to Biscayne Bay has become a regional water supply allocation issue closely linked to similar issues facing the major coastal environments of the modern-day modified drainage basin, which includes metropolitan Miami and Everglades National Park (ENP).

Salinity variations and the hydrodynamic regime, in part established by the freshwater runoff, have been important controls on the type and health of biota and flora found in the bay (see Berkeley and Campos, 1984; Serafy et al., 1997; Ault et al., 1999a, b). Substantial changes in the volume and timing of freshwater outflows into coastal bays will undoubtedly affect many key recreational and commercial inshore and coral reef fish populations directly and indirectly through environmental changes and food-web interactions. In most cases, however, the relative importance of different bay habitats in south Florida has rarely been quantified (Rubec et al., 1999, 2001). This is of direct public concern since fishes are obvious measures of management performance and ecological success, and fisheries are the ultimate downstream integrators of environmental changes and human uses.

Seatrout is one of the populations most sensitive to environmental changes (Ault and Harwell, 1995; Harwell et al., 1995) and is of great concern because individuals spend their entire lifecycle within a particular bay. Thus, seatrout populations are an essential and conspicuous component of the south Florida coastal marine ecosystem, supporting important commercial, recreational, and aesthetic uses (Murphy and Taylor, 1994). Quantitative understanding of the role of cross-shelf ontogeny, essential habitats, and animal survivorship in the community dynamics of the regional ecosystem is critical to management of the sustainability and conservation of these key natural resources (Bohnsack and Ault, 1996; Lindeman et al., 1999, 2000).

Traditionally, water quality, critical habitats, and fish stocks have each been treated as separate management issues. However, pervasive resource declines and widespread habitat destruction have emphasized the importance of taking a more holistic view to resource management. Clearly, innovative predictive tools are needed to help evaluate mechanisms for effective spatial fishery management. Everglades restoration, severe overfishing, habitat health, and water quality are driving factors linked to water movement and exchange. Success of Everglades restoration and other targeted fishery management strategies will be reflected in changes in the size and abundance structure of fisheries and species composition of the marine resource communities. To better understand the effects of human controls and interventions, we extend here the spatial dynamic community model of Ault et al. (1999b) to the development of a generalized, age-structured predator–prey model for seatrout–shrimp interactions applicable on relatively wide spatial scales across the southeastern U.S. The model is based on fundamental principles of bioenergetics, population ecology, and community trophodynamics linked to a well-calibrated Biscayne Bay hydrodynamic model (Wang, 1978; Wang et al., 1988, 2002).

The coupled spatial biophysical model is used to examine system sensitivity to changes in bay salinity stemming from management alternatives of regional surface and groundwater redistribution. We also use the model to understand how physics and biology contribute to changes in population growth, production, and dynamics by focusing our analysis on a key trophodynamic linkage between an important predator (spotted seatrout, *Cynoscion nebulosus*) and their prey (pink shrimp, *Farfantepenaeus duorarum*) in the tropical waters of Biscayne Bay, Florida. Finally, we test some relatively straightforward ecological goals for Biscayne Bay by using the biophysical model to evaluate risks to a seatrout population and fishery from proposed regional water management strategy.

METHODS

In this section we begin by describing the physical and biological environments of Biscayne Bay, including data assembly for modeling the physical and biological components of the coastal marine environment. We overview the structure of the spatial predator–prey ecosystem model and then define the experimental design to assess the consequences of system "restoration" and management efforts.

PHYSICAL AND BIOLOGICAL ENVIRONMENTS

Biscayne Bay is an interconnected, shallow (< 4 m), subtropical coastal marine lagoonal system situated adjacent to Miami on the southeastern coast of Florida (Figure 15.1). Although it is technically a larger system, Biscayne Bay is defined here as constituting the portion south of the extensively dredged and filled north bay, i.e., south of Rickenbacker Causeway. A few kilometers to the east of Biscayne Bay is the northern boundary of the Florida Keys coral reef tract. The benthos of the 750-km^2 lagoonal system is composed of a wide variety of substrates (e.g., rocky outcrops, sand, silt–clay) that provide a mosaic of habitats for associated floral and faunal assemblages (e.g., seagrasses, sponges, soft corals, and mangroves) and more than 150 species of fishes and macroinvertebrates (Ault et al., 1999a, 2001a).

Along the bay's western shore is an extensive network of water management canals that regulate freshwater discharges into it. Canals facilitate agriculture and provide flood control; however, episodic human-controlled freshwater releases contribute to the development of ephemeral salinity gradients that range from freshwater on the bay's western side to undiluted seawater to the east. Water temperatures range from 17°C in winter to 32°C in summer. Currents are driven by winds and semi-diurnal tides (Figure 15.2), while terrestrial runoff (90% in the form of canal discharges) is too small to affect circulation directly. Water exchange with the ocean is by way of numerous passes between the eastern barrier islands or Keys, and typical residence times range between weeks and months. Salinity patterns fluctuate seasonally between wet (June to November) and dry (December to May) seasons (Chin-Fatt, 1986).

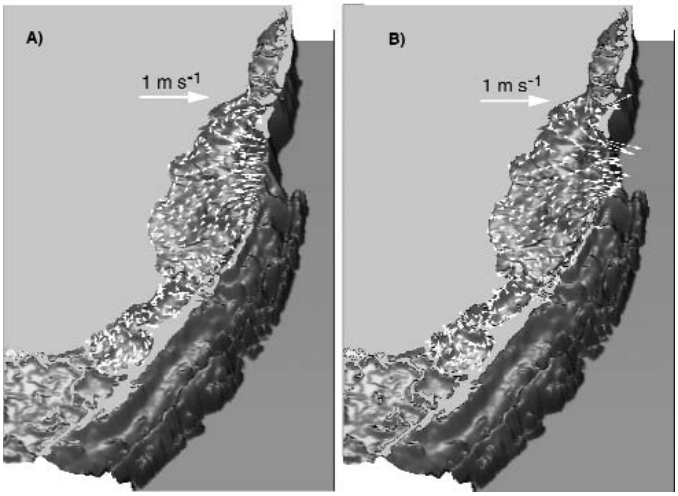

FIGURE 15.2 Biscayne Bay hydrodynamic model outputs showing current vectors for (A) flood and (B) ebb tidal cycles. Length of vector indicates current speed.

The vertically averaged finite element model of hydrodynamic circulation and salinity of Biscayne Bay (Wang, 1978; Wang et al., 1988, 2002) was used to simulate the physical environment and mass transport. The physics-based model uses principles of conservation of mass and momentum and possesses predictive capabilities without the need for parameter adjustments. The model space domain consisted of 6364 triangular elements and 3407 nodes, with grid spacings between nodes on the order of 500 m.

Pink shrimp (prey) and spotted seatrout (predator) utilize similar nearshore bay environments as nursery areas. However, adult pink shrimp spawn offshore (Munro et al., 1968; Kennedy and Barber, 1981), where fertilized ova hatch and progress through a series of planktonic larval stages while being transported towards the coast by prevailing ocean currents (Jones et al., 1970). Postlarvae settle onto relatively shallow (< 1 m) seagrass beds in coastal bays (Costello et al., 1986). Juvenile pink shrimp occupy this habitat until the onset of sexual maturity, which occurs at about 6 months of age and 85 mm total length (TL) (Eldred et al., 1961). Individuals then move to offshore grounds, where they remain through adulthood (maximum age about 3 years) and where they are intensively fished (Iversen and Idyll, 1960; Tabb et al., 1962; Beardsley, 1970). Pink shrimp are omnivores, feeding mainly on detritus, algae, small benthic worms, molluscs, and crustaceans (Eldred et al., 1961). They are the principal food of spotted seatrout (Pearson, 1929; Tabb, 1961; Hettler, 1989) and many other fishes harvested in the bays and coral reefs (Costello and Allen, 1970; Bielsa et al., 1983).

Spotted seatrout spend their entire life within coastal bays, and adults spawn in seaward entrance channels (Saucier and Baltz, 1993). Fertilized ova hatch in about a day and within 2 weeks progress through planktonic larval stages as they are advectively transported shoreward by currents (Peebles and Tolley, 1988). Larvae settle onto nearshore seagrass beds and nonvegetated silt–clay substrates (McMichael and Peters, 1989; Rutherford et al., 1989). Juveniles remain in these nearshore habitats for several months (Rutherford et al., 1989) and then gradually move to vegetated bottoms throughout the bay as they grow older and larger (McMichael and Peters, 1989). Seatrout reach sexual maturity at about 2.5 years, recruit to the fishery at 380 mm TL (about 3.5 years), and live to a maximum age of 9 years (Johnson and Seaman, 1986; Maceina et al., 1987; Murphy and Taylor, 1994). Seatrout population dynamics reflect those of the broader sciaenid community (e.g., red drum, black drum, etc.) and a host of other important coastal fishery species like tarpon, bonefish, and permit, thus influencing their choice as the "model" species.

ECOSYSTEM MODEL DESCRIPTION

To simplify the presentation, we begin development of the coupled biophysical model by presenting aspects of the predator–prey dynamics through introduction of a spatial individual patch interaction model whose conceptual underpinnings are shown in Figure 15.3. The model is object-oriented, with population–community dynamics considered in terms of the independent variables of age and time but also two-dimensional (x,y) space dependency. The spatial dynamic model divides each of n population cohorts into a number of patches and follows each of these patches over space and time with fewer tactical assumptions about animal behavior than those of individual-based models.

The model also explicitly links coastal hydrodynamics and mass transport via the Wang et al. model (1988, 2002) and habitat dynamics through spatial maps of resources. Environmental variability and prey are dynamically linked to predator production through a spatial distribution of growth rate potential (see Brandt et al., 1992) to explore the extent to which physics and biology couple to determine spatial and temporal effects on the growth and survival of each patch. In addition, by summing individual patches over space, we can obtain information on the survivorship and variability of cohort growth and recruitment. Summing the patches and cohorts projects the population, while comparison of prey and predator reflects community dynamics. The numerical version of the spatial dynamic model tracks cohorts of spotted seatrout (predator) and pink shrimp (prey) at age a and time t in horizontal space, from spawning through settlement and recruitment and as they grow through maturity to maximum size and age. A brief model summary is presented below; further details of model parameterizations are found in Ault et al. (1999b).

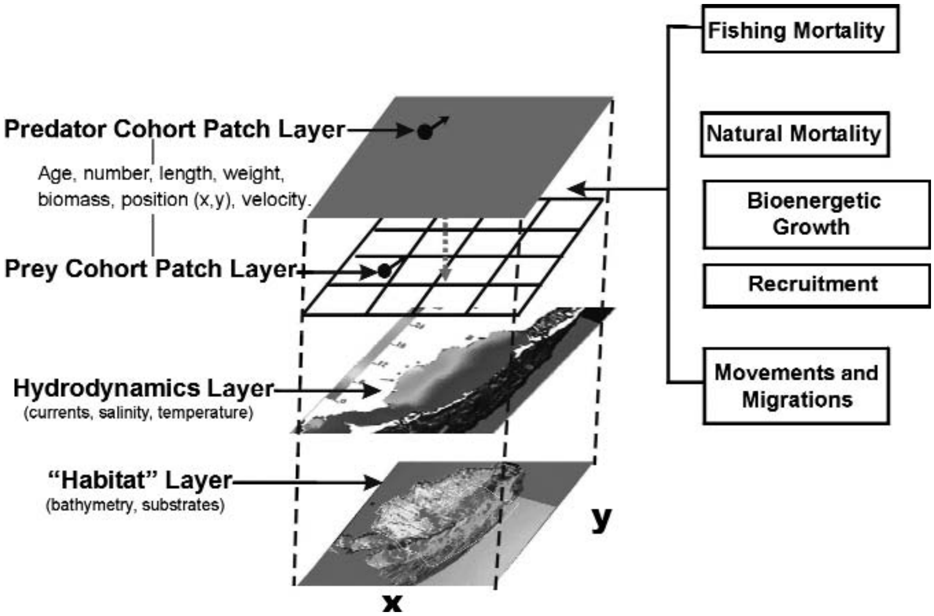

FIGURE 15.3 Conceptual diagram of two-dimensional spatial patch interaction model used for seatrout (predator)–shrimp (prey) community dynamics. Shown also are hydrodynamics and habitat layers overlain by predator and prey cohort object spatial domains.

