



Fish communities of estuarine salt marshes of eastern North America, and comparisons with temperate estuaries of other continents

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Contents

Abstract	page 281
Introduction	282
Materials and methods	283
Salt marshes	
Geographic regions covered	
Findings and discussion	286
Estuarine salt marsh fishes from eastern North America	
Life history patterns of salt marsh fishes	
Cape Cod as a zoogeographic boundary	
The Florida peninsula as a zoogeographic boundary	
Seasonal patterns of abundance and diversity	
Times of reproduction	
Temperature and salinity relationships	
Temperature x salinity, and other environmental interactions	
Nonindigenous species in salt marshes	
Profile of estuarine salt marsh resident fishes – eastern North America	
Fishes of estuaries of western Europe	
Fishes common to estuaries of eastern North America and western Europe	
Comparisons of life history groupings among continents	
Fish families common to estuaries on four continents	
Applications	
Summary/Conclusions	317
Acknowledgements	318
References	319

Key words: estuarine fishes, life history characteristics, nonindigenous species, salinity and temperature tolerances

Abstract

Twenty eastern North American estuarine/salt marsh locations, for which published inventories of inhabiting fishes were available, were selected for study. The geographic range of systems extended from south Texas on the west; North River, FL. on the south; to Prince Edward Island, Canada on the east; and James and Hudson Bays, Canada at the north. A total of 237(±) species of fishes were associated with these systems. Life history groupings included: permanent residents (9.3%); marine nursery species (17.7%); diadromous fishes (5.5%); marine transients (52.3%); and freshwater transients (15.2%). The most widely distributed species were primarily permanent residents and marine nursery species. The fraction of resident species did not vary significantly over the latitudinal range, but the fraction of marine migratory (MN + MT) species decreased with latitude. An increasing fraction of diadromous (anadromous) species may compensate for the decreasing fraction of marine migratory species. Permanent residents, marine nursery species, and marine transients all showed extended periods of spawn-

ing. Permanent resident species showed the widest ranges of ambient salinity tolerances or of ambient salinity ranges of occupied habitats, with marine nursery species second. Patterns with respect to ambient temperature tolerances were associated with geographic ranges rather than life history groups. A general profile was produced of characteristics of species that live as permanent residents in salt marsh estuaries of eastern North America.

Species and family relationships of fishes from a group of 17 and another of 25 estuaries located along the west coast of Europe were compared with the eastern North American group. European estuaries showed higher species richness per system than did those of eastern North America. Family representations of eastern North American and western European estuaries were compared with a series of estuaries located in southwestern Australia and South Africa. This showed significant overlap in family representation, with two species being common among the four continents.

Introduction

Considerable attention has been given to estuarine fish communities. These faunas consist of mixtures of: permanent residents (PR); developmental stages of marine (SW) fishes that spend varying amounts of time in these habitats taking advantage of inherent resources and conditions (marine nursery, MN); diadromous fish species (D) that move through those systems that are associated with rivers, some individuals spending appreciable amounts of time in the estuary, in some cases as adults as well as in developmental stages; a diversity of young and/or adults of marine species (marine transients, MT) that are not developmentally tied to estuaries as nursery grounds, but enter especially during periods of low rainfall when salinities are approximately those of SW, or during periods when nearshore waters are rapidly cooling; and young and adults of freshwater (FW) species, generally in small numbers, frequently during periods when salinities are reduced by rainfall (freshwater transients, FT). The occurrence of various fish species in estuarine systems varies throughout the year following features of local climate and weather, and spawning and development patterns of the regional fish fauna. This heterogeneous aggregation of fishes that inhabit such fluctuating but highly productive (Odum, 1980) environments has received attention from scientists interested in many kinds of biological questions, especially from fisheries scientists whose interests are stimulated by the large number of commercially important marine species that are ontogenetically associated with estuarine environments (Gunter, 1967; Blaber, 1997; Elliott and Hemingway, 2002). However, it has been pointed out that marine fishes generally found in temperate estuarine waters are also frequently found to develop successfully in adjacent marine waters. While many of these species

may benefit from their sojourn in estuaries, they would survive in the absence of estuaries, so they are not totally limited to developing in such areas. The term "estuarine opportunist" has been substituted by some authors to describe the estuarine relationship of species that are not strictly limited to an estuarine habitation at some point in the life cycle (Lenanton and Potter, 1987).

The purposes of this review are: to further evaluate the fish faunas of estuarine salt marsh systems over a wide latitudinal range, focused on the temperate zone of the east coast of North America; to determine the distributions in such estuarine/salt marsh systems of those species over the selected latitudinal range; to evaluate the extent to which each is tied to those systems in its life cycle; and to elucidate behavioral, ecological, and physiological characteristics of the principal species of fishes occupying such estuarine/salt marsh habitats in an effort to better understand how those fishes are equipped to utilize such potentially stressful habitats. Secondly, the faunas of eastern North American estuarine salt marshes will be compared with those of analogous systems in other temperate regions of the world, especially of western Europe.

Selected for present analyses are a series of estuarine systems located along the coast of eastern North America, ranging from south Texas and south Florida, northward to James and Hudson Bays, limiting analyses primarily to systems or those portions of estuarine systems that were identified as including salt marshes. Using existing literature, fish species known to use these environments were identified, defining when and how each used the estuarine salt marsh. Information was synthesized on spawning patterns and on physiological capabilities with respect to variations in ambient temperature and salinity of the principal species of fishes occupying those systems.

Behavioral, ecological, and physiological patterns of species that showed an estuarine dependence (PR and MN species) were compared with those of transient species (MT, FT, and D species) that occurred in those estuarine marshes. The question was asked whether estuarine-dependent species responded differently to environmental variations than did the transient species because of differences in physiological capabilities and/or differences in life history patterns. Finally, a “profile” of the characteristics of estuarine permanent resident species was produced.

A number of comprehensive works have evaluated estuarine biotas, frequently with emphasis on the fishes, but also have considered aspects of dynamics of environmental and biotic interactions in such systems (e.g., Kinne, 1963, 1964, 1966, 1967; McHugh, 1967; Haedrich, 1983; Potter et al., 1990; Kneib, 1997; Blaber, 1997, 2000; Whitfield, 1999; Mathieson et al., 2000; Elliott and Hemingway, 2002). A significant problem in drawing generalizations in such systems has been the multiple definitions of an estuary. The need for a precise definition, one that will also allow for consistent classification of estuarine systems was stressed by Elliott and McLusky (2002), who pointed out the existing difficulties of communication among individuals and groups involved in estuarine management. The definition that was followed here was: “An estuary is a partially enclosed coastal body of water which is either permanently or periodically open to the sea, and within which there is a measurable variation of salinity due to the mixture of sea water with fresh water derived from land drainage” (Day, 1980, as modified from Pritchard, 1967). A further limitation was imposed, restricting, where possible, the portions of estuarine systems evaluated to those referred to as estuarine salt marshes or salt marshes.

Both riverine estuaries and those developed where the freshwater discharge emanates from nonpoint overland flow and/or seepage into a semi-enclosed coastal basin show gradients of physical and chemical features, especially of salinity. Accompanying or influenced by such gradients are biological features including those of resident aquatic and terrestrial vegetation. Numerous studies have analyzed estuarine systems from the standpoint of vegetation (e.g., Jackson, 1952; Kurz and Wagner, 1957; Chapman, 1960; Pool et al., 1977; Odum, 1980). Estuarine habitats of particular interest in this paper, estuarine salt marshes, are generally defined on the basis of supported vegetation. Those usually develop in shal-

lower areas of estuaries where ambient temperatures and salinities tend to be most variable (Durako et al., 1985). While salt marshes are not uniform with respect to plant species composition, or to physical or chemical features, that more restrictive habitat description allowed focusing on areas with more common features, while excluding others. Characteristics of fish biotas of North American estuarine salt marshes were compared with those of western Europe with respect to species and of families reported, numbers, distributions, and life history categories (“ecological guilds”). Finally, fish faunas in estuaries of eastern North America and western Europe were compared with those of temperate regions of South Africa and Australia.

Materials and methods

Salt marshes

Salt marshes were defined (Penfound, 1952) as sedge-grass-rush communities of brackish habitats, with typifying plant genera including *Spartina*, *Distichlis*, *Juncus*, and *Sporobolus*, although other genera may be found in such habitats. Salt marshes develop along margins of estuaries where wave energy is low (Durako et al., 1985). Principal species composing floras of salt marshes along the Atlantic and Gulf coasts of North America, in addition to grasses, sedges and rushes, include mangroves along the coasts of Texas, Louisiana, Mississippi, and southern portions of the Florida peninsula (Carlton, 1975). Plant zonation in salt marshes is mainly controlled by tidal amplitude and salinity, interacting with composition of the substratum, soil chemistry, temperature, and freshwater inflow, as well as other factors (Durako et al., 1985). In areas climatically compatible with mangrove growth, those species generally intergrade with or replace typical salt marsh vegetation. Some of the typical salt marsh species, especially *J. roemerianus* (black rush or needle rush), function as colonizers of open habitats, being replaced by mangroves, where they occur, in plant succession (Eleuterius, 1976). While the distributional limits of the three principal species of mangroves (*Avicennia germinans*, *Laguncularia racemosa*, and *Rhizophora mangle* – black, white, and red mangrove, respectively) extend northward along the western coast of the Gulf and more than half the distance along both coasts of the Florida peninsula, those species are regularly killed back in

northern portions of their ranges in colder winters (Carlton, 1975).

Historically, *J. roemerianus*, a principal salt marsh species, was distributed from areas along the Mexican coast and coasts of Caribbean islands, northward to Connecticut, but was most prevalent, generally in bands, along the south Atlantic and Gulf coasts of the eastern United States, between 25° and 42°N latitude (Eleuterius, 1976). Salt marsh systems were somewhat discontinuous along the coasts of the Gulf of Mexico and the north Atlantic of North America, with most of the salt marsh area of the Gulf coast along the Mississippi River delta. There was relatively little salt marsh vegetation associated with the lagoons and estuaries of the Florida panhandle. Areal extent of such systems has been greatly reduced by human activities in recent time (Eleuterius, 1976; Durako et al., 1985). Along the east coast of Florida, tidal marshes are dominated by *S. alterniflora* (smooth cord grass) and, as was previously mentioned, in the southern part of the Florida peninsula where the coastal systems are dominated by mangroves, the predominant salt marsh species is *J. roemerianus* (Durako et al., 1985). Significant areas of salt marsh are found along the Atlantic coast of North America actually as far north as the coast of Maine, and the Nova Scotia and New Brunswick coasts of the Bay of Fundy (Cranford et al., 1987; Jacobson et al., 1987).

Geographic regions covered

Data incorporated into this review were taken from publications containing lists of fishes collected in estuaries (a few of which, as will be noted, did not include salt marshes; however, the overall range of ambient salinities in those collections was generally similar to other locations – FW to ≥ 25) of coastal eastern North America. Those ranged (following Briggs, 1974) from subtropical/tropical (a south Florida location) to Arctic regions (James and Hudson Bays), and primarily focused on ichthyofaunas of the pools and channels of salt marsh portions of estuarine systems. In all, data from 20 North American locations were included in the analyses with two or more collecting sites combined in some cases: Texas, 1; Louisiana, 1; Florida, 5; Georgia, 1; South Carolina, 1 (composite of 2); North Carolina, 1; Virginia, 2; New Jersey, 1; Connecticut, 1; Massachusetts, 2; Rhode Island, 1; Maine, 1; Prince Edward Island, 1; and James and Hudson Bays, 1 (several sites combined). The sites ranged latitudinally from 25°20'N (south Florida) to

58°30'N (Hudson Bay). The range of longitude of included estuarine systems was from Prince Edward Island, ca. 62–65°W, to the Texas location, ca. 97°W, a significant range in east-west distance as well as in north-south distance. Details of specific locations, environmental conditions, numbers of families represented at each station, and authors of works cited are found in Table 1. The inclusion of a large number (5) of sites in Florida was based primarily on questions of possible differences between the fish fauna of the subtropical/tropical zoogeographical region of south Florida and the warm temperate areas to the north along both coasts of the Florida peninsula. The southern tip of the Florida peninsula has extensive mangrove systems and limited salt marsh development, so may act as a barrier to interchanges of fishes between warm temperate regions to the north on the Gulf and Atlantic coasts of the Florida peninsula (Reid, 1954; Briggs, 1974).

Only one of the 20 locations included an extensive development of mangrove in conjunction with salt marsh, that of North River, FL (Odum and Heald, 1972). Locations to the west around the Gulf of Mexico were from salt marshes, with the exception of the Texas location. Locations along the east coast of the Florida peninsula and northward to Maine were primarily in salt marshes, with most in riverine tidal areas that supported salt marshes. The two most northern locations, Prince Edward Island, and James and Hudson Bays did not include salt marshes.

Estuarine systems evaluated from the west coast of Europe were located in three biogeographical regions: Baltic/Skagerrak, Boreal, and Mediterranean (Pihl et al., 2002). At least 15 of those 25 systems were noted to include some area of salt marsh.

Published information was incorporated, as available, on species presence; stage of maturity of individuals present; time of year found to be present; duration of stay; season, temperature, and salinity of spawning locations; ambient salinities and temperatures encountered in the salt marsh system (referred to as occupancies); and/or known salinity and thermal tolerance limits of various life history stages of those species as measured under controlled conditions.

Life history categories of species were developed using background from previous works (e.g., Haedrich, 1983; Dando, 1984; Wallace et al., 1984; Kneib, 1997; Collette and Klein-MacPhee, 2002), following general categories of McHugh (1967), with the modification that adventitious visitors were split as either FW or SW transient species. Resulting category design-

Table 1. Locations, chemical and physical features, numbers of families and species of Eastern North American estuaries

Location	Latitude	Disch. to	Salinity Range	Temp. Range °C	Human Alter.	No. of Fam.	No. of Sp.	Source/s
Port Aransas, Texas (TX)	ca. 27°45'–28°15'N	Gulf of Mexico	9.1–31.5 Mo. means	13.41–29.86 Mo. Means	No	27	53	Gunter, 1945
Barataria Basin, Louisiana* (LA)	ca. 29°12'–29°29'N	Gulf of Mexico	4–28	16–34 spr., sum.	Yes	26	42	Rakocinski et al., 1992
St. Marks, FL* (SM)	ca. 30°07'N	Gulf of Mexico	3.9–29.0	11–36	No	18	26	Subrahmanyam and Drake, 1975
Cedar Key, FL* (CK)	29°10'N	Gulf of Mexico	<0.5–38	7–38	No	21	42	Kilby, 1955; Nordlie, 2000a
Tampa Bay, FL* (TB)	27°32'–28°00'N	Gulf of Mexico	3.2–35.1	10.0–38.2	Yes	30	59	Springer and Woodburn, 1960
North River, FL** (NR)	25°20'N	Whitewater Bay to Gulf of Mexico Adjacent areas in Everglades	FW-29	No data 6–7 – 35–37	Yes	30	57	Odum, 1971 Loftus and Kushlan, 1987
Indian River Lagoon, [#] and adjacent waters, FL	26°58'–29°05'N	Atlantic Ocean	0.15–42	11.0–37.9	Yes		609 (704)	Gilmore, 1977
Indian River, FL,* Impoundments (IR)	27°35'–27°36'N	Indian River to Atlantic Ocean	2–200 closed 25–38 open	13.5–34	Yes	20	44	Gilmore et al., 1982
Georgia,* Sapelo-St. Catherines (GA)	31°30'–31°43'N	Atlantic Ocean	0.0–34.0	3.5–31.7	Yes	43	86	Dahlberg, 1972
South Carolina, Edisto*	32°35'N	Atlantic Ocean	26–33	15–36	No	22	33	Crabtree and Dean, 1982
South Carolina, Bozuz* (SC–B & E combined)	33°20'N	Atlantic Ocean	25–34	7–25	No	26	43	Shenker and Dean, 1979
North Carolina,* Cape Fear (NC)	33°49'–34°13'N	Atlantic Ocean	1.7–24.9	17.4–21.1	No	38(24)	80(50)	Weinstein et al., 1980
Virginia, 6 rivers (VC)	36°50'–39°05'N	6 rivers tributary to Chesapeake Bay	FW → 14	No data	No	17	26	Massman, 1954; Dovel, 1967
Virginia, Eastern shore (VE)	37°05'–38°00'N	Eastern Shore of Delmarva peninsula	9.28–32.64	<4–31.5	No	13	20	Richards and Castagna, 1970
New Jersey* Marsh creeks (NJ)	ca. 39°35'N	Atlantic Ocean	23–33	8.0–28.0	No	41	61	Rountree and Able, 1992
Connecticut, Mystic River (CN)	41°20'–41°24'N	Mystic river estuary	3–30	0.8–25	No	37	51	Pearcy and Richards, 1962
Massachusetts* Slocum River (MS)	ca. 41°30'N	Buzzards Bay to Atlantic Ocean	1–36	0–25	Yes	38(35)	54(47)	Hoff and Ibara, 1977
Massachusetts* Waquoit Bay (MW)	41°32'N	Vineyard Sound to Atlantic Ocean	No data	–1–30, Mean 13.9	Yes	31	49	Ayvazian et al., 1992
Rhode Island,* Bissel Cove (RI)	ca. 41°33'N	Narragansett Bay to Atlantic Ocean	16–23	>0–30.5	Yes	14	19	Nixon and Oviatt, 1973
Maine* Wells Harbor (MH)	43°22'N	Atlantic Ocean	No data	0–26 Mean 11.4	Yes	16	24	Ayvazian et al., 1992
Prince Edward Island (PE)	46°00'–46°30'N	Gulf of St. Lawrence	0–29.5	0–22	No	16	22	Johnston and Morse, 1988
James-Hudson Bay (JH)	52°00'–58°30'N	Atlantic Ocean by Hudson Straits	0–25	<0–? Ice breakup May 1–June 20	Yes	16(14)	38(29)	Morin et al., 1980

*Salt Marsh Systems; **Primarily Mangrove; [#]For Reference.

Note: Human alteration indicates whether there was mention of such in the references cited.

nations were: (1) estuarine permanent residents (PR); (2) marine nursery species (MN, including species that spawn in estuaries but do not reside there); (3) diadromous species (D, Myers, 1949; McDowall, 1987, 1997); (4) saltwater transients (MT); and (5) freshwater transients (FT). In attempting to assign each species to one of these life history categories, classifications given by authors of works on the selected locations were noted, as well as was information from others (McLane, 1955; Hellier, 1967; McHugh, 1967; Ager, 1971; Dahlberg and Conyers, 1973; Swift et al., 1977; Worgan and FitzGerald, 1981; Haedrich, 1983; Dando, 1984; Peebles and Flannery, 1992; Kneib, 1997; Collette and Klein-MacPhee, 2002). Where there was serious disagreement among authors regarding the nature of estuarine use by a particular species, that was indicated in Table 2, and disparities were also discussed in the narrative. In cases where two values were cited for numbers of species and families from a particular estuarine system, generally because certain stations were not considered to be in a salt marsh, the lesser values were used in making calculations of representation by life history categories in those systems. Questions of nomenclature were resolved using appropriate works (Robins et al., 1991; Nelson, 1994; Eschmeyer, 1998). Salinities are expressed using the Practical Salinity Scale, and are therefore presented as dimensionless numbers.