POPULATION AND COMMUNITY ABUNDANCE AND BIOMASS DYNAMICS

For each population cohort, we used a spatial bioenergetic framework that facilitates spatially-explicit coupling with the physical and biological environments. This framework was formulated into a model partial-differential equation based on conservation of mass expressed in terms of population i cohort abundance $N_i(a,t,x,y)$, for example, of predator (spotted seatrout) N_{ST} or prey (pink shrimp) N_{PS}, each as a function of age a, time t, and two-dimensional space (x and y), following (Ault and Olson, 1996; Ault et al., 1999b; Humston et al., 2000)

$$\frac{dN_i}{dt} = \underbrace{\left(\frac{\partial N_i}{\partial a}\right)}_{\substack{\text{Reaction}\\ \text{kinetics}}} + \underbrace{K\left(N_i\right)\left(\frac{\partial^2 N_i}{\partial x^2} + \frac{\partial^2 N_i}{\partial y^2}\right)}_{\substack{\text{Density-dependent}\\ \text{diffusion}}} + \underbrace{\chi\left(\vec{h}\right)\nabla\left[B\left(\vec{h}\right)\right]N_i}_{\substack{\text{Environmental}\\ \text{taxis}}}$$

where dN_i/dt is a material derivative expressing the local rate of change and advection of N_i as a function of:

1) reaction kinetics, i.e., births minus age-specific deaths in time, where birth rates (recruitments) are modulated by physical transport (e.g., advection during egg–larval transition);
2) density-dependent diffusion $K(N_i)$ (i.e., age-specific competition for resources at local carrying capacities); and
3) behavioral migrations and movements via an environmental taxis function

$$\chi(\vec{h}),$$

driven by the gradient of a "habitat" feature function

$$B(\vec{h}),$$

$$\vec{h}$$

where $\vec{h}$ is the vector of environmental characteristics. Presentation of the fully coupled biophysical model is organized by abundance dynamics, growth dynamics, larval transport, postsettlement movements, and habitat dynamics.

The reaction kinetics component of cohort abundance at age over time was represented by

$$\frac{\partial N_i}{\partial t} = -Z\left(\sum N_i\right)N_i = -\left(M\left[1-\gamma\left(\frac{W(a,t)-W_{opt}(a)}{W_{opt}(a)}\right)\right]+F\right)N_i$$

where N_i is population cohort abundance, a is age ($a = 1,..., \lambda,$), t is time, total instantaneous mortality rate $Z(\sum N_i)$ is a size- and density-dependent function constituting the sum of age-specific, density-dependent interactions, and F is the instantaneous fishing mortality rate.

The base instantaneous natural mortality rate M (in units of numbers per unit time) for average environmental conditions for both species was estimated using maximum average life span methods (Ault et al., 1998). The realized natural mortality rate was determined as the base rate modulated by physical (e.g., "habitat quality") and biological (e.g., predator and prey densities) environmental features. In our model, we linked predator natural mortality to growth by the factor shown in the above equation, where $W(a,t)$ is the current weight of a fish at age and $W_{opt}(a)$ is the optimum weight at age a of a fish growing in an environment with no competitive effects (i.e., unlimited food resources) and is a scale factor to weight the mortality response.

Prey natural mortality rate M was separated into environmental M_H and predation M_P components. Benthic detritus production likely influences shrimp survivorship and growth; however, data were not available to quantify the functional dependency formally on currents or salinity regimes. To compute prey environmental mortality rates, we made the rate magnitude proportional to features of the environment such as depth, salinity, and bottom substrate at location (x,y) at time t relative to observed shrimp survey densities. Using a conservation of biomass principle, predation mortality was proportional to the consumption rate calculated in the predator energetic submodel, the functional response of predator-to-prey density, and a mortality weighting factor. This arrangement makes prey mortality a function of the redistribution of predators due to changing environmental fields.

The mortality rates of predator and prey were higher while searching to reflect the basic foraging-movement risk notion that most juvenile mortality is likely to occur while feeding or dispersing, creating an explicit link between feeding and age-specific mortality rates. Total mortality Z was computed from catch curve analysis of abundance estimates from our fishery-independent trawl surveys conducted in Biscayne Bay during November 1996 and March 1997 (Ault et al., 1999a, 2001a). Fishing mortality F was obtained by difference, i.e., $F = Z - M$, and adjusted for gear size selectivity.

Growth models describe the rate of change in the size of fish with respect to time, usually as the difference between tissue synthesis (anabolism) and degeneration (catabolism) (see von Bertalanffy, 1949; Ault and Olson, 1996). Anabolism (tissue synthesis) is the assimilation of new energy converted into somatic tissue and relates to the proportionality between gut surface area of digestion and body volume, whereas catabolism (tissue degeneration) is usually assumed to be proportional to body volume. Anabolic and catabolic rates are normally allometric functions of individual weight (Jobling, 1994); thus, weight-specific growth rate at age is modeled as

$$\frac{dW(a,t)}{W(a,t)dt} = \lambda W(a,t)^{m-1} - \eta W(a,t)^{n-1}$$

This equation provides the quantitative basis for a bioenergetic modeling framework (e.g., Adams and Breck, 1990; Jobling, 1994; Ault et al., 1999b). Now consider that C is consumption, E is egestion, U is excretion, and R is respiration or total metabolic costs; let rate functions E and U be expressed as relative proportions of C, following Hewett and Johnson (1992), such that $E = C \cdot p_E$ and $U = C \cdot p_U$, where each proportion function ranges between 0 and 1. Combining these ideas, we have

$$\frac{dW(a,t)}{W(a,t)dt} = C - (E - U - R) = \left[C - C \cdot p_E - C \cdot p_U\right] - R = C \cdot A - R$$

where $A = (1 - p_E - p_U)$ is food assimilation efficiency, a quantity that reflects what is consumed minus what the body cannot process or does not use, and $A \geq 0$.

Consumption rate C was modeled as a function of seatrout weight $W(a,t)$, water temperature T, salinity S, and prey abundance N_{PS}. The maximum consumption rate C_{max} was considered to be an allometric function of weight and a function of several environmental variables: water temperature T dependence as defined by the Thornton and Lessem (1978) algorithm, salinity S dependence derived from various field and laboratory experiments, and predator dependence following a functional response that relates the average spatial arrangement of predators to prey (Cosner et al., 1999). Predator $N_{ST}(a,t)$ and prey $N_{PS}(a,t)$ abundances were distributed homogeneously in a model unit area, i.e., the numerical response of the predator-to-prey density of Gutierrez (1996). Predator respiration rate R was modeled as an allometric function of body weight, water temperature T, salinity S, and average swimming speed V. Combining these notions captures fundamental bioenergetic growth principles into an ensemble weight equation:

$$\frac{dW_{ST}(a,t)}{W_{ST}(a,t)dt} = \alpha_C\left[f_C\left(T,S,N_{PS}\right)\right]W_{ST}(a,t)^{\beta_C} - \alpha_R\left[f_R(T,S,V)\right]W_{ST}(a,t)^{\beta_R}$$

where α_C is the maximum consumption rate of a 1-g fish at the optimal temperature and salinity; β_C is the exponent for the weight dependence of consumption; α_R is the standard respiration rate of a 1-g fish at the optimal temperature and salinity; and β_R is the exponent for the weight dependence of respiration. Stock biomass at age is the product of abundance (i.e., numbers at age) times ensemble weight at age. Since weight at age is an environment-dependent function, this arrangement implicitly makes predator stock biomass a function of predator density, prey density, age, time, location, bottom type, salinity, temperature, and swimming speed. While it would have been desirable to model shrimp growth as a bioenergetic function of salinity, temperature, and food quality, these functional relationships were not available. Therefore, we modeled pink shrimp growth following Ault et al. (1999b), using the temperature-dependent, length-on-age piecewise linear function of Smith (1997), where weight dependence on length followed an allometric relationship (Diaz et al., 2001).

LARVAL TRANSPORT AND RECRUITMENT USING A LAGRANGIAN DRIFT MODEL

To estimate the Lagrangian drift for both passive and biologically active behavioral particles, we modeled horizontal particle movements in continuous two-dimensional space as the distance change along the x and y coordinate axes during a time interval dt via the ordinary differential equations

$$\frac{dx}{dt} = X = X_c + \left(X_r + X_b\right)$$

$$\frac{dy}{dt} = Y = Y_c + \left(Y_r + Y_b\right)$$

where X and Y are the x and y coordinate velocities for a postlarval "patch" containing 100,000 postlarvae moving together in concert. Subscripts c and r, respectively, denote velocity components due to water currents X_c, Y_c (i.e., passive advective movements) and density-dependent diffusion X_r, Y_r (simulated as a two-dimensional random walk). Water current velocity components at a position (x,y) were obtained from the finite element velocity solution for the element in which a particle was located. The b subscript denotes behavioral taxis components X_b and Y_b, which were directed movements toward optimal conditions by active swimming. The spatial movement of each patch was then tracked during the pelagic larval transport period, which began with the event of immigration and concluded with the event of demersal settlement.

Postlarval shrimp initial population abundance spatial distributions were precisely determined by fishery independent stratified random sampling surveys (Ault et al., 1999a). Numbers of immigrating shrimp postlarvae were obtained from abundance data back projections combined with immigration seasonal pattern data from Allen et al. (1980). Parameters for the drift transport model can be found in Ault et al. (1999b) and Wang et al. (2002). We defined "larval immigration" as the arrival of fertilized eggs (seatrout) or postlarvae (shrimp spawned on the coral reefs) to the safety valve entrance channel on Biscayne Bay's eastern edge (Figure 15.1). For both populations, total immigrants in a cohort were divided into 1000 patches of equal density, and then these were distributed in rectangles 100 patches long by 10 patches wide, covering the entire safety valve entrance channel. The initial east-to-west and north-to-south interpatch distance was 125 m.

Pink shrimp postlarvae patches were modeled to perform three-dimensional taxis behaviors consisting of vertical diel migrations and horizontal swimming toward preferred environmental conditions (i.e., lower salinity habitats). This was because postlarvae were known to remain on the sea bottom during the day and vertically migrate and enter the water column at night (Tabb et al., 1962; Hughes, 1968). The horizontal behavioral taxis component was composed of two parts: swimming speed and a net resultant angular direction of movement (i.e., the angle of motion). This idea was modeled in polar coordinates using a function that modulated maximum average swimming speed by the salinity gradients along x- and y-coordinate axes. A normally distributed random deviate was included in the direction function to account for behavioral error in directional movement. We assumed no horizontal movements when shrimp stayed at the bottom during the day, and we assumed that water current (X_c, Y_c), behavioral (X_r, Y_r), and random velocities were invoked only at night when shrimp were in the water column.