Findings and discussion

Estuarine salt marsh fishes from eastern North America

The western-most of the selected series of 20 North American estuarine locations, near Port Aransas, TX on the Gulf of Mexico (ca. 97°W long.), did not include a salt marsh (Gunter, 1945). A total of 53 species of fishes representing 27 families was reported in that study. Other locations on the Gulf of Mexico included Barataria Basin, LA (Rakocinski et al., 1992), St. Marks, FL (Subrahmanyam and Drake, 1975), Cedar Key, FL (Kilby, 1955; Nordlie, 2000a), and Tampa Bay, FL (Springer and Woodburn, 1960). All of those included extensive areas of salt marsh (those locations for which fishes were included for Tampa Bay were from salt marsh areas). The largest number of species of fishes was reported from the Tampa Bay area, 59, representing 30 families, and

the fewest species among this group of estuaries was reported from St. Marks, 26, representing 18 families.

The one subtropical/tropical system included was the North River on the southwest tip of the Florida peninsula. Upper reaches of the North River were of marsh, largely vegetated by *J. roemarianus* with mangrove downstream from there to the coast (Odum, 1971; Odum and Heald, 1972). Salinities in the headwater in that system varied from 25 in dry years to FW from mid June to late fall in rainy years, with salinities at the mouth ranging from 27 to 29 during dry months of April and May, to FW in wet months. That fish fauna was very similar to those of more typical salt marsh stations to the north on both Florida coasts, and consisted of 57 species of fishes belonging to 30 families (Odum and Heald, 1972), none of the families being unique to that location. There were only two typically FW families represented in those collections, Centrarchidae and Lepisosteidae, and a total of only seven typically FW species. *Fundulus similis* was not present in collections from North River, although the species was reported from adjacent areas (Kilby and Caldwell, 1955; Loftus and Kushlan, 1987), and so was included here for the region.

The only estuarine location included from the east coast of Florida was that of impoundments associated with the Indian River system (a tidal river), from which a total of 44 species of fishes representing 20 families was reported (Gilmore et al., 1982).

The largest number of species reported taken at any of the 20 estuarine locations was from Georgia, in the region of Sapelo Island (Dahlberg, 1972), with 86 species representing 43 families taken from salt marsh waters. Actually, a total of 136 species was reported in that study that included collections from nine different habitats ranging from a beach station to a FW creek, but the species from only four of those habitats (high marsh, middle and upper reaches of the estuary, tidal canal, and low salinity tidal pools) were included here. Salinities in those areas ranged from 0.4 to >30.

Data from three separate studies were combined in evaluating fishes of South Carolina salt marshes. Those included a study of the Edisto River marshes (Crabtree and Dean, 1982), and two evaluations of the Bozuz marshes (Shenker and Dean, 1979; Bozeman and Dean, 1980). Data for the Edisto and Bozuz systems were given separately and in combination, with totals of 43 species representing 26 families for the two areas combined.

Collections that yielded the second highest number of species were from the Cape Fear River estuary of

Table 2. Species of fishes from salt marshes of Eastern North America

Class, family, species	Locality																					
	Code	TX	LA	SM	CK	TB	NR	IR	GA	SC	NC	VC	VE	NJ	CN	MS	MW	RI	MH	PE	JH	
CLASS AGNATHA																						
Family Petromyzontidae																						
<i>Petromyzon marinus</i>	D															X						
CLASS CHONDRICHTHYS																						
Family Carcharhinidae																						
<i>Carcharhinus leucas</i>	MT**						X															
<i>Mustelus canis</i>	MT**													X								
Family Dasyatidae																						
<i>Dasyatis sabina</i>	MT*	X		X	X	X	X		X													
Family Rajidae																						
<i>Raja eglanteria</i>	MT													X								
<i>Raja erinacea</i>	MT														X	X						
CLASS OSTEICHTHYES																						
Family Acipenseridae																						
<i>Acipenser fulvescens</i>	D																				X	
Family Lepisosteidae																						
<i>Lepisosteus osseus</i>	FT								X													
<i>Lepisosteus platyrhincus</i>	FT						X															
<i>Lepisosteus spatula</i>	FT	X																				
Family Elopidae																						
<i>Elops saurus</i>	MT**		X	X	X	X	X	X	X		X						X					
<i>Megalops atlanticus</i>	MT**				X	X	X	X	X													
Family Anguillidae																						
<i>Anguilla rostrata</i>	D					X	X		X		X		X	X	X	X	X	X	X			
Family Congridae																						
<i>Conger oceanicus</i>	MT													X	X							
Family Ophichthidae																						
<i>Myrophis punctatus</i>	MT**		X			X			X	X												
Family Clupeidae																						
<i>Alosa aestivalis</i>	D								X	X	X			X		X	X		X			
<i>Alosa mediocris</i>	D													X								
<i>Alosa pseudoharengus</i>	D											X		X	X	X	X		X	X		
<i>Alosa sapidissima</i>	D								X		X			X			X					
<i>Brevoortia patronus</i>	MN	X	X			X																
<i>Brevoortia smithi</i>	MN					X		X	X													
<i>Brevoortia tyrannus</i>	MN							X	X	X	X	X	X	X		X	X					
<i>Clupea harengus</i>	MT**													X			X	X	X		X	
<i>Dorosoma cepedianum</i>	FT	X							X	X	X											
<i>Dorosoma petenense</i>	FT	X		X					X	X	X											
<i>Harengula jaguana</i>	MT			X																		
<i>Harengula humeralis</i>	MT	X																				
<i>Harengula pensacolae</i>	FT?					X	X		X													
<i>Opisthonema oglinum</i>	MT						X		X		X											
<i>Sardinella aurita</i>	MN?													X								
Family Engraulidae																						
<i>Anchoa hepsetus</i>	MN	X	X	X		X			X	X	X	X		X			X					
<i>Anchoa mitchilli</i>	MN**	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X					

Table 2. Continued

[illegible]

Table 2. Continued

Class, family, species	Locality																					
	Code	TX	LA	SM	CK	TB	NR	IR	GA	SC	NC	VC	VE	NJ	CN	MS	MW	RI	MH	PE	JH	
Family Centropomidae																						
Centropomus pectinatus	MT						X															
Centropomus undecimalis	MN**					X	X	X	X													
Family Moronidae																						
Morone americana	D											X		X		X	X	X		X		
Morone saxatilis	D									X						X						
Family Serranidae																						
Centropristis striata	MT								X				X	X			X					
Epinephelus itajara	MT						X															
Mycteroperca microlepis	MT									X	X											
Family Centrarchidae																						
Lepomis gibbosus	FT										X					X						
Lepomis gulosus	FT						X															
Lepomis macrochirus	FT				X	X					X					X						
Lepomis microlophus	FT						X															
Lepomis punctatus	FT						X															
Micropterus salmoides	FT					X	X									X						
Family Percidae																						
Stizostedion vitreum	FT																				X	
Family Pomatomidae																						
Pomatomus saltatrix	MT								X	X	X			X	X	X	X	X				
Family Rachycentridae																						
Rachycentron canadum	MT													X								
Family Echeneidae																						
Echeneis naucrates	MN?														X							
Family Carangidae																						
Alectis crinitis	MN														X							
Caranx hippos	MT	X	X				X		X		X			X		X	X					
Caranx latus	MT					X					X											
Chloroscombrus chrysurus	MT	X				X			X													
Oligoplites saurus	MN			X		X	X		X	X												
Selene vomer	MT										X			X								
Seriola zonata	MN														X							
Trachinotus carolinus	MT								X													
Trachinotus falcatus	MN?							X	X		X			X		X						
Family Lutjanidae																						
Lutjanus griseus	MT		X		X	X	X		X	X	X			X								
Lutjanus synagris	MT									X	X											
Family Gerreidae																						
Diapterus auratus	MT							X														
Diapterus olisthostomus	MN								X													
Diapterus plumieri	MN					X	X	X														
Eucinostomus argenteus	MT**		X	X	X	X	X	X	X	X	X											
Eucinostomus gula	MT**		X?		X	X	X	X			X											
Eucinostomus melanopterus	MT**									X	X											
Gerres cinereus	MN							X														
Family Pomadasyidae																						
Orthopristis chrysopterus	MT	X		X					X	X	X											

Table 2. Continued

Class, family, species	Locality																				
	Code	TX	LA	SM	CK	TB	NR	IR	GA	SC	NC	VC	VE	NJ	CN	MS	MW	RI	MH	PE	JH
Family Sparidae																					
<i>Archosargus probatocephalus</i>	MT	X	X		X	X	X	X	X												
<i>Lagodon rhomboides</i>	MT**	X	X	X	X	X	X	X	X	X	X										
<i>Stenotomus chrysops</i>	MT													X	X	X	X	X			
Family Sciaenidae																					
<i>Bairdiella chrysoura</i>	MN	X	X		X	X	X	X	X	X	X	X	X	X	X						
<i>Cynoscion arenarius</i>	MN	X	X	X	X																
<i>Cynoscion nebulosus</i>	MN**	X	X		X	X	X		X	X	X	X									
<i>Cynoscion nothus</i>	MN	X																			
<i>Cynoscion regalis</i>	MT*								X		X	X	X	X							
<i>Leiostomus xanthurus</i>	MN	X	X	X	X	X		X	X	X	X	X	X	X	X						
<i>Menticirrhus americanus</i>	MT	X				X			X												
<i>Menticirrhus littoralis</i>	MT	X	X						X												
<i>Menticirrhus saxatilis</i>	MT								X					X	X						
<i>Micropogon undulatus</i>	MN	X	X			X		X	X	X	X	X									
<i>Pogonias cromis</i>	MN	X			X	X		X	X		X		X								
<i>Sciaenops ocellata</i>	MN**	X	X		X	X	X	X	X		X										
<i>Stellifer lanceolatus</i>	MT?	X							X		X										
Family Mullidae																					
<i>Mullus auratus</i>	MT														X						
Family Ephippidae																					
<i>Chaetodipterus faber</i>	MT	X	X						X		X										
Family Chaetodontidae																					
<i>Chaetodon ocellatus</i>	MT													X							
<i>Chaetodon striatus</i>	MT															X					
Family Labridae																					
<i>Tautoga onitis</i>	MT										X			X	X	X	X	X			
<i>Tautoglabrus adspersus</i>	MT														X	X	X			X	
Family Mugilidae																					
<i>Mugil cephalus</i>	MN**	X	X	X	X	X	X	X	X	X	X		X	X	X	X	X	X	X		
<i>Mugil curema</i>	MN**	X			X	X		X	X		X		X	X			X				
<i>Mugil gyrans</i>	MN				X	X															
Family Sphyraenidae																					
<i>Sphyraena barracuda</i>	MT						X	X			X										
<i>Sphyraena borealis</i>	MN?													X	X						
Family Polynemidae																					
<i>Polydactylus octonemus</i>	MT	X		X																	
Family Uranoscopidae																					
<i>Astroscopus guttatus</i>	MT										X										
<i>Astroscopus y-graecum</i>	MT								X	X	X										
Family Blenniidae																					
<i>Chasmodes bosquianus</i>	MT**		X							X	X	X									
<i>Hypsoblennius hentzi</i>	MT								X	X	X										
<i>Hypsoblennius ionthas</i>	MT		X							X											
Family Stichaeidae																					
<i>Lumpenus fabricii</i>	MT**																				X
<i>Ulvaria subbifurcata</i>	MT																			X	
Family Pholidae																					
<i>Pholis gunnellus</i>	PR														X		X		X		

Table 2. Continued

Class, family, species	Locality																					
	Code	TX	LA	SM	CK	TB	NR	IR	GA	SC	NC	VC	VE	NJ	CN	MS	MW	RI	MH	PE	JH	
Family Ammodytidae																						
<i>Ammodytes americanus</i>	MT													X	X	X	X		X			
<i>Ammodytes dubius</i>	MT**																				X	
<i>Ammodytes hexapterus</i>	MT																				X	
Family Eleotridae																						
<i>Dormitator maculatus</i>	D						X	X														
Family Gobiidae																						
<i>Bathygobius soporator</i>	MT				X		X															
<i>Evorthodus lyricus</i>	MT**						X?	X														
<i>Gobionellus boleosoma</i>	PR*	X	X				X		X	X				X								
<i>Gobionellus hastatus</i>	MT**					X		X			X											
<i>Gobionellus shufeldti</i>	PR*									X	X											
<i>Gobionellus smaragdus</i>	PR?							X														
<i>Gobionellus stigmaturus</i>	MT										X											
<i>Gobiosoma bosci</i>	MT*	X	X		X	X		X	X	X	X	X	X	X	X		X					
<i>Gobiosoma ginsburgi</i>	MT					X					X				X							
<i>Gobiosoma robustum</i>	MT**						X	X														
<i>Microgobius gulosus</i>	PR*		X	X	X	X	X	X			X											
<i>Microgobius thalassinus</i>	MT**										X	X										
Family Trichiuridae																						
<i>Trichiurus lepturus</i>	MT	X																				
Family Scombridae																						
<i>Scomber scombrus</i>	MT															X				X		
<i>Scomberomorus maculatus</i>	MT					X				X				X								
Family Stromateidae																						
<i>Peprilus alepidotus</i>	MT								X			X										
<i>Peprilus triacanthus</i>	MT	X							X							X						
Family Triglidae																						
<i>Prionotus carolinus</i>	MT										X				X	X	X					
<i>Prionotus evolans</i>	MT*								X					X			X					
<i>Prionotus scitulus</i>	MT								X		X											
<i>Prionotus tribulus</i>	MN	X				X	X		X	X	X											
Family Cottidae																						
<i>Cottus cognatus</i>	FT																				X	
<i>Cottus ricei</i>	FT																				X	
<i>Myoxocephalus aeneus</i>	MT*														X	X	X		X	X		
<i>Myoxocephalus octodecimspinosus</i>	MT*														X							
<i>Myoxocephalus quadricornis</i>	PR*																				X	
<i>Myoxocephalus scorpioides</i>	MT**																				X	
<i>Myoxocephalus scorpius</i>	MT*															X					X	
Family Cyclopteridae																						
<i>Cyclopterus lumpus</i>	MT														X				X	X		
Family Liparidae																						
<i>Liparis atlanticus</i>	MT?														X					X		
<i>Liparis inquilinus</i>	MT^																			X		
Family Paralichthyidae																						
<i>Ancylosetta quadrocellata</i>	MT								X		X											
<i>Citarichthys macrops</i>	MT										X											

Table 2. Continued

Class, family, species	Locality																					
	Code	TX	LA	SM	CK	TB	NR	IR	GA	SC	NC	VC	VE	NJ	CN	MS	MW	RI	MH	PE	JH	
<i>Citharichthys spilopterus</i>	MT	X	X						X													
<i>Etropus crossotus</i>	MT**	X							X		X				X							
<i>Paralichthys albigutta</i>	MT			X	X	X				X?	X											
<i>Paralichthys dentatus</i>	MT**								X	X	X	X		X	X		X					
<i>Paralichthys lethostigma</i>	MT**	X	X	X					X?	X	X											
<i>Paralichthys oblongus</i>	MT														X							
Family Scophthalmidae																						
<i>Scophthalmus aquosus</i>	MT								X		X			X	X	X	X	X		X		
Family Pleuronectidae																						
<i>Hippoglossoides platessoides</i>	MT																			X		
<i>Limanda ferruginea</i>	MT																X			X		
<i>Pleuronectes putmani</i>	MT																		X			
<i>Pseudopleuronectes americanus</i>	MN**											X	X	X	X	X	X	X	X	X		
Family Achiridae																						
<i>Achirus fasciatus?</i>	MT	X									X											
<i>Achirus lineatus</i>	MN	X	X		X	X	X	X														
<i>Trinectes maculatus</i>	MN**				X	X	X		X		X	X		X		X	X					
Family Cynoglossidae																						
<i>Symphurus plagiusa</i>	MN	X	X		X	X			X	X	X											
Family Balistidae																						
<i>Aluterus</i> spp.	MT													X								
<i>Balistes caprisacus</i>	MN												X									
<i>Monacanthus hispidus</i>	MT								X		X			X		X						
Family Tetraodontidae																						
<i>Sphoeroides maculatus</i>	MT**								X					X	X	X	X					
<i>Sphoeroides spengleri</i>	MT?	X																				
<i>Sphoeroides nephelus</i>	MT**				X																	
<i>Sphoeroides parvus</i>	MT**		X																			
Family Diodontidae																						
<i>Chilomycterus schoepfi</i>	MT	X							X		X			X	X							

Note: key to abbreviations of locations and of sources of information are given in Table 1.

? Question about presence / identification.

Codes: PR – permanent resident; MN – marine nursery; D – diadromous; MT – marine transient; FT – freshwater transient. * – frequently found in estuaries, sometimes in FW; ** – some populations are permanent residents in estuaries; ^ – lives in mantle cavity of a scallop.

North Carolina (Weinstein et al., 1980), and included 80 species belonging to 38 families. When stations with continuously high salinities were excluded, the totals dropped to 50 species and 24 families.

Listings of fishes from FW and brackish waters of the James, Chickahominy, Pamunkey, Mattaponi, and Rappahannock rivers of Virginia, all tidally influenced, included only euryhaline and SW species taken in FW, and excluded diadromous species (Massman, 1954). Those data were combined with data from another study (Dovel, 1967), that identified fish eggs and larvae taken in tidal river collections of

the region. Fishes of other Virginia estuarine waters closer to the Atlantic identified in a study conducted along the eastern shore were also included (Richards and Castagna, 1970). Those collections represented several habitats, and included a total of 70 species belonging to 39 families. Information included here from that study was limited to species taken in tidal creeks, reducing the number of species to 20, representing 13 families.

Northward, the next system was of New Jersey marsh creeks (Rountree and Able, 1992) in which 61 species of fishes belonging to 41 families were identi-

fied. Fishes of the Mystic River estuary, CT (Pearcy and Richards, 1962) included 51 species belonging to 37 families. Two systems in Massachusetts were included, Slocum River adjacent to Buzzards Bay (Hoff and Ibara, 1977), with 54 species belonging to 38 families (with 35 families and 47 species considered to be part of the shallow estuarine system), and Waquoit Bay (Ayvazian et al., 1992), where 49 species belonging to 31 families were identified. A single location was available for Rhode Island, Bissel Cove (Nixon and Oviatt, 1973), with a sparse representation of 19 species belonging to 14 families. Maine was represented by the fauna at Wells Harbor (Ayvazian et al., 1992), with, again, a limited fauna, including 24 species representing 16 families.