Laboratory studies by Hughes (1969) suggested that nocturnal vertical movements by pink shrimp postlarvae were modulated by the prevailing tidal cycle in several ways: postlarvae could detect relatively small salinity changes, typically less than or equal to 1 psu; during flood tides, they vertically migrated in response to increasing salinity; and during ebb tides, they remained on the bottom in response to decreasing salinities. In the model, vertical migration was assumed to begin after dusk, coinciding with the onset of flood tides; once suspended in the water column, postlarvae could not detect subsequent tidal cycle shifts that occurred during the rest of the night. Therefore, horizontal movements occurred until dawn, when postlarvae migrated to the sea floor. After each nocturnal transport period, a proportion of postlarvae within a given patch settled out. For larvae less than 11 mm TL, settling probability was described as a multiplication of three independent component probability functions based on bottom substrate type, depth, and postlarvae total length, in accordance with field and laboratory observations (Hughes, 1969; Allen et al., 1980; Costello et al., 1986). At 11 mm TL, all postlarval shrimp, settled regardless of substrate and depth.

We modeled seatrout spawning events (i.e., egg immigration) to occur at night on the incoming tide. Seatrout patch movements were tracked over a continuous spatial domain at 10-minute time intervals until all individuals either settled on the bottom or died. For seatrout eggs and yolksac larvae, we assumed that horizontal movements were advective and diffusive, but not behavioral (i.e., $X_b = Y_b = 0$) and that no vertical movements occurred during the seatrout pelagic life stage. At 5 to 8 days of age, seatrout larvae will actively settle onto seagrass in depths less than 2 m (Peebles and Tolley, 1988). For larvae more than 6 and fewer than 9 days old, settling probability was described by a multiplication of independent probability functions based on bottom substrate type and total length. At 9 days postspawn, we modeled seatrout larvae to settle, regardless of substrate and size.

JUVENILE AND ADULT ONTOGENETIC MOVEMENTS AND MIGRATIONS

Juvenile and adult movements and migrations were based on the idea that animals could detect gradients of habitat quality, which provide the stimuli for predator and prey movement behaviors. These spatially explicit mosaics of habitat quality within model unit cells directly influenced population-dynamic rates of growth and mortality. Factors affecting seatrout spatial growth-rate potential (Ω), measured as *dW/Wdt*, were components of an essential habitat vector that included time-dependent physical variables such as salinity, prey density, temperature, and substrate. Mathematically, this complex dynamic vector can be resolved in a single variable (i.e., Ω, the expected growth for an animal occupying that cell during a given time step) for each model cell. All point computations within the model domain produced a spatial map of Ω, which represents a quantitative spatial index of habitat quality over time and space (Brandt et al., 1992; Rubec et al., 1999, 2001; Chapter 14, this volume). We modeled behavioral movements based on an optimization search by the fish at its present location relative to the spatial growth rate potential of adjacent habitat cells in the surrounding environment. Movement of fish patches on continuous two-dimensional coordinate space can be described by two velocity-vector components that are dependent on Ω:

$$X_b(\Omega) = \left(\tilde{V}(a,t) \left[1 - e^{\Phi\left(\frac{\Omega(t)-\Omega_{max}}{\Omega_{max}}\right)} \right] \right) \left(\cos\left[\theta_{max} + \xi\pi\right] \right)$$

$$Y_b(\Omega) = \left(\tilde{V}(a,t) \left[1 - e^{\Phi\left(\frac{\Omega(t)-\Omega_{max}}{\Omega_{max}}\right)} \right] \right) \left(\sin\left[\theta_{max} + \xi\pi\right] \right)$$

where X_b, Y_b are coordinate velocity components due to behavior, ζ is a random normal variate, Ω_{max} is the maximum growth rate potential within the detection range of the fish, $\tilde{V}(a,t)$ is the net displacement velocity of the fish at age *a*, Φ is a scalar multiplier, and θ_{max} is the heading to the location of maximum growth rate potential within the detection range of the fish.

The first term in parentheses on the right-hand side of the above equation represents the fish speed as a function of growth rate potential Ω, while the second term is the directional heading of fish as a function of the perceived proximal habitat quality. The net displacement speed is the actual distance moved between two points from the start and end of one time step, recognizing that substantial searching may occur during this time. We assumed that, to determine movements, animals evaluated their local environment daily and that juvenile and adult fish movements were not influenced by hydrodynamic currents.

Postsettlement pink shrimp movements were modeled by a discrete transform two-dimensional cellular automaton method that divides the spatial domain into *j* grid cells, each with dimensions 0.0025° latitude by 0.0025° longitude (i.e., approximately 278 by 250 m). Each day a proportion of animals move to and from neighboring grid cells; the probability of an individual of length *L* staying in cell *j* at time *t* depends on the respective habitat, animal size, and a random-stay probability. The habitat probability is a function of environmental variables (e.g., depth, substrate, salinity) that define habitat quality measured by observed animal density distributions. As pink shrimp grow, the probability of movement increases. The random-stay probability function was based on the notion that a proportion of those animals that did not move from a cell, based on environmental features, still migrated due to random forces. Once an animal matures, it preferentially moves toward cells with higher salinity, higher currents, and greater depths, in accordance with the studies of Hughes (1969) and Beardsley (1970).

To parameterize the spatial model and provide initial population conditions in space and time, we developed a comprehensive habitat and fishery-independent survey database. At progressively smaller spatial scales, numerous habitat types can be defined by structural (e.g., depth and benthic substrates, etc.) and by water quality attributes (Lindeman et al., 1999, 2000). Since April 1996, we have conducted quarterly bay-wide fishery-independent trawl surveys of fish and macroinvertebrate populations in Biscayne Bay (Ault et al., 1999a; Diaz, 2001; Diaz et al., 2001; Ault et al., 2001a). This was the primary biological data source for model initial conditions of animal densities by habitat type and season used in the model development and parameterization.

To assess shrimp and fish abundance and habitat preferences, essential fish habitats were described as a feature vector comprising six principal variables: topography, substrate type, water temperature, water currents, salinity, and prey or predator density. Gridded bathymetry data for Biscayne Bay were obtained from the National Ocean Service topographic database (NOAA National Geographic Data Center, Boulder, Colorado) and the Office of Naval Research. Areal benthic habitat coverages for Biscayne Bay were provided by Dade County and the Florida Marine Research Institute. Daily temperature was modeled by a periodic function fit to observations for 1990 to 1994. The hydrodynamics model was parameterized for calendar years 1995 to 1998 using tides predicted from harmonic constants, wind observations from the Fowey Rocks CMAN (Coastal Marine Automated Network) station, and canal freshwater discharge data from the SFWMD (J. Obeysekera, personal communication). These physical data were used to drive biological recruitment simulations. March 1997 fishery-independent survey data were used to initialize pink shrimp spatial densities for model simulations.

We also used the fishery-independent database to validate model simulation results empirically. Model parameters, functional forms, and initial conditions were developed from a number of published field and laboratory sources to represent the population dynamics and spatial movement behaviors for spotted seatrout and pink shrimp and are reported in Ault et al. (1999b). For the water management scenario testing for years 1965 to 1995, we ran the hydrodynamic model using wind measurement from Miami International Airport, canal delivery outputs from the SFWMD water management model (www.sfwmd.gov), and USGS groundwater inputs (C. Langevin, personal communication). The hydrodynamic model simulated water current velocities and salinity distributions at 1-minute time steps. The scientific data visualization package IDL (Interactive Data Language, Research Systems Inc., Boulder, CO) was used on a COMPAQ Alpha workstation to view the data and animate the coupled biophysical model simulations.

SCENARIO TESTING AND EXPERIMENTAL DESIGN

Steps in a comparative assessment of population risks start with model simulations of management scenarios that involve two water management strategies proposed under the Everglades restoration plan. The 95Base reflects historical environmental and human water uses and actual 1995 regional human population and socioeconomic conditions. The D13R considers operational changes in water management and the water uses for population size projected to occur in 2050 (see www.sfwmd.org).

In the 95Base, the 1965 to 1995 climate record was used in conjunction with the 1995 physical system state for evaluations of the existing condition, with rainfall and potential evapotranspiration the key climatic inputs. Scenario D13R corresponds to the Comprehensive Everglades Restoration Plan (CERP) and attempts to capture additional water discharged to tide (i.e., the coastal marine waters of south Florida) and return it to the natural terrestrial Everglades system. Key scenario features include increasing storage capacities and adjusting water-management operations to better redistribute the additional water to Everglades National Park and Biscayne Bay. Under the D13R scenario, structures S197 and S20G (Figure 15.1) will be removed and more freshwater will be diverted to the mid-bay region at canal structures S123, S21, and S21A (Table 15.1a). Similarly, more surface waters will be delivered to mid-bay under the D13R scenario (Table 15.1b). The water management model of SFWMD was set up to run 31-year simulations

TABLE 15.1
Comparison of Freshwater Deliveries to Biscayne Bay under 95Base and D13R Water Management Scenarios via (A) Gated Canal Control Structures and (B) Ground and Surface Sheet Flows

(A)

	Canal Structure								
Scenario	**G93**	**S22**	**S123**	**S21**	**S21A**	**S20G**	**S20F**	**S197**	**Total**
95Base	131.78	93.17	53.11	124.51	39.85	12.83	81.62	7.93	544.79
D13R	68.93	88.05	80.11	144.17	120.47	0	72.59	0	574.30

(B)

	Ground and Surface Water								
Scenario	**North**			**Mid-Bay**				**South**	**Total**
95Base	9.60	9.79	13.16	17.83	15.6	16.10	-2.34	51.28	131.03
D13R	8.79	10.25	12.32	15.46	24.25	21.38	7.56	32.01	132.04

Note: Values are 31-year averages in millions of cubic meters of freshwater per year. Delivery volumes for (B) are arranged from north to south along the western boundary of the model domain, where each column represents freshwater inflows along about 10 km of linear shoreline of Biscayne Bay.

from 1965 to 1995 under 95Base and D13R scenarios, thereby providing the canal flows and ground and surface inputs for the Biscayne Bay hydrodynamic model simulations of the same time period (Table 15.1).

Biophysical model simulations were conducted under the two water management scenarios to evaluate their ecological effects. The biophysical model used hydrodynamic outputs to assess the consequences of either strategy. Simulation experiments were conducted, varying several factors to explore the model's dynamic behavior. Larval behavior of fishes (both passive pelagic larvae and motile larvae) was input into the model with current, salinity, and canal discharges to provide an estimate of larval recruitment pathways in Biscayne Bay. The individual and population growth and production dynamics of the seatrout and pink shrimp populations were evaluated with two fishing exploitation rate experiments (normal fishing and doubled fishing mortality).

RESULTS

Comparisons of salinity from hydrodynamic model simulations indicate significant physical and water quality differences between the Base95 and D13R CERP water management strategies (Color Figure 15.4*). The differences in freshwater deliveries between the scenarios are summarized in Table 15.1. In general, the D13R scenario produces lower-salinity regimes in the middle Biscayne Bay than Base95 due to increased freshwater from recycling, but it produces higher salinity regimes in southern Biscayne Bay due to the removal of the C-111 canal structure.