Collections at Prince Edward Island, Canada were not made in a salt marsh system, but taken in ichthyoplankton sampling in the area (Johnston and Morse, 1988). Included were 22 species representing 16 families. That group could have included species that would not normally survive and develop in estuarine habitats. Major species present among estuaries of James and Hudson Bays, Canada (Morin et al., 1980) included a diversity of salmonids (7 species) and of cottids (6 species, one an obligate FW species). Also represented were species belonging to other families generally showing colder water affinities (Nelson, 1994), including Osmeridae, Ammodytidae, and Stichaeidae, as well as such cold FW families as Hiodontidae and Percopsidae. Again, those collections were not made in salt marsh systems, and some of the collections were from areas of very low salinity in river mouths, resulting in FW species being included. Some almost exclusively marine species were included as collecting stations extended well offshore. Individual listings of fishes taken from James and Hudson Bays were combined for simplicity. The fish fauna included 29 species belonging to 14 families, not including nine obligate FW species (Morin et al., 1980). Overall, the mean number of species per estuarine location was 42.5 (44.8 if stations with higher salinities were included, Table 1), representing a mean of 25.0 (or 25.9) families.

The number of fish species included in the overall set of 20 locations (including Prince Edward Island and James and Hudson Bays) was 237 (with a few questions of identification), representing 80 families (Table 2). Diadromous species were not always included by authors, and some FW species taken only in upper reaches of an estuarine system, where the water was consistently FW were also excluded.

Families represented among locations varied from 13 in the Virginia eastern shore collections (Richards and Castagna, 1970), to 43 families in the Georgia collections (Dahlberg, 1972). Species richness ranged from 19 in collections from Bissel Cove, Rhode Island (Nixon and Oviatt, 1973) to 86 species in Georgia collections (Dahlberg, 1972; Table 1). The hypothesis that numbers of species per estuary would decrease with increasing latitude was tested, regressing species numbers of the included estuaries on latitude. This analysis was done in two parts: the first used numbers of species that excluded what were judged to be freshwater species that were taken only in freshwater reaches of riverine estuaries; and the second included those freshwater species. The first of these regressions was marginally significant ($Y = 77.915 - 0.981X$, $p = 0.0495$), while the second was not significant ($Y = 75.538 - 0.852X$, $p = 0.1301$). The trend in the marginally significant regression does suggest a reduction in species richness with increasing latitude, but with extensive scatter. Variations in types of collecting gear, differences in total collecting efforts, and differences in physical features among the estuaries influence the numbers of species collected in any location. Numbers of species taken per estuarine system over a narrow range of latitude, and for a more homogeneous set of circumstances in England and Wales, showed a strong decrease in species numbers with increasing latitude. However, the results there were noted to be confounded by the fact that salinities of these estuaries also decreased with increasing latitude (Henderson, 1989). Problems of making such comparisons were further discussed by Elliott and Dewailly (1995).

Overall distributions of species and of families over this range of 20 estuarine systems was determined, and extent of distribution was indicated by the fraction of the 20 estuaries in which a species or a family was represented (Table 3). A total of 22 families was found to be represented by species present in 8 or more of the 20 estuarine locations. The most widely distributed of families were Atherinidae, Clupeidae, Cyprinodontidae, Mugilidae, Engraulidae, Sparidae, and Gobiidae, all with representation in 15 or more of the estuarine systems. Also included (Table 3) were individual species most widely distributed among the 20 sites. The most widely distributed of species among these estuaries were *F. majalis* (including *F. similis* or *F. m. similis*), *Cyprinodon variegatus*, *Mugil cephalus*, *Anchoa mitchelli*, *Menidia beryllina*, *Bairdiella chrysoura*,

Table 3. Most widely distributed[#] fish families and species* represented in salt marshes/estuaries of eastern North America

Families	Species
Atherinidae 18 (19)	<i>Fundulus majalis</i> ¹ 17
Fundulidae 18	<i>Cyprinodon variegatus</i> 17
Clupeidae 17 (19)	<i>Mugil cephalus</i> 17
Cyprinodontidae 17	<i>Anchoa mitchelli</i> 16
Mugilidae 17	<i>Menidia beryllina</i> 13
Engraulidae 16	<i>Bairdiella chrysoura</i> 13
Sparidae 15	<i>Leiostomus xanthurus</i> 13
Gobiidae 15	<i>Gobiosoma boscii</i> 13
Sciaenidae 14	<i>Menidia menidia</i> 12
Syngnathidae 13 (14)	<i>Fundulus heteroclitus</i> 11
Belontiidae 13	<i>Anguilla rostrata</i> 11
Carangidae 13	<i>Lucania parva</i> 11
Paralichthyidae 12	<i>Anchoa hepsetus</i> 10
Achiridae 12	<i>Strongylura marina</i> 10
Anguillidae 11	<i>Lagodon rhomboides</i> 10
Batrachoididae 11	
Triglidae 10	
Phycidae 9(10)	
Elopidae 9	
Gerreidae 9	
Pleuronectidae 8 (9)	
Pomatomidae 8	

[#]Widely distributed for families is defined here in terms of being represented in more than 50% of the estuarine systems included in the analyses (9 or more of the 18 North American locations between Texas and Maine. Number in parenthesis indicates total number of systems in which the family was represented out of 20 when Prince Edward Island and James and Hudson Bays are included).

*Widely distributed for species includes all 20 estuarine sites distributed from the Texas coast to James and Hudson Bays.

Total number of families represented among the estuaries = 80.

Total number of species includes = 237.

¹*Fundulus majalis* here includes *F. m. similis*.

Leiostomus xanthurus, and *Gobiosoma boscii*, all of which were taken at 13 or more of the 20 sites.

Families of highest species richness represented in this series of estuarine salt marsh systems were Clupeidae, 15 species; Sciaenidae, 13; Gobiidae, 12; Fundulidae, 10 (2 rarely taken in brackish waters); Carangidae, 9; Paralichthyidae, 8; Salmonidae, 7 (several of which are rarely found in brackish waters); Gerreidae, 7; Cottidae, 7; Centrarchidae, 6 (none truly estuarine); and Gadidae, Phycidae, and Gasterosteidae, 5 species each. (Table 4).

Table 4. Fish families represented by largest numbers of species*, estuaries of eastern North America and of western Europe

North America		Europe	
Family	No. of species	Family	No. of species
Clupeidae	15	Cyprinidae	26
Sciaenidae	13	Gobiidae	20
Gobiidae	12	Sparidae	18
Fundulidae	10	Gadidae	10
Carangidae	9	Labridae	10
Paralichthyidae	8	Soleidae	10
Salmonidae	7	Syngnathidae	8
Gerreidae	7	Salmonidae	7
Cottidae	7	Pleuronectidae	7
Centrarchidae	6	Clupeidae	6
Gadidae	5	Phycidae	6
Phycidae	5	Mugilidae	6
Gasterosteidae	5	Blenniidae	6
		Scophthalmidae	6
		Rajidae	5
		Cottidae	5
		Triglidae	5

*Only those families represented by five or more species were listed here.

Life history patterns of salt marsh fishes

Key features of life history categories of the various species found in estuarine salt marshes were based on places of spawning and development, and of regular patterns of migration (Table 2). Each of the 237 species was assigned to one of the five life history categories used. Criteria applied for inclusion of a species in a particular life history group varied among authors of the included studies; thus, life history assignments made here were based on what seemed to be the most consistent or general life history pattern for each species, interpreting existing information. However, in a number of cases a species was noted as potentially varying in the category to which it could be assigned, depending on geographical area or particular estuarine system being addressed. Superscript notations were used to indicate variations in (or in opinions as to) categories to which a species should be assigned, especially where information suggested there were interdemographic variations in life history characteristics. A conservative approach was used in making assignments to all life history categories. A fundamental criterion used with respect to the assignment to the permanent resident category (PR) was whether

individuals of a species generally remained in the salt marsh habitat, or regularly and predictably migrated elsewhere for a portion of the life cycle, including for spawning. That was a difficult decision, as over much of the latitudinal range covered in these analyses individuals of many species were said to move from the estuary to deeper waters during colder periods of the year. Perhaps the most arbitrary decision was between including a species in the marine nursery category or that of marine transient, the distinction being with respect to whether the sojourn in an estuarine environment was an obligate stage in the life cycle (estuarine dependence) or one followed by some, but not most/all of the young of a species.

A total of 22 species representing eight families was included in the permanent resident category (Table 2). The largest single group of these belonged to the family Fundulidae, *Adinia xenica*, *F. confluentus*, *F. grandis*, *F. heteroclitus*, *F. luciae*, *F. majalis*, *F. similis* (or *F. m. similis*), and *Lucania parva*. Other cyprinodontoids that were included in this group were *C. variegatus* and *Floridichthys carpio*, both belonging to the family Cyprinodontidae; *Rivulus marmoratus*, belonging to the family Aplocheilidae, and *Poecilia latipinna*, belonging to the family Poeciliidae. In addition, there were four species belonging to the family Gasterosteidae, *Apeltes quadracus*, *Gasterosteus aculeatus*, *G. wheatlandi*, and *Pungitius pungitius*; four belonging to the Gobiidae, *Gobionellus boleosoma*, *G. shufeldti*, *G. smaragdus*, and *Microgobius gulosus*; one species belonging to the Pholidae, *Pholis gunnellus*; and one belonging to the Cottidae, *Myoxocephalus quadricornis*. There were questions about the inclusion or exclusion of some of these species in the permanent resident category. A number of examples of questions or problems, but not an exhaustive list, will be given here.