Postsettlement pink shrimp cohort dynamics is represented by the dynamics of its habitat utilization in the bay (Color Figure 15.5*). At recruitment, postlarvae settle in concentrated bands on seagrass beds along the western side of Biscayne Bay (Color Figure 15.5a*). At 150 days postsettlement, pink shrimp are about 85 mm total length and still concentrated in grassbeds, but the total spatial abundance distribution has expanded and diffused outward into deeper waters (Color Figure 15.5b*). At about 180 days or 6 months postsettlement, shrimp have begun an easterly ontogenetic migration in which they begin inhabiting deeper channelized areas with high salinity and strong currents (Color Figure 15.5c*). By age 270 days, the majority of a pink shrimp cohort has left the bay in favor of oceanic habitats for adult feeding and spawning grounds (Color Figure 15.5d*).

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* Color insert figures follow page 242.

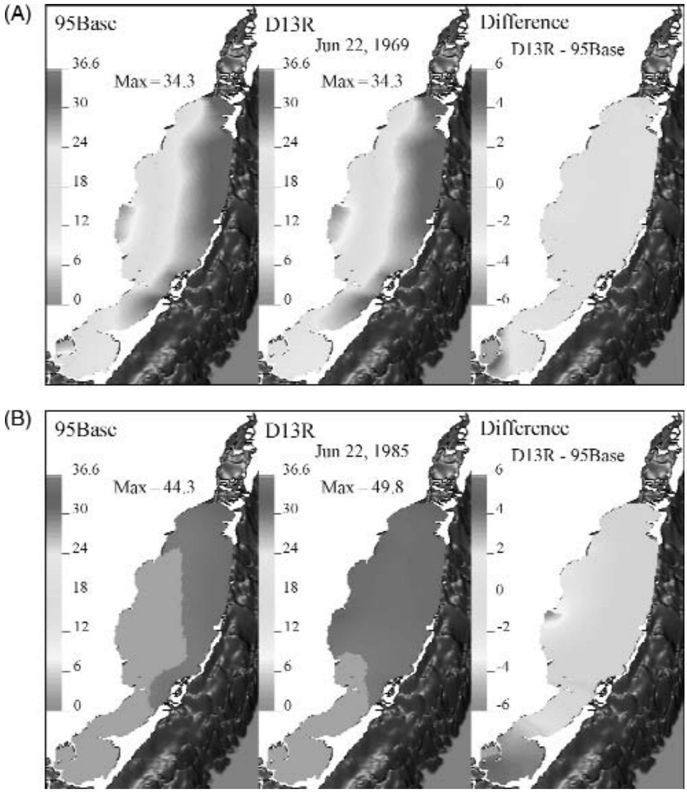

FIGURE 15.4 Comparison of modeled surface salinities resulting from 95Base (left panel) and D13R (middle panel) scenarios and their difference (right panel) for CERP water management alternatives. Surface salinities for (A) June 22, 1969, during a characteristic wet year, and (B) June 22, 1985, during a characteristic dry year. Pink areas indicate surface salinity ≥ 36.6 psu.

The empirical shrimp spatial density distribution (number of shrimp per 600 m^2), sample locations, and the distribution of average size at those sampling locations, estimated from stratified sampling surveys for November, 1996, are shown in Color Figure 15.6b*. Highest shrimp densities were found in relatively shallow seagrass beds located on the western side of the bay in areas of moderate salinity regimes (10 to 20 psu). The center of abundance moves somewhat between August and November, presumably influenced strongly by varying salinity regimes. Comparisons of shrimp spatial distributions suggests relatively good agreement between empirical and modeled observations (Color Figure 15.6*).

SEATROUT GROWTH-RATE POTENTIALS

Ecological consequences of 95Base and D13R water management scenarios can be represented by the comparison of simulated spatial growth rate potential for spotted seatrout and its population dynamics under 95Base and D13R scenarios. Our results indicate that the highest growth rate potentials for seatrout always occurred on the bay's midwestern side in both water management scenarios (Color Figure 15.7a,b),* due to the combination of available seagrass beds, high prey densities (i.e., shrimp), and suitable salinity regimes. In comparing these two scenarios, D13R produced slightly higher daily spatial growth rate potentials than 95Base (Color Figure 15.7c*) as the result of more

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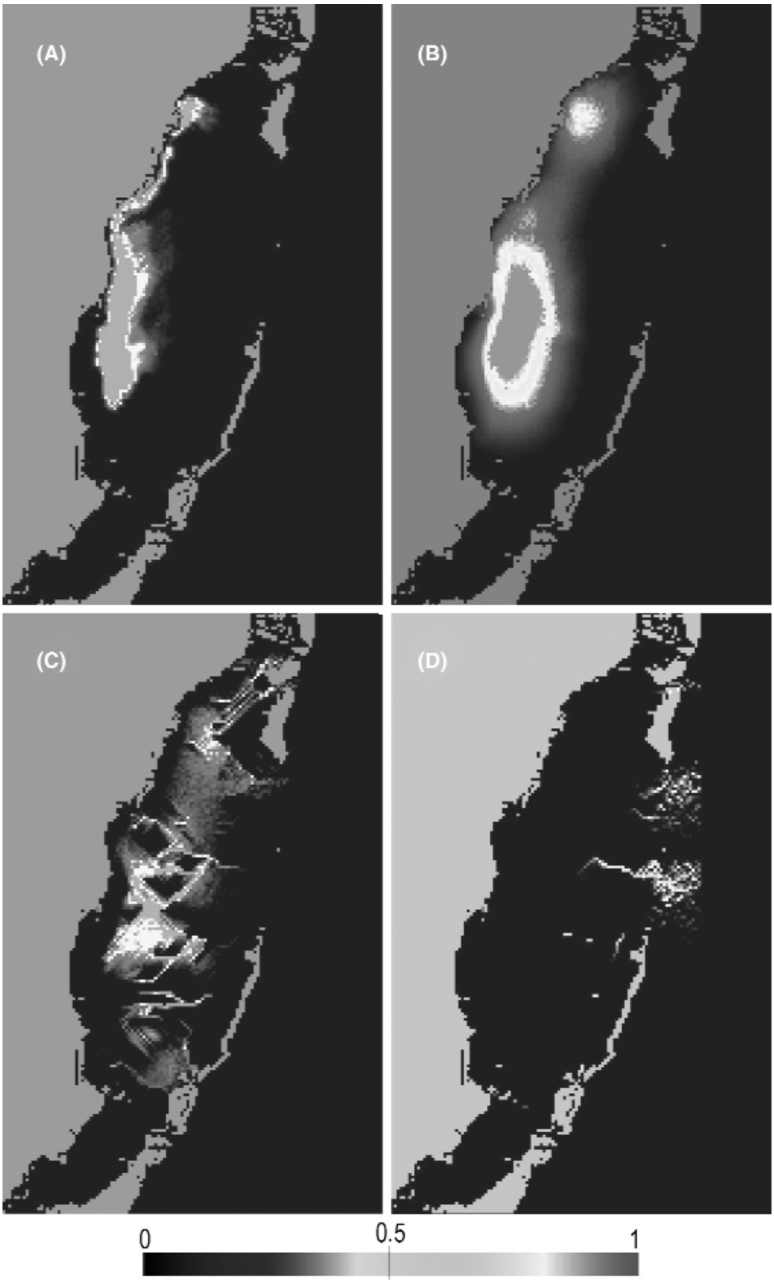

FIGURE 15.5 Simulated shrimp population spatial abundance distributions over time for a June cohort immigrating into Biscayne Bay: (A) Day 0 (settlement), (B) Day 150, (C) Day 180, (D) Day 250. Note that all animals from a given cohort are assumed to have left the bay by 270 days after birth. Color scale indicates densities ranging from 0 to 1.0 shrimp m.$^{-2}$

freshwater inputs. These daily differences were magnified if a fish stayed in a given cell for its entire lifetime. However, individual fish actually traveled through the complex seascape at different stages of life span and accumulated growth over different habitats. Therefore, it is not possible to compare individual fish to determine which regime was better; however, by summing the patches

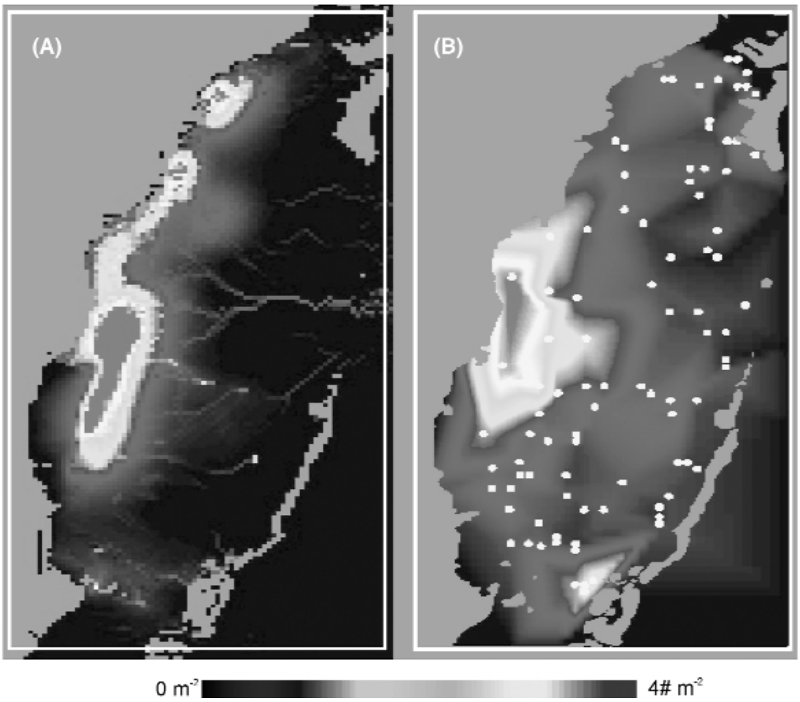

FIGURE 15.6 Time synchronized comparisons of (A) spatial patch interaction model spatial estimates of shrimp densities (number of shrimp per m^2) relative to (B) stratified random survey shrimp density estimates. (From Ault et al., *North Am. J. Fish. Manage*., 19(3):696–712, 1999a.)

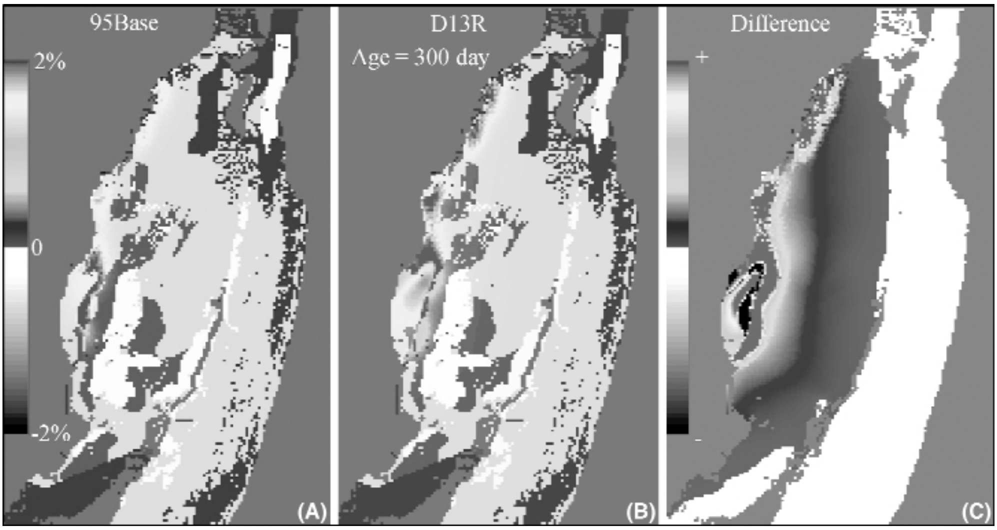

FIGURE 15.7 Modeled spatial growth potential or habitat quality for seatrout in typical scenario runs of (A) 95Base (B) D13R, as well as (C) the difference between scenarios expressed as 95Base minus D13R.