A number of species have been included in the permanent resident category in particular situations but were not included here as such because their life history pattern was more commonly of another type including: *Dasyatis sabina*, *D. hastata*, **Syngnathus scovelli*, **Strongylura marina*, **M. beryllina*, *Morone saxatilis*, **M. gulosus*, and **G. bosci*, all of which were considered to have "non-migratory" populations (St. Johns River, FL; those marked * represent relic populations locally isolated in the St. Johns system; McLane, 1955). Other examples of species and/or systems in which certain species could have been included as permanent residents in particular estuarine systems included: *A. mitchelli*, *B. chrysoura*, and

Trinectes maculatus (Chesapeake estuary; McHugh, 1967); *M. beryllina* (Lake Okeechobee, FL; Ager, 1971); *A. mitchelli*, *Opsanus tau*, *S. marina*, *M. beryllina*, *M. menidia*, *S. fuscus*, *G. bosci*, and *Prionotus evolans* (New Jersey; Rountree and Able, 1992); *M. thalassinus*, (Magothy River estuary, VA; Dovel, 1967) and *Paralichthys lethostigma* (Escambia and Apalachicola estuaries, FL; Beecher and Hixon, 1982). Examples of species that might qualify as belonging to either the permanent resident or diadromous category, depending on the system, included the sticklebacks, *A. quadracus*, *G. aculeatus*, and *P. pungitius* (Audet et al., 1985, 1986; Ayvazian et al., 1992; Hoff and Ibara, 1977; Smith and Paulson, 1977), all of which were included here as permanent residents along with *G. wheatlandi* (Audet et al., 1985, 1986; Ayvazian et al., 1992; Worgan and FitzGerald, 1981).

Species, the vast majority of which spawn in marine waters, and whose young enter estuarine salt marsh habitats and remain there for varying periods of time for successful development, have been defined as marine nursery species (MN). The second largest fraction of species reported here to utilize estuarine salt marsh habitats belonged to that group. Widely distributed members of the group included: *Brevoortia tyrannus*, *A. mitchelli*, *M. beryllina*, *B. chrysoura*, and *L. xanthurus* (Table 2). Two popular sport fishes, *Cynoscion nebulosus* and *Sciaenops ocellata*, both with extended distributions from the Gulf of Mexico and along the Atlantic coast of the eastern US, were among the species that were difficult to assign to a single life history category. Both have been cited as permanent residents of estuaries, especially along portions of the Gulf coast (e.g., Tabb, 1966; Schwartz et al., 1981; Brown-Peterson et al., 2002). They are generally considered marine nursery species (as indicated here, Moody, 1950; Pattillo et al., 1997; Renfro, 1960), but sometimes as marine transients in areas from the Georgia coast at least to Chesapeake Bay, as some populations apparently develop outside of estuarine waters (Dahlberg, 1972; Herke et al., 1984; Hoese, 1973) and also some populations have been observed to migrate north and inshore in spring, and south and offshore in fall following the seasonal changes in water temperature (reviewed in Mercer, 1984a, b). Information was especially inconsistent for *S. marina*, reported to be a permanent resident in the St. Johns and Apalachicola Rivers of Florida (McLane, 1955; Swift et al., 1977), to be an anadromous species (Yerger, 1977), or a marine

nursery species in other systems (Ayvazian et al., 1992; Hellier, 1967; Rountree and Able, 1992; Collette, 2002), the category used here, and has also been considered to be a marine transient (Pearcy and Richards, 1962). *M. beryllina*, *M. menidia*, and *M. peninsulae* were considered permanent residents in some salt marshes; however, the argument was made that all atherinids make annual migrations to marine waters (Kneib, 1997), so despite the fact that they may spawn in, and spend much of the developmental period and a considerable period of adult life in salt marshes, they should be considered marine nursery species. Thus, they were included in the latter category. No FW species was reported to be an obligate user of salt marshes as a nursery area.

Diadromous species (D) included 13 species belonging to eight families (Table 2). The diverse group of anadromous species included sea lamprey, *Petromyzon marinus*, sturgeon, *Acipenser fulvescens*, and Atlantic salmon, *Salmo salar*, among others. The young of many anadromous species also utilize salt marsh systems as nursery grounds. Only a single catadromous species, *Anguilla rostrata*, was taken in estuaries included here. *Dormitator maculatus*, an eleotrid, was considered to be amphidromous (as the term was interpreted by McDowall, 1987, 1997), spending much of its adult life in fresh waters of riverine systems, and part of its developmental period in salt marshes, with adults returning to lower portions of estuaries to spawn (Nordlie, 1979, 1981). *M. cephalus* might well have been included in the diadromous (amphidromous) category rather than as a marine nursery species, as young of that species, hatched at sea, enter estuarine waters where they may remain for up to 6 months or more (Kilby, 1955), with adults frequently moving back and forth between marine waters, brackish waters, and fresh waters, often into coastal rivers and springs (Herald and Strickland, 1949; Odum, 1953; McLane, 1955; Hellier, 1967). However, it has also been suggested (Potter et al., 1990) that *M. cephalus* should be considered to be a marine transient (estuarine-opportunist species), rather than an estuarine-dependent one, as its young successfully develop in coastal marine areas that are devoid of estuaries.

Transient species included those species for which there was information that indicated they showed successful development whether or not they entered estuaries, or for which there was little or no information to indicate any developmental requirement was being met in estuarine salt marsh systems (Table 2).

The marine transient category (MT) included the largest total among the five groupings, with a smaller number of freshwater transients (FT).

Some possible variations indicated in the life history assignments of species reflected incomplete information. Even among species that were considered to be permanent residents, spawning locations for the species were not always completely limited to salt marshes, though alternative sites were immediately adjacent to the marshes. It was noted that within a small group of species generally considered to be permanent residents in salt marshes at Cedar Key, FL (Gulf coast of northwest Florida), only one species, *A. xenica*, appeared to be totally limited to such environments for all of its requirements including reproduction (Nordlie, 2000a).

The present scheme of life history classifications resulted in including 22, or 9.3%, of the 237 species in the permanent resident category, species that normally spawn in and complete their life cycles in salt marshes/estuaries. Marine nursery species numbered 42, or 17.7%, most of which spawn in marine areas (a few may spawn in salt marshes), and whose young spend varying developmental periods in salt marshes, ultimately leaving the system to return to marine waters where they spend a portion of the life cycle. Included as marine transients were 124 species, or 52.3% of the total, so the majority of species reported from these estuaries occurred in a salt marsh habitat for some not completely predictable portions of the year, and/or with significantly less than all of the developing individuals being found in estuarine salt marsh environments, those not in that habitat successfully developing elsewhere. It seems likely that the large percentage of species included in the marine transient category may be at least partially a result of the difficulties in demonstrating that normal development requires some period of residence in an estuarine system, especially in a salt marsh. A total of 36 species were identified as freshwater transients, 15.2% of the total, and 13 were included as diadromous species, 5.5% of the total (Figure 1).

Among the 15 most widely-distributed species from these estuaries/salt marshes of eastern North America (Table 3), four (*F. majalis* including *F. similis* or *F. m. similis*, *C. variegatus*, *F. heteroclitus*, and *L. parva*) were identified as estuarine permanent residents, eight (*M. cephalus*, *A. hepsetus*, *A. mitchelli*, *M. beryllina*, *M. menidia*, *B. chrysoura*, *L. xanthurus*, and *S. marina*) were marine nursery species, one (*A. rostrata*) was a diadromous species, and two

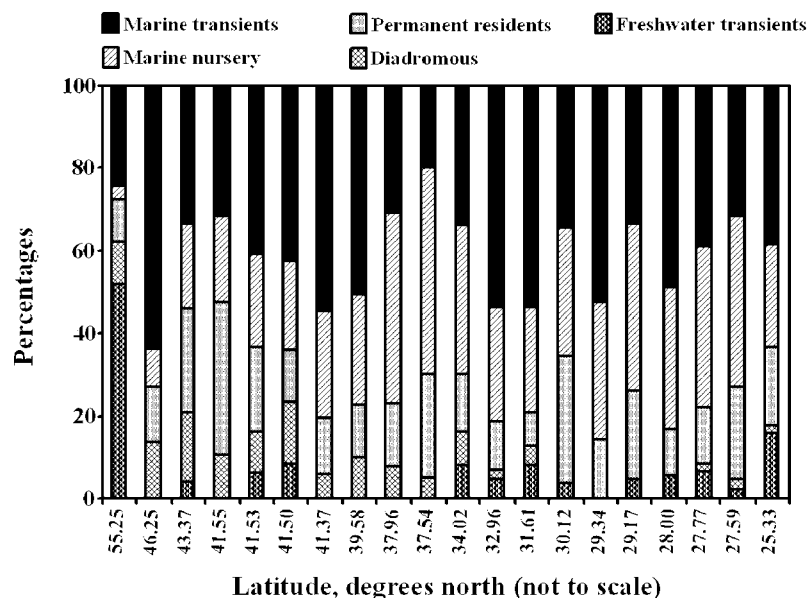


Figure 1. Representation of life history groups over latitude for the 20 estuarine systems of eastern North America (where more than a single system was included for a particular location, the mean latitude is given here). Names of estuaries for corresponding latitudes are found in Table 1. Life history groups: FT, freshwater transient; D, diadromous; PR, permanent resident; MN, marine nursery; MT, marine transient.