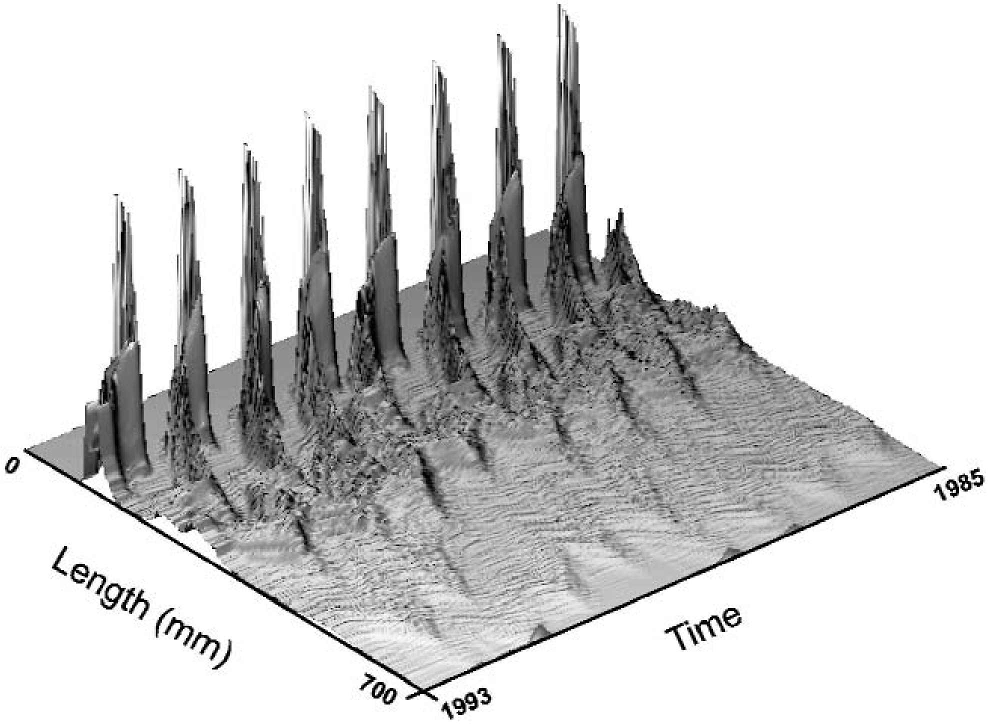

FIGURE 15.8 Simulated seatrout population-abundance structure by size during the period 1985 to 1993, using the 95Base water-management scenario.

over the spatial domain, we can compare simulation results at the population level. Fuller comprehension of the overall dynamics of multicohort populations can be gained by viewing a graphic of the abundance surface over size and time (Figure 15.8). For comparative analysis, the abundance surfaces were summarized (digitized) into a series of cohort time tables: weight (Table 15.2), length (Table 15.3), abundance (Table 15.4), and biomass (Table 15.5).

SEATROUT SIZE COMPARISONS

Seatrout weights at age varied among the years but, in general, the D13R scenario resulted in larger fish for all age classes than 95Base (Table 15.2) scenarios did. Mean weights of age-1 fish ranged from 16 to 34 g, and for age-8 fish ranged from 719 to 1667 g under the 95Base with no exploitation (Table 15.2a). Under the D13R water management scenario with no exploitation (Table 15.2b), mean weights of age-1 fish ranged from 19 to 39 g, and for age-8 fish ranged from 1622 to 2065 g. Table 15.2c to d gives similar information for an exploited seatrout population in which the fishing mortality rate is equal to natural mortality. Comparisons of Tables 15.2a and15.2c, 15.2b and 15.2d shows no clear effect of fishing mortality on seatrout weight at age under the mortality values used in this study. The results of seatrout lengths at age (Table 15.3) were similar to those for weight at age, but with smaller differences due to the power function of the length–weight relationship.

SEATROUT ABUNDANCE AND BIOMASS COMPARISONS

Even though the recruitments at age-0 in our simulations were the same for all years and all scenarios, differences in abundances resulted from year-to-year changes in water deliveries and from the scope of the changes between the water-management scenarios (Table 15.4). The differences in abundance among years were small compared to differences in abundance between the water-management scenarios (Table 15.4a vs**.** 15.4b). The D13R scenario resulted in greater abundances for all age classes and all years compared to the 95Base under no exploitation. The introduction of fishing mortality not only decreased the abundances in age classes 3 and older but also decreased the observed differences in population abundance between the water-management scenarios (Tables 15.4c,

TABLE 15.2
Seatrout Cohort Weights (g) Resulting from Scenario Simulations: (A) 95Base; (B) D13R; (C) 95Base with Exploitation; and (D) D13R with Exploitation

(A)

				Year				
Age	**1986**	**1987**	**1988**	**1989**	**1990**	**1991**	**1992**	**1993**
1	29	19	23	16	20	23	23	34
2	174	176	157	136	134	165	165	214
3	320	267	269	226	243	259	265	337
4	414	433	327	273	286	307	324	425
5	799	579	637	347	325	363	376	508
6	1333	1019	849	799	437	420	452	602
7	1587	1434	1263	1009	1055	572	544	741
8	1667	1594	1555	1289	1240	1298	719	851

(B)

				Year				
Age	**1986**	**1987**	**1988**	**1989**	**1990**	**1991**	**1992**	**1993**
1	34	29	25	19	23	29	27	39
2	195	218	172	135	140	168	183	218
3	366	350	330	237	255	272	277	347
4	480	682	550	363	308	353	364	436
5	1170	879	1148	749	494	412	496	619
6	1654	1625	13	9	1074	772	636	899
7	1878	1929	1827	1423	1549	1463	1107	1162
8	1972	2065	1971	1669	1589	1783	1689	1622

(C)

				Year				
Age	**1986**	**1987**	**1988**	**1989**	**1990**	**1991**	**1992**	**1993**
1	27	19	23	17	21	25	24	39
2	176	166	160	138	145	170	186	224
3	333	257	258	220	239	261	255	356
4	406	455	302	263	271	303	319	404
5	889	533	651	305	308	336	357	509
6	1386	1112	739	807	357	385	407	595
7	1596	1449	1341	889	1034	461	486	700
8	1674	1567	1536	1345	1120	1300	606	814

(D)

				Year				
Age	**1986**	**1987**	**1988**	**1989**	**1990**	**1991**	**1992**	**1993**
1	35	28	27	19	27	28	29	38
2	211	224	189	156	169	191	188	224
3	370	364	317	249	277	288	294	346
4	519	644	546	346	332	382	383	461
5	1157	931	1052	717	502	455	570	657
6	1687	1567	1359	1267	1072	807	736	1026
7	1883	1878	1756	1445	1564	1448	1200	1283
8	1974	1986	1934	1630	1658	1806	1678	1697

d). Biomass is the product of fish abundance and weight and, as a result, the differences among years, ages, and scenarios are magnified (Table 15.5). When we summed biomass for all age classes and plotted it over the time for each of the scenarios, the dynamics over the years and the differences among the scenarios could be easily seen (Figure 15.9).

TABLE 15.3
Seatrout Cohort Lengths Resulting from Scenario Simulations: (A) 95Base; (B) D13R; (C) 95Base with Exploitation; and (D) D13R with Exploitation

(A)

	Year							
Age	**1986**	**1987**	**1988**	**1989**	**1990**	**1991**	**1992**	**1993**
1	150	131	142	126	135	141	141	160
2	268	270	259	248	245	264	266	289
3	331	310	313	295	303	308	311	336
4	355	359	330	314	318	327	331	360
5	427	389	398	332	330	340	345	378
6	515	465	437	427	353	353	361	397
7	553	533	505	465	470	382	379	421
8	563	555	549	513	502	509	412	438

(B)

	Year							
Age	**1986**	**1987**	**1988**	**1989**	**1990**	**1991**	**1992**	**1993**
1	160	151	145	132	141	152	149	168
2	280	292	270	249	251	267	276	292
3	345	340	334	301	308	314	317	340
4	374	416	386	342	328	341	344	365
5	492	451	492	421	371	358	377	403
6	558	554	519	519	475	424	406	451
7	586	590	579	534	549	530	481	493
8	595	604	595	564	554	575	562	553

(C)

	Year							
Age	**1986**	**1987**	**1988**	**1989**	**1990**	**1991**	**1992**	**1993**
1	148	133	141	127	136	144	143	167
2	270	265	261	249	252	266	276	294
3	335	307	309	293	301	309	308	343
4	352	363	323	311	314	325	327	356
5	443	378	399	322	324	334	340	377
6	522	482	414	426	335	345	352	396
7	554	535	517	439	464	360	367	414
8	564	552	547	521	477	506	390	432

(D)

	Year							
Age	**1986**	**1987**	**1988**	**1989**	**1990**	**1991**	**1992**	**1993**
1	161	149	149	134	148	152	152	166
2	288	294	278	260	266	279	278	295
3	346	343	330	306	316	320	322	340
4	382	406	384	337	335	349	349	370
5	489	457	475	414	374	368	391	409
6	562	547	521	509	473	432	424	471
7	586	585	571	536	548	529	497	510
8	595	596	591	560	561	577	561	563

Table 15.4
Sea cohort abundance (millions of fish) resulting from scenario simulations: (A) 95Base; (B) D13R; (c) 95Base with exploitation; and, (D) D13R with exploitation.

(A)

	Year							
Age	**1986**	**1987**	**1988**	**1989**	**1990**	**1991**	**1992**	**1993**
1	489.4	496.8	484.0	464.4	470.2	475.8	480.1	511.8
2	280.4	294.3	288.6	275.6	262.2	270.5	283.2	302.3
3	159.0	145.2	147.9	139.2	137.7	132	131.7	169.1
4	78.9	82.4	72.0	69.5	69.0	69.0	64.6	78.1
5	34.9	39.8	39.6	33.3	34.1	34.4	33.7	38.2
6	21.9	17.3	18.9	18.0	15.9	16.7	16.6	19.4
7	15.3	11.7	8.7	8.8	8.7	7.6	8.0	9.5
8	6.2	8.3	6.3	4.3	4.4	4.4	3.6	4.4

(B)

	Year							
Age	**1986**	**1987**	**1988**	**1989**	**1990**	**1991**	**1992**	**1993**
1	516.7	516.2	496.5	489.6	489	511	513.2	517.7
2	300.9	327.1	306.0	298.4	287.8	296.8	312.8	328.4
3	180.4	181.4	171.6	160.4	162.1	160.6	165.2	193.8
4	95.9	109.5	94.2	85.0	86.5	89.6	88.1	102
5	52.2	57.5	58.6	45.2	43.5	47.8	49.6	53.0
6	32.4	31.2	31.4	31.1	22.8	22.9	26.6	29.0
7	20.2	19.5	17.2	16.9	17.5	12.5	12.3	15.7
8	9.6	12.0	10.5	9.0	9.5	10.0	6.9	7.3

(C)

	Year							
Age	**1986**	**1987**	**1988**	**1989**	**1990**	**1991**	**1992**	**1993**
1	490.9	496.2	482.7	466.6	465.2	477.4	480.3	511.2
2	280.6	297.3	289.1	279.8	265	267.0	283.9	302.7
3	135	131.4	138.1	130.8	130.7	122.2	116.5	145.9
4	51.4	52.9	57.2	56.9	59.2	55.8	49.0	56.2
5	15.3	18.3	19.0	22.0	24.3	24.2	20.9	21.5
6	6.9	5.5	6.4	6.2	8.7	9.4	8.7	8.8
7	3.6	2.6	2.1	2.1	2.2	3.2	3.2	3.6
8	1.1	1.4	1.0	0.7	0.7	0.8	1.0	1.3

(D)

	Year							
Age	**1986**	**1987**	**1988**	**1989**	**1990**	**1991**	**1992**	**1993**
1	515.9	512.8	496	486.6	488.1	509.4	509.7	518.7
2	296	321.3	305.7	294.3	285.7	298.2	311.5	324.1
3	148.5	151.2	144.6	149.9	145.7	144.6	145.0	168.6
4	58.5	63.3	58.5	58.2	67.7	64.8	61.7	67.3
5	21.1	23.9	23.7	20.2	22.8	27.9	25.4	26.3
6	9.6	8.8	9.2	8.8	7.4	8.7	10.9	10.3
7	4.7	4.0	3.5	3.5	3.5	2.9	3.3	4.5
8	1.5	2.0	1.6	1.3	1.4	1.5	1.1	1.4

TABLE 15.5

Seatrout Cohort Biomass (mt) Resulting from Scenario Simulations: (A) 95Base; (B) D13R; (C) 95Base with Exploitation; and (D) D13R with Exploitation

(A)

	Year							
Age	**1986**	**1987**	**1988**	**1989**	**1990**	**1991**	**1992**	**1993**
1	13988.3	9226.2	11320.9	7470.0	9523.2	11036.9	10981.3	17527.1
2	48646.1	51668.2	45384.8	37411.6	35236.5	44580	46821.4	64690.5
3	50938.9	38730.3	39772.6	31483.7	33502.6	34202.1	34922.5	56932.6
4	32629.3	35645.7	23529.4	18991.8	19772.2	21191.9	20941.8	33175.8
5	27887.9	23091.2	25238.8	11563.9	11098.8	12506.1	12663.5	19377.2
6	29212.3	17644.3	16073.2	14364.1	6944.1	7025.2	7515.3	11694.5
7	24298.3	16835.2	11039	8911.1	9177.5	4366.2	4332.1	7011.8
8	10375.7	13307.3	9832.7	5594.6	5510.1	5660.7	2600.2	3786

(B)

	Year							
Age	**1986**	**1987**	**1988**	**1989**	**1990**	**1991**	**1992**	**1993**
1	17457.8	14725.3	12292.8	9187.1	11342.5	14754.3	13892.2	20372.6
2	58617.1	71157.3	52509.3	40383.5	40376.3	49748.1	57334.1	71706.3
3	66020.5	63419.1	56618.8	38071.3	41349.8	43751.8	45710.3	67265
4	45994.3	74618.6	51815	30874.8	26643.7	31606.7	32124.1	44454.6
5	61079.2	50588.7	67254.7	33833.3	21496.1	19712.1	24609.6	32785.1
6	53568.1	50781.5	41762.7	41055.6	24526.4	17690.8	16890.8	26087.8
7	37858.9	37610.2	31422.2	24108.3	27035.7	18228.1	13561.6	18236.5
8	18837.5	24796.5	20760.1	5044.2	15052.3	17888.2	11680.3	11860.7

(C)

	Year							
Age	**1986**	**1987**	**1988**	**1989**	**1990**	**1991**	**1992**	**1993**
1	13334.9	9456.5	11150.8	7754.0	9628.2	11867.9	11496.5	20044.5
2	49359.2	49339.3	46140.2	38589.8	38295.1	45357.6	52898.9	67864.2
3	44924.9	33739.8	35665.7	28752.2	31238.2	31894.6	29666.8	51923.7
4	20897.8	24053.7	17278.4	14984.8	16042.9	16887.7	15633.1	22675.2
5	13635.1	9776.5	12381.6	6704.4	7463.7	8140.6	7453	10959.5
6	9594.2	6108.2	4698.8	5026.5	3108.6	3604.7	3544.3	5260.8
7	5799.9	3781.5	2752.5	1838	2261.6	1455.5	1555.9	2505.8
8	1896	2194.3	1546.2	1006.6	819.5	1024.1	635.2	1042.3

(D)

	Year							
Age	**1986**	**1987**	**1988**	**1989**	**1990**	**1991**	**1992**	**1993**
1	17972.9	14153.0	13334.0	9431.2	13007.3	14509.7	14662.8	19780.9
2	62541.8	71827.6	57894.6	46002.4	48242.3	57031	58463.8	72741.6
3	54991.9	55086.1	45788.9	37362.8	40386.5	41599.7	42574.9	58378.2
4	30369.4	40752 3	1932.8	20128.3	22472.1	24764.3	23636.3	30986.6
5	24442.8	22251.4	24896.8	14470.3	11471.2	12714	14463.5	17303.8
6	16151.9	13814.1	12496.4	11183.1	7948.7	6988.3	8023.9	10614.4
7	8883.9	7546.3	6106.8	5071.8	5511.9	4177.7	4011.8	5832.3
8	3028.0	3889.0	3054.2	2132.7	2325.5	2625.4	1926.7	2417.6

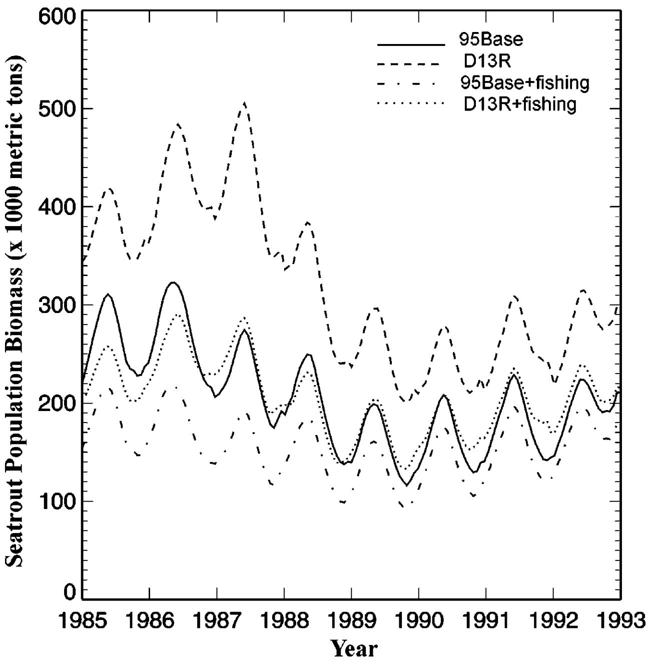

FIGURE 15.9 Simulated seatrout stock biomass model outputs for the period 1985 to 1993, using 95Base and D13R scenarios with and without exploitation.

TOTAL INSTANTANEOUS MORTALITY RATES (Z)

Total mortality rates were estimated (Table 15.6) from modeled seatrout abundances (Table 15.4). In the biophysical model simulations, each seatrout patch, with or without fishing, encountered a variable natural mortality rate as determined by the habitat quality. When fishing occurred, it did so as a density-dependent rate component. Therefore, the total mortalities were different among years, ages, and scenarios. As one would expect, the D13R scenario resulted in lower mortality for all years and all ages for exploited and nonexploited populations.

SHRIMP ABUNDANCES

As a point of comparison between predator and prey populations, shrimp abundances were grouped into three size classes: < 45, 45 to 85, and > 85 mm (Table 15.7). These results indicated that differences among the years were much greater than the differences between any scenario, meaning that shrimp population abundances were principally driven by seasonal and interannual variability (i.e., independent of the scenario).

DISCUSSION

Our dynamic spatial model to assess fish population risks from exploitation and environmental changes is still in early stages of development, requires a large number of parameters derived from empirical studies, and must make important assumptions as to which attributes of the ecosystem should be modeled. At several junctures in developing the spotted seatrout–pink shrimp model, we made many simplifications to avoid an unmanageable number of state variables. Our results indicate that, despite these simplifications, the coupled biophysical model presented here provides a quantitative framework for assessing predator–prey population responses to dynamic physical and biological environments.

TABLE 15.6

Seatrout Cohort Total Instantaneous Mortality Rate (Z) from Scenario Simulations: (A) 95Base; (B) D13R; (C) 95Base with Exploitation; and (D) D13R with Exploitation

(A)

Age	Year							
	1985	**1986**	**1987**	**1988**	**1989**	**1990**	**1991**	**1992**
1	0.48	0.46	0.49	0.53	0.52	0.51	0.50	0.43
2	0.51	0.51	0.54	0.56	0.57	0.55	0.52	0.46
3	0.58	0.66	0.69	0.73	0.69	0.69	0.72	0.52
4	0.58	0.66	0.70	0.75	0.70	0.69	0.72	0.52
5	0.66	0.68	0.73	0.77	0.71	0.70	0.72	0.53
6	0.59	0.70	0.74	0.79	0.74	0.71	0.73	0.55
7	0.52	0.62	0.68	0.76	0.73	0.73	0.74	0.56
8	0.53	0.61	0.62	0.70	0.69	0.69	0.75	0.58

(B)

Age	Year							
	1985	**1986**	**1987**	**1988**	**1989**	**1990**	**1991**	**1992**
1	0.42	0.43	0.46	0.48	0.48	0.44	0.43	0.42
2	0.48	0.46	0.52	0.51	0.53	0.50	0.49	0.45
3	0.52	0.51	0.64	0.65	0.61	0.58	0.59	0.48
4	0.53	0.50	0.66	0.70	0.62	0.59	0.60	0.48
5	0.57	0.51	0.62	0.74	0.67	0.59	0.59	0.51
6	0.50	0.51	0.61	0.63	0.68	0.64	0.59	0.54
7	0.48	0.51	0.60	0.62	0.58	0.61	0.63	0.53
8	0.49	0.52	0.62	0.65	0.58	0.55	0.59	0.52

(C)

Age	Year							
	1985	**1986**	**1987**	**1988**	**1989**	**1990**	**1991**	**1992**
1	0.48	0.47	0.49	0.53	0.53	0.50	0.50	0.44
2	0.51	0.50	0.54	0.55	0.57	0.56	0.52	0.46
3	0.75	0.76	0.77	0.79	0.76	0.77	0.83	0.67
4	0.83	0.94	0.83	0.89	0.79	0.85	0.91	0.73
5	0.97	1.03	1.02	0.96	0.85	0.89	0.98	0.82
6	0.93	1.03	1.06	1.12	0.93	0.95	1.02	0.86
7	0.87	0.98	0.98	1.12	1.05	1.02	1.07	0.89
8	0.87	0.95	0.95	1.01	1.04	1.02	1.10	0.92

(D)