(*G. bosci*, and *Lagodon rhomboides*) were included in the marine transient category, though *G. bosci* was considered to be an estuarine resident in some situations and *L. rhomboides* was included as a marine transient rather than as a marine nursery species because of apparent variability in its areas of development. Thus, it appears that species that demonstrate associations with estuarine systems over a wide geographical range generally show more than casual utilization of those habitats.

Cape Cod as a zoogeographic boundary

Fish faunas of Waquoit Bay, MA, south of Cape Cod, and of Wells Harbor estuary, ME, north of Cape Cod, both estuarine systems, were compared (Ayvazian et al., 1992), elaborating on the concept (Bigelow and Schroeder, 1953; Ekman, 1953; Briggs, 1974) that Cape Cod serves as a biogeographic boundary. It was pointed out that several species of fishes from warmer waters to the south were not found beyond the Cape, with the ichthyofauna to the north of Cape Cod consisting of more cold-tolerant boreal species. To enhance comparisons in the present analyses, data were also included for Prince Edward Island in the Gulf of St. Lawrence (Johnston and Morse, 1988), another location north of the Cape. Using these data, 27 species of tele-

osts were found to drop out of the estuarine fauna between Waquoit Bay and Wells Harbor (plus Prince Edward Island). That group included, among others, some fishes that were the most widely encountered among the 20 eastern North American estuarine locations reviewed here: *B. tyrannus*, *A. mitchelli*, *S. marina*, *F. majalis*, *C. variegatus*, *Pomatomus saltatrix*, *M. curema*, *G. bosci*, and *T. maculatus* (Table 2). Notable among widely distributed species whose distributions extended northward beyond the Cape were: *A. rostrata*, *F. heteroclitus*, *M. beryllina*, *M. menidia*, *S. fuscus*, and *M. cephalus*.

Another idea that had been proposed was that fish faunas of more northern systems include a greater fraction of estuarine resident species compared to more southern estuaries, which would be expected to have more migratory species (Bigelow and Schroeder, 1953; Ekman, 1953; Whitlatch, 1982). That hypothesis was tested (Ayvazian et al., 1992), comparing life history group representation in Waquoit Bay, MA, south of Cape Cod, with that of Wells Harbor, ME, north of the Cape. Results of the study suggested that ca. 33% of the species taken in Waquoit Bay, south of Cape Cod, were estuarine residents, compared with ca. 42% in the Wells Harbor estuary, north of Cape Cod, supporting the hypothesis of greater influence of migrants in southern estuaries. Estuarine residents made up the largest single fraction of species of fishes

in both estuaries following their classifications, with marine nursery species and marine transients each making up ca. 23% of the species in Waquoit Bay, compared with ca. 21% nursery species and ca. 17% marine visitors in Wells Harbor. Diadromous species constituted ca. 17% of the total with <5% being added by freshwater transients in Wells Harbor compared with diadromous plus marine and freshwater transient species totaling ca. 20% of the species in Waquoit Bay.

The hypothesis that the fraction of permanent estuarine residents increased with latitude was tested here, regressing percentages of permanent residents on latitude. Including values for all 20 estuarine systems produced the regression, $Y = 19.353 - 0.047X$, which was not significantly different from 0 ($p = 0.8370$). Next, the hypothesis that the fraction of marine migratory species (MN + MT) decreased with increasing latitude was tested, regressing percentages of marine migratory species in the faunas of each of the 20 estuarine systems on latitude. The resulting regression was $Y = 109.884 - 1.118X$ ($p = 0.0021$), indicating a significant negative relationship between the fraction of marine migratory species and latitude, consistent with the general concept (Bigelow and Schroeder, 1953; Ekman, 1953; Whitlatch, 1982; as tested by Ayvazian et al., 1992). Regressing marine nursery species separately from marine transients revealed a strong significant relationship for the marine nursery species ($Y = 64.633 - 0.989X$, $p = 0.0014$), while the regression of marine transients on latitude was not significant ($Y = 45.250 - 0.128X$, $p = 0.7173$). Because of apparently conflicting results among these regressions, a regression of percentages of diadromous species on latitude was run ($Y = -13.915 + 0.559X$, $p = 0.0001$). It was concluded that there was an exchange in fractional representation in the estuarine fish faunas between marine nursery species and diadromous species, which increased in percentage representation at higher latitudes (see Figure 1). This is more-or-less consistent with another viewpoint, that marine fishes (species derived from a marine ancestry) generally dominate the ichthyofaunal assemblages of north temperate estuaries, both numerically and in terms of species richness (Haedrich, 1983; Greenwood et al., 2002), but does not deal with Arctic estuarine systems. While fewer species of fishes were taken in the more northern areas, the Hudson and James Bay data (Morin et al., 1980) indicated that the largest fraction of species occurring in those very cold estuarine areas were freshwater transients (not represented in regressions because of inconsistencies

in their inclusion in the various data sets used in the analyses).

The Florida peninsula as a zoogeographic boundary

Zoogeographic boundaries (provinces) along the coast of North America have been proposed by several authors, with disagreement as to where they should be located (Ekman, 1953; Briggs, 1974). Some of the disagreement has resulted from the particular animal group being considered (Hedgpeth, 1954, 1957; Hayden and Dolan, 1976), some specific to fishes based on what groups of fish were being evaluated, e.g., species from deeper waters or species that inhabit the nearshore waters. The reality seems to be that there is no consistency among various marine groups in where species become a part of or drop out of the fauna (Briggs, 1974). Only the tropical/subtropical-temperate boundaries will be considered here. Distribution limits of inshore fish faunas, in this case including those associated with salt marshes (especially permanent residents and marine nursery species), vary among the Florida Keys, the Florida peninsula as the eastern boundary of the Gulf of Mexico, and the east coast of the Florida peninsula. The warm-temperate region of the Gulf of Mexico is generally assumed to extend from Cape Rojo, Mexico, around the Gulf to Cape Romano, just north of the Ten Thousand Islands on the lower southwest coast of Florida (Briggs, 1974). However, various arguments have suggested that the boundary on the Florida coast could be from a location as far north as Tampa Bay, to one well south of Cape Romano. On the Atlantic coast the boundary has been proposed for locations from as far south as Biscayne Bay to Cape Hatteras or even to Cape Cod (Briggs, 1974). It was suggested that the area between Cape Kennedy on the south and Cape Hatteras on the north be considered the warm-temperate region along the Atlantic coast of North America (Briggs, 1974). Examining known distributions of species associated with estuaries/salt marshes of the Gulf and east coasts of Florida (not all of which were actually common in the series of estuaries examined here), a number of species were identified as illustrating distributional limits associated with areas along that portion of the coast of eastern North America (distributional information from Robins and Ray, 1986). These were organized into two groups, the first of which includes species whose distributions extend around the Gulf of Mexico, reaching a distributional limit somewhere

along the Florida coast. Examples included: *Harengula humeralis* (south Florida); *O. beta* (Florida, south of Cape Canaveral); *Gunterichthys longipenis* (Gulf coast to Florida Keys); *F. carpio* (southeast Florida); *Centropomus pectinatus* (south Florida); and *Sphoeroides parvus* (northwest Florida). Species whose distributions extend southward along the Atlantic coast reaching a distributional limit somewhere along the Florida coast are exemplified by: *Alosa aestivalis* (northeast Florida); *B. tyrannus* (east coast of Florida); *O. tau* (east coast of Florida); *Ophiodon marginatum* (northeast Florida); *S. fuscus* (northeast Florida); *P. evolans* (northeast Florida); *P. dentatus* (northeast Florida); *Scophthalmus aquosus* (northeast Florida); and *S. maculatus* (northeast Florida).

More detailed examples of changes in the salt marsh fish faunas for five families are also given as illustrations. Four species belonging to the family Clupeidae, *B. gunteri*, *B. patronus*, *B. smithi*, and *B. tyrannus*, illustrate disparities in distribution patterns, with *B. gunteri* and *B. patronus* limited to Gulf waters (Dahlberg, 1970; Pattillo et al., 1997); *B. smithi* distributed along both coasts of Florida and along the Atlantic coast as far north as North Carolina (Dahlberg, 1970; Pattillo et al., 1997); and *B. tyrannus* distributed from Jupiter Inlet, FL northward along the Atlantic coast to Nova Scotia (Dahlberg, 1970). *B. gunteri*, which was not reported in any of the studies included here, is found in the western Gulf of Mexico from Louisiana to the Gulf of Campeche, Mexico (Dahlberg, 1970). Among members of the family Belontiidae, *S. marina* has a continuous distribution from Maine to Brazil around the Florida peninsula, while *S. notata*, a more southern species, gets as far north as mid-Florida (both coasts) and as far south as Central America. A third species, *S. timucu*, shows a distribution very similar to that of *S. notata* (Robins and Ray, 1986). Several examples are also found among members of the family Fundulidae. The small species, *A. xenica*, has a distribution extending from Texas around the Gulf of Mexico to Big Pine Key in the Florida Keys, but is not present northward of Miami on the Atlantic coast (Relyea, 1975). Both *F. grandis* and *F. similis* (or *F. majalis similis*) are widely distributed around the Florida peninsula and around the Gulf of Mexico, but drop out along the east coast of Florida (Relyea, 1983). In the case of *F. grandis*, its distribution is from Laguna de Tamiagua, Mexico, around the Gulf of Mexico, northward to Amelia Island on the Georgia border, with a possible gap in the distribution in south Florida