Age	Year							
	1985	**1986**	**1987**	**1988**	**1989**	**1990**	**1991**	**1992**
1	0.43	0.43	0.47	0.48	0.48	0.44	0.44	0.42
2	0.49	0.47	0.52	0.52	0.53	0.49	0.49	0.45
3	0.70	0.67	0.80	0.71	0.70	0.68	0.72	0.61
4	0.83	0.85	0.95	0.91	0.79	0.81	0.85	0.77
5	0.91	0.89	0.98	1.06	0.94	0.89	0.94	0.85
6	0.85	0.87	0.96	0.99	1.00	0.97	0.94	0.90
7	0.82	0.87	0.93	0.96	0.92	0.94	0.95	0.88
8	0.83	0.88	0.93	0.98	0.92	0.89	0.92	0.85

TABLE 15.7
Pink Shrimp Size Class Abundance (in Millions) from Scenario Simulations: (A) 95Base; (B) D13R; (C) 95Base with Exploitation; and (D) D13R with Exploitation

(A)

Size class	**Year**							
mm	**1986**	**1987**	**1988**	**1989**	**1990**	**1991**	**1992**	**1993**
< 45	112.6	231.0	141.5	113.8	235.6	144.6	113.3	235.2
45–85	146.0	115.2	245.0	154.7	115.0	242.0	152.8	114.2
> 85	239.6	150.1	114.0	235.2	144.9	111.9	224.8	135.5

(B)

Size class	**Year**							
mm	**1986**	**1987**	**1988**	**1989**	**1990**	**1991**	**1992**	**1993**
< 45	100.4	186.8	98.6	102.6	184.4	92.7	103.6	186.1
45–85	93.1	105.4	196.6	104.5	104.1	197.7	106.6	107.6
> 85	204.7	112.2	105.7	198.1	108.2	107	193.3	103.7

(C)

Size class	**Year**							
mm	**1986**	**1987**	**1988**	**1989**	**1990**	**1991**	**1992**	**1993**
< 45	112.7	229.9	140.2	113.4	231.9	141.5	113.2	232.9
45–85	143.7	115.1	241.0	150.5	114.9	238.6	148.9	113.5
> 85	235.7	147.2	113.0	232.4	143.5	110.4	221.1	133.4

(D)

Size class	**Year**							
mm	**1986**	**1987**	**1988**	**1989**	**1990**	**1991**	**1992**	**1993**
< 45	109.2	212.6	120.1	110.8	210.4	116.4	110.8	215.8
45–85	122.0	112.1	219.3	126.5	110.6	218.2	126.3	111.7
> 85	214.2	119.9	109.0	210.9	120.3	104.4	196.8	111.2

The principal goal of our model development was to assess seatrout population risks associated with current and proposed water management alternatives for restoration of the south Florida ecosystem. In our analysis, we found that the proposed D13R strategy seemed to favor seatrout population production, resulting, on average, in bigger fish and more fish. In comparison, however, the D13R scenario did not result in substantially more freshwater reaching Biscayne Bay but did result in a different timing pattern of freshwater discharges as well as location of those deliveries (Table 15.1). In the physical circulation and mass transport model, these differences produced decreased average salinities (more favorable) over the middle portion of the bay. It also reduced the areal extent of hyper-saline waters (i.e., > 36.6 ppt).

Wind transport drives water circulation and hydrodynamic flows in Biscayne Bay, and thus wind effects dominated advective transports and thereby variability in recruitment observed in model runs (Ault et al., 1999b). To control for input variability, in model runs we purposely set all patches constituting a cohort for each specific population (i.e., seatrout and shrimp) to be equal in the numbers of initially recruiting animals and their respective population demographics. Thus, any differences in either abundance or growth between patches observed in later life stages of a given population were due strictly to environmental and ecosystem forcing.

We found that the spatial effects and responses in growth and mortality in a cohort were regulated by the explicit coupling of the biophysical environment and that these linkages resulted in seasonal variations in stock biomass. To that extent, an important physical variable driving population dynamics and production was variation in salinity fields caused by seasonal and interannual variations in rainfall, which directly and indirectly drove the extent and quality of suitable habitats and abundance dynamics of the prey. The D13R scenario resulted in increased areas of suitable habitats and promoted expansion of areas with higher fish growth rate potentials, because changes in freshwater regime expanded the range and duration of favorable salinity environments over favorable physical habitats for shrimp. These expanded salinity ranges were also more favorable for seatrout.

Comparing seatrout biomass variability between the scenarios (Figure 15.9), we noted differences in seatrout population dynamics that resulted from interannual variability that exceeded the maximum differences in these quantities observed between any of the scenarios. For example, the maximum difference in total seatrout stock biomass between the years of 1985 and 1993 under D13R ranged from 200,000 to 510,000 mt, a difference of 310,000 mt. On the other hand, the maximum difference between any two of the scenarios was only 230,000 mt because the difference between freshwater deliveries according to scenario differences was less than the differences observed due to climate variability. Probably the more important effects of the physical environment resulted from variations in wind-induced transport in the bay (Wang et al., 2002).

In model runs we found that variations in seatrout sizes-at-age (Tables 15.2 and 15.3) were consistent with those results reported from other field studies conducted in Florida (Tabb, 1961, 1966; Stewart, 1961; Moffett, 1961; Klima and Tabb, 1959; Maceina et al., 1987). Four out of five of these studies reported seatrout total lengths ranging from 144 to 163 mm for age-1, 228 to 267 mm for age-2, 290 to 373 mm for age-3, and 367 to 398 mm for age-4 fish. These reported size-at-age relationships closely matched the observed ranges from our model simulations (126 to 168 mm for age-1, 245 to 295 mm for age-2, 295 to 346 mm for age-3, and 314 to 406 mm for age-4 fish (Table 15.3)), covering all four scenarios. The reported field studies were conducted at different locations (i.e., on different populations) and also during different years.

Maceina et al. (1987) argued that discrepancies in back-calculated lengths among different studies may be due to several factors — including differences in annulus interpretation between scales and otoliths, different methodologies used to compute back-calculated lengths, size-selective gear biases — or to some combination of these factors. Since our simulations were conducted at the same virtual location and using the same methodology, all variations reported in this study resulted from year-to-year climate variations. Therefore, we feel strongly that variations observed from field studies may have been the result of climate variability. On the other hand, reductions in growth also resulted from physical environmental variability and from spatial mismatches of predators with prey density distributions. These reductions led to decreased survivorship that directly modulated the spread of size-at-age distributions. The upper end of the distribution is dominated by individuals that have found favorable environmental conditions for growth and survivorship over their lifetimes.

The magnitude of interannual variability appeared similar to the intracohort levels because all age groups experienced the same environmental conditions during a given year. The reality is that factors that force the predator–prey populations were principally habitat-based and reflected the habitat mosaic they experienced over their lifetimes, suggesting that small variations in the physical and biological environments resulted in relatively large variations in the growth of fish from the same spawning date. Traditional quantitative approaches to virtual cohort analysis assume that factors affecting an age-structured population in equilibrium are the same as those that a single cohort experiences over a lifetime (see Ricker, 1975). However, when directly coupled to a biophysical environment, our results show that this assumption is fatuous because of the dynamic nature of growth when linked to temporal variation in environmental features. Interannual variation in the environment, and thus habitat quality and spatial growth rate potential, produced wide variations in cohort growth, survivorship, and abundance.

Our results also indicated substantial variation in natural mortality rates among years, ages, and scenarios. In the 95Base scenario, natural mortality was greater for all sizes of seatrout because of lower biophysical habitat quality, which lead to smaller fish sizes at age. More favorable environmental conditions for seatrout in the D13R scenario produced significantly lower natural mortality rates, particularly for large (i.e., age 3+) seatrout. Differences between scenarios were attributed to availability of higher quality habitat, despite generally lower prey availability. This suggests that seatrout experienced lower metabolic demands under D13R, were larger at age, and had reduced natural mortality rates. The addition of exploitation on seatrout resources obviously reduced their abundance and biomass but, in general, appeared to increase the average size of individuals at age. This could be viewed as a density-dependent compensatory response that allowed more food per capita, which was particularly true for age-2 fish. However, density dependence decreased with age because fish spread out over the seascape. Fishing also reduced the variability between scenarios, suggesting that variation was in some ways proportional to population size.

The proposed D13R water management scenario was designed to reduce seasonal effects of rainfall; more water collected over the landscape during wet seasons would be subsequently stored and discharged with a delay to the coastal bays. South Florida experiences about 150 cm of rainfall per year, with a strong seasonal component between wet and dry seasons. About 75% of the annual rainfall occurs during the wet season (June to November).

This chapter focused on modeling efforts on seatrout because of broad interest in the important ecological and fishery resource and because of the focus of this book. While the D13R scenario produced larger and more abundant seatrout, as a management strategy it may be unwise generally to consider this optimal for the broader range of important fisheries in the coastal marine waters of south Florida, given the apparent biological and socioeconomic tradeoffs in the ecosystem. Such a strategy is fine for maintaining longer hydroperiods over the vast expanses of the Everglades; however, it may deleteriously compromise a host of ecologically and economically important juvenile coral reef and coastal fishes (or stenohaline organisms) because of extended individual physiological stresses on these recruiting fishes and the ultimate reductions of valuable populations of mature adults occupying the coral reefs of the Florida Keys.

On the other hand, water stored for greater periods of time and delivered through sheet flows under the D13R scenario may be higher quality and bear a reduced load of nutrients and pollutants, a condition that could have ecological benefits extending through the coral reef system. Due to the broad interconnections in the south Florida ecosystem that extend from the land to the coastal bays to the coral reefs (see Bohnsack and Ault, 1996; Ault and Luo, 1998; Ault et al., 2001a, b; Lindeman et al., 2000), clearly some extended thought must be given to more comprehensive risk analyses that include a broader range of community effects than those that focus somewhat myopically on coastal bay resources. These analyses must also factor in the explosive regional human population growth and its effects on growth of the fishing fleets and exploitation pressures, particularly for those resources already serially overfished (Ault et al., 1997, 1998, 2001a, b); these extensive human uses will continue to place extraordinary demands on the ecosystem and its performance.

Further development of the evolving class of models presented here and elsewhere (e.g., Rothschild and Ault, 1996; Luo et al., 1996; Giske et al., 2001; Werner et al., 2001; Meester et al., 2001) will require improved population-dynamic and bioenergetic parameters covering the breadth of the trophodynamic community representative of the principal ecosystem components. To estimate model parameters in this study, we used relatively precise data from our fishery-independent field surveys (Ault et al., 1999b) and information from published literature on pink shrimp and spotted seatrout or related species (such as weakfish, *Cynoscion regalis*) when data for the target species were not available. We also believe that further testing of model sensitivity is warranted. For example, it will be important to spread out the introduction of recruit patches during the year, since intra-annual variations in physical conditions produced substantial variations in cohort strengths. As a result, the predicted outputs presented here are not intended to necessarily represent realistic spotted seatrout–pink shrimp community dynamics *per se*, but are representative of the kinds of dynamics a predator–prey community with these demographic and behavioral characteristics would be expected to display in coupled physical and biological environments. Better predictions of predator and prey spatial and temporal dynamics will require more precise demographic, bioenergetic, and movement data that facilitate a deeper understanding of inter- and intraspecific relationships.

Our model undoubtedly has other potential basic science and management applications. A number of possibilities exist for linking our numerical model into other regional hydrodynamic circulation models and coupling these to a broader biophysical model domain to incorporate the biological interconnectedness of inshore coastal lagoonal bays with the offshore Florida Keys coral reef tract. For example, linking our model to potential climate change scenarios could facilitate study and improve understanding of the dynamic linkages between water management, the coastal bay bait-shrimp fishery, and impacts on habitats, fish community dynamics and production, and commercial food shrimp production in the Keys and Dry Tortugas region. Our biophysical model can also be used to assess the ecological consequences of specific spatial management actions like use of marine protected areas in meeting resource performance goals.

In the long run, our model's utility will be enhanced through a systems science approach that integrates empirical field and laboratory study with monitoring and analytical modeling efforts in a rigorous quantitative framework. This approach will likely provide the basis for more precise and accurate data and improved mechanistic models that fully represent ecosystem structure, function, and dynamics and that support management efforts to build sustainable fisheries and conserve marine biodiversity.

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16 Spotted Seatrout as a Potential Indicator of Estuarine Conditions

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CONTENTS

INTRODUCTION

This book began with a premise: a summary of our knowledge and understanding of the basic life history and biological features of the spotted seatrout would aid in any decision or attempt to use its life history parameters to evaluate estuarine conditions. Before we evaluate this species' potential to serve in such a manner, it is appropriate to consider the features of estuaries that would optimally be evaluated by life history parameters.

ATTRIBUTES OF ESTUARINE INDICATORS

Estuaries (as well as inshore bays, lagoons, and bayous) are subject to a wide variety of varying environmental conditions that are either natural or anthropogenic (Day et al., 1989). Important to understanding the arguments here is to appreciate that estuaries can vary spatially and temporally, each at different scales. Each estuary varies spatially relative to the location, intensity, and duration of various inputs such as storm water runoff, point discharges, and normal freshwater–saltwater exchanges (Estevez, 2000). Temporally, the scale of variation is expansive from minutes to centuries (and beyond). It is incumbent on those who would monitor estuarine systems using a biological indicator (such as the life history parameters of a fish species) to be mindful of the extent, duration, frequency, and scale of the variation of estuarine features. Thus, when preparing to monitor estuarine conditions, we must first assert our intent of comparing differences between estuaries (spatial) or trends over time within estuaries (temporal).

Indicator organisms should possess certain attributes that lend them to the purpose of using life history features to evaluate differences between estuaries. Ideally, one would look for broadly distributed species occurring in several estuaries that are genetically similar between estuaries and regions; they should necessarily display little genetic commingling between estuaries with other populations. This helps insure that differences observed are not due to differences in genotypically mediated responses. Additionally, their life history features should show little association with

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changes in latitude, because variation in life history parameters should be independent of latitude *per se*. Biological response variables should reflect environmental differences between estuaries, but they must be clearly ascribable to environmental characters such as temperature and amount of daylight. Concomitantly, a species should show consistent responses for several characters and the responses for each variable should be consistent for similar environmental conditions.

When using species' life history traits to evaluate trends within an estuary, our quest is to determine if differences in environmental conditions are responsible for (or at least associated with) the observed biological response differences. Therefore, we also should require reasonable genetic isolation from other estuarine populations. Interestuarine comparisons help assure that observed changes are not unduly influenced by differences induced by genetic differentiation. There should be genetic homogeneity with the intraestuarine population regardless of whether the species broadly distributes its gametes or retains clutches for a high degree of parental care. Comparisons of changes within the system could be spatial (i.e., the impact of localized perturbations) or temporal (i.e., time-based trends reflecting additive disturbance impacts). In either case, because estuaries are spatially and temporally variable, it is important that the scale of biological response should match the scale of environmental disturbance. Moreover, the response that we wish to evaluate should not be influenced by natural-scale biological responses.

In looking for spatial differences within an estuarine system, the ideal species would be broadly distributed within the estuary, but individuals would show little dispersal and movement within the system. To determine if microhabitat features are associated with observed biological responses, adults (once settled) ideally should remain in reasonable proximity to the initial settling site. Spatially, for example, a suspected point source of nutrients that results in higher primary productivity and secondary productivity could be demonstrably detected by higher growth rates in the consumers. Salinities are usually spatially associated in an estuary because higher salinities are usually located proximate to the sea entrance and lower salinities are proximate to the freshwater input. If consumers' growth rates are influenced more by salinity than nutrient impacts, then comparing growth rates in the consumers from different salinity regimes within an estuary would not be likely to detect the impact of the suspected nutrient point-source.

In a temporally directed investigation, a gradual increase in nutrient load due to a generalized, nonpoint source (in keeping with our trophic example) may not be detected if the cumulative impacts of the changed trophodynamics are examined for only a season. It may take several years for the growth parameters of the consumer to reflect the energy-transfer alteration.

In summary, it is essential that any assessment of estuarine conditions be based on species with genetic and ecological features that do not void certain assumptions upon which the evaluation is based. Below we use spotted seatrout attributes to effectively evaluate estuarine conditions and trends, with consideration given to overall biological features as well as the specific life history attributes elucidated in this volume.

ATTRIBUTES OF SPOTTED SEATROUT AS ESTUARINE INDICATORS

Spotted seatrout have attributes that serve to compare conditions between estuaries. The genetic studies offered here, coupled with referenced studies on migration, indicate a strong, estuarine-based residential habit. This is tempered with additional information that indicates little within-region genetic differentiation of populations. Apparently, gene flow is sufficient to counter interestuarine differentiation. Between zoogeographic regions, the value of accepting a premise of reasonably similar genetic stock structure becomes more suspect. The utility of using spotted seatrout parameters within an estuary is potentially meaningful because of limited movement between estuaries. This suffices for assumptions needed for within-estuary trend speculation relative to temporal influences. However, evidence presented in this volume indicates considerable daily and seasonal movements of spotted seatrout within an estuary. Thus, the usefulness of spotted seatrout in evaluating within-estuary spatial impacts of altered environmental conditions is diminished.

Currently available age and growth data for the species are substantial and have the potential to provide a basis for interestuary comparisons. There is evidence that some correction or compensation may have to be offered to accommodate clinal temperature or day length effects on growth. The usefulness of age and growth data may therefore be better realized when comparing attributes of fish between estuaries of similar latitude (i.e., along the northern Gulf of Mexico). Nevertheless, longitudinally ordered estuaries that are proximate and at least within similar zoogeographic regions may be compared using the age and growth responses of spotted seatrout.

A caveat indicated by the authors here is that comparisons using age and growth data should be based on fish with demonstrably similar age- and size-specific fishing mortality. In some situations careful inspection may determine that data gathered from sampling methods that differ in selective fishing mortality (i.e., catchability) may be used, but it is necessary to qualify such data.

Data on the reproductive aspects of spotted seatrout have the potential to allow comparisons between estuaries. As noted, substantial differences often exist in reproductive parameters between populations of spotted seatrout within various parts of its range. As with comparisons based on age and growth, a potential bias could be introduced by using different sampling techniques to obtain specimens. Reproductive information could serve to compare estuarine conditions within zoogeographic regions, especially within a single year, while comparisons based on age and growth data may be useful in examining long-term conditions between estuaries.

Time-based trends in estuarine conditions lend themselves to utilizing both age and growth and reproductive data. Again, selective capture could negate these study results, but time series of data could readily serve as an indicator on long-term trends in estuarine conditions.

Especially important when using biological information from a single species to evaluate environmental conditions is the consideration that must be given to acclimation to local conditions. Information presented indicates that we are beginning to understand the significance of environmental acclimation on life-history parameters such as distribution, abundance, growth, and mortality. This effect must be understood in order to explain observed differences in the biological responses.

Intensity and incidences of parasitism and disease have been used by fisheries scientists to help establish stock limits for some species. Because of their restricted interestuarine movements, spotted seatrout may be able to serve as one of the premier examples as to how useful this biological feature can be to delineate zoogeographic regions and intraregional relationships.

The two modeling studies in this volume present very different but complementary approaches to using spotted seatrout to indicate estuarine conditions between estuaries or time-based trends within estuaries. The Habitat Suitability Index model can serve to determine if there has been an appreciable alteration in suitable habitat for spotted seatrout, which will go far in assessing trends in declining habitat conditions of a general nature. Importantly, this model may effectively indicate the success of estuarine restoration efforts. The Spatial Ecosystem model incorporates the trophic relationships of spotted seatrout and should prove useful in examining ecosystem structure alterations that could be influenced by broad-based changes in estuarine physical conditions or impacts induced by fishing activities. This model should prove useful in assessing impacts of "estuary specific fishery management plans" — something called for by several authors here.

FUTURE RESEARCH NEEDS

As a result of the effort to compile and summarize biological information on the spotted seatrout, the potential to use its life history parameters to help evaluate interestuarine conditions spatially and intraestuarine conditions temporally is evident. The adage that "more data are needed" is easily offered, but some careful delineations must be added before the use of spotted seatrout as an estuarine condition monitor can be realized. First, a better understanding of the exact degree of genetic isolation and exchange should be established for within- and between-estuary examinations. More exact elucidation of genetic exchange may even permit inter-regional comparisons, as well. Age and growth studies have the potential to serve as the most widely applicable life history feature for these purposes because substantial historical data on these characters are available. With these (and all other variables), it is essential that common methods should be adopted to enable comparable data for specific analyses. Also important, as a part of methods, is the recognition that differences in sampling methods can render the comparability of these data useless. Therefore, an effort needs to be made to gather specimens via methods that have the same selectivity features relative to the measured parameter.

The arguments for age and growth are mirrored for using reproductively based life history features to facilitate estuarine condition evaluations. Differences in sampling methodology and measurement abound among previously conducted studies. Future research efforts should aim toward methodological consistency as well as refinement toward a set of variables that can be accurately and precisely measured.

Perhaps the least well documented of any of the life history features of spotted seatrout is habitat utilization. This may be due, in part, to their quite variable habitat preference. It could be due to minor (but significant) changes in local conditions and behavioral preference. It could also be due to our inability as scientists to measure habitat preferences accurately. Nevertheless, accurately determining microhabitat preference, in the sense of biotope choice, may remain a difficult task. More useful, however, is the potential of specific habitat preference to major variables such as salinity, temperature, and substrate type. Additional studies are needed at the adult stage, as well as a refinement of the data currently available on the juvenile life stage, to make habitat preference studies more exacting and, therefore, useful for estuarine monitoring.

Long-term changes in spotted seatrout parasite faunal attributes have not been assessed but clearly have potential to be extremely useful as a time-series monitor of local conditions. A greater effort directed toward a more rigorously established sampling schedule to obtain parasite and disease information on spotted seatrout throughout its range and over time should prove fruitful in assessing larger scale estuarine conditions.

The modeling studies offered here demonstrate a viable direction for the future of using the biological aspects of species to serve as environmental monitors. Most environmental modelers currently use parameters based on an amalgamation of studies that are not estuary specific. The accumulation of inter- and intraestuarine, species-specific data has enormous utility in serving to detect significant environmental effects. Perhaps more important is the ability to make projections of estuarine conditions on anticipated changes in life history parameters. On the other hand, they could be used to set limits or levels for biological parameters in order to achieve a desired estuarine condition. Setting and achieving these limits or levels is the job of the fisheries resource manager. Thus, whether it is deemed a species problem or a habitat problem, effective management of our estuaries will require input and expertise from a variety of fields.

In total, our present examination of spotted seatrout biology is incomplete; it may never be complete. However, the effort points to a direction for future studies and the valuable utility that such information may have on the large-scale issue of estuarine condition assessment. Caring for our natural resources requires constant vigilance. The task at hand is to develop effective and reliable tools with which to conduct the vigil. Making use of the biological features of indigenous fauna to conduct assessments can be a reliable and meaningful tool.

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