(Relyea, 1983). Its distribution overlaps with that of *F. heteroclitus*, whose distribution extends roughly from Mosquito Lagoon on the east coast of Florida, northward to Canada. A biochemical analysis demonstrated that the two, *F. grandis* and *F. heteroclitus*, are distinct species (Duggins et al., 1989). The situation with respect to the other two species, *F. majalis* and *F. similis*, is slightly different, as results of a biochemical analysis indicated that they are conspecifics, and to the north of the region of the Matanzas Inlet along the northeast coast of Florida a '*majalis*'-like species begins its distribution which extends northward along the Atlantic coast to New Hampshire. Southward from this area a '*similis*'-like species extends its distribution around the Florida peninsula and the Gulf of Mexico to an area just north of Tampico, Mexico (Relyea, 1983; Duggins et al., 1994), with the area of differentiation pointed out to be roughly where the northern *Juncus-Spartina* salt marshes are replaced or joined by mangroves. Among members of the family Atherinidae, *M. beryllina* shows a wide distribution along the Atlantic coast of North America and into the Gulf of Mexico, while *M. menidia* shows a similar distribution along the Atlantic coast but southward only to northern Florida, and is not present in the Gulf of Mexico. A third species, *M. peninsulae*, shows a limited distribution in the northeastern Gulf of Mexico, but does not reach south Florida. The final example deals with two species belonging to the family Sciaenidae, *C. regalis* and *C. arenarius*. *C. regalis* is found southward along the east coast of Florida, and northward to Nova Scotia (Robins and Ray, 1986; Klein-MacPhee, 2002b). The distribution of *C. arenarius* extends from southeast Florida around the Gulf of Mexico to the Bay of Campeche (Robins and Ray, 1986). However, it was concluded that *C. arenarius* is actually a subspecies of *C. regalis* (Weinstein and Yerger, 1976), with the area of transition between subspecies along the lower east coast of Florida.

Based on these examples it would appear that the Florida peninsula does restrict the distributions of some inshore species to the Gulf of Mexico, perhaps because of environmental conditions, including warmer temperatures, and possibly because of unavailability of suitable habitat, in part associated with the presence of mangrove rather than *Juncus-Spartina* marshes along the coast of southwestern Florida. Examples presented here also show zones of changes in distributions of species that extend from the southern tip of the Florida peninsula to south Georgia on the Atlantic side.

Seasonal patterns of abundance and diversity

A principal factor of interest in seasonal occupation of estuaries/salt marshes is of immature stages of marine fishes that move into and occupy these shallow areas for varying periods of time in their developmental stages. Thus, a major factor determining species composition and abundance of fishes in such areas is correlated with reproductive patterns of species using the system. For example, it has been shown in the Elbe estuary that annual cycles of presence of particular species, especially of marine species, at particular times and places varies among years, not necessarily being tied to variations in ambient salinities (Thiel and Potter, 2001). It has been suggested by a number of authors (Dahlberg and Odum, 1970; McErlean et al., 1973; Hoff and Ibara, 1977; Weinstein, 1979; Thorman, 1986a, b) that abiotic factors may outweigh biotic factors in determining both the species present in shallows of an estuary/salt marsh, in a particular life stage of individuals of those species, as well as in the abundance of individuals of the species present. The principal abiotic factors structuring such communities have been found to be water temperature and salinity (Thorman, 1982; Thorman and Wiederholm, 1984; Thorman, 1986a, b). Extremes of environmental conditions found among northern estuaries discussed here probably can be exemplified by those of Hudson and James Bays, where the estuaries are under ice cover for a considerable portion of the year. In such circumstances it is likely that some shallower areas are frozen to the bottom, at least following the coldest portion of the year, rendering those areas uninhabitable. The overall annual range of water temperatures in such areas would be quite limited, never reaching levels far above those of freezing (Morin et al., 1980). However, it has been suggested that water temperature may be more appropriately regarded as an indicator of potential interactions of a number of abiotic and biotic characteristics, rather than as a direct influence on abundance and diversity of fishes in shallow marine habitats (Magill and Sayer, 2002). While abiotic factors may exert significant influences, directly or indirectly, in determining species associations in such systems, biotic factors, also exert impacts in determining species associations through such interactions as both inter- and intraspecific competition for available food and space, and through predation. Again, biotic forces may be exerted directly or indirectly in concert with abiotic forces.

The other geographic extreme among estuaries considered here is that of North River, FL, in a subtropical region. The annual temperature range there is also somewhat limited, in this case to warmer temperatures (Table 1). The more significant annual cycle in that environment is of rainfall, altering ambient salinity levels (Odum, 1971). However, it was suggested that the numbers of species in temperate and subtropical estuaries peak in spring and summer due to annual patterns of temperature, while seasonal cycles of abundance in tropical estuarine systems, as exemplified by Brazilian mangrove creeks, are related to seasonal variations in salinities (Barletta-Bergan et al., 2002).

In extensive studies of a number of shallow marine habitats and estuaries along the east and west coasts of Sweden, it became apparent that water temperature and salinity were major limiting factors (along with environmental heterogeneity and exposure to predators) in the occupation of these habitats by fishes, generally limiting fish populations below levels at which food would become limiting. Evidence was presented (Thorman, 1986b) that salinity limited the species that could inhabit such areas, and water temperature limited the abundance of individuals of those species. Fish assemblages were found to differ between areas in a single year and between years in the same area. Some of the areas evaluated froze to the bottom each winter, so that they were recolonized each spring following melting of the ice, again, an extreme situation of an abiotic factor determining the pattern of habitat utilization. We will first discuss annual reproductive cycles of selected species from the various life history groups, keeping in mind seasonal variations in temperature and salinity over their ranges of distribution, and then consider water temperature and ambient salinity as potential abiotic limiting factors to the distributions and abundances of various species, including potential changes in their vulnerability to variations and extremes of these conditions in various life stages.

Times of reproduction

The body of information and completeness regarding spawning (or live birth) patterns of the various species of fishes included here varied from extensive, with details on places, times, environmental conditions, and the like, to unknown or almost so. It would be very difficult to consider all of the details even of those estuarine species for which such informa-

tion was available. The approach taken was to select representative species from three of the five life history groups (diadromous species were not included and there were no freshwater transients that regularly spawned in estuarine salt marshes), and make comparisons among those spawning patterns, especially with respect to seasonality and to variations over the latitudinal ranges of widely distributed species. It was pointed out (Dando, 1984; Nordlie, 2000a), and previously mentioned here, that there are few true resident fishes in estuarine salt marshes when inclusion in that group is only of species that are totally restricted to breeding in those habitats as well as residing there throughout their lifetime. However, it has also been pointed out (Blaber, 2000) that this is dependent on the estuarine definition followed.

The first group considered was those identified as permanent estuarine residents. *P. gunnellus*, a resident of colder, but not the coldest, estuaries, was reported (Chenoweth, 1973) to deposit demersal eggs in the upper portion of Sheepscot estuary, ME, with hatchings between January and June, and showing peak spawning activity in February and March, during a cold period of the year. *A. xenica*, a species limited to tropical/subtropical and warm temperate areas of the Gulf coast of the United States, spawns at least during the months of February through September, and may spawn year-round in warmer areas (Kilby, 1955; Hastings and Yerger, 1971; Cunningham and Balon, 1985). *C. variegatus*, a species with an extensive distribution along the Gulf and Atlantic coasts of North America, was said to spawn from April through November in Florida (Raney et al., 1953; Kilby, 1955; Loftus and Kushlan, 1987). However, the spawning season was found to be more limited in Delaware, extending from May–August, with peaks of activity in early May and again in mid July (Warlen, 1964). That pattern was similar to *F. heteroclitus*, another species with a wide distribution along the Atlantic coast. It was found to spawn from early spring through summer, but the timing of spawning varied with the subspecies (Denoncourt et al., 1978; Samaritan and Schmidt, 1982; Taylor, 1986; Able, 2002). Spawning of *F. heteroclitus* in Florida waters, at the southern end of its distribution, was found to extend from February–October (Kneib and Stiven, 1978), with a spawning season extending from the end of May to mid-June in Nova Scotia, at the northern end of its range (Penczak, 1985). Thus, timing of reproductive activity of the species chosen as representative of permanent resident species gener-

ally extended from spring through summer, with that of some species (e.g., *P. gunnellus*) beginning earlier, and a few either widely distributed or limited to the southern portion of the latitudinal range considered here, possibly showing year-round spawning activity. Limited spawning in estuaries in winter by permanent residents or other species may be a result of low and variable temperatures in such shallow areas, coupled with low primary production at this time of year. It has been noted that for estuaries of temperate regions of the American Atlantic coast that peak abundance and diversity of fish species in estuaries occurs during summer months (Merriner et al., 1976). Permanent resident species included some live bearers as well as benthic or nest spawners, the latter of which either attached eggs in or to the substratum, to vegetation, or placed eggs in a constructed nest. Species that are permanent residents of estuarine salt marshes exhibit a number of strategies that prevent their eggs and young from being swept out of the estuary (Dando, 1984; Elliott and Dewailly, 1995; Nordlie, 2000a).

Among those species considered to be marine nursery species (estuarine-dependent in development), timing of spawning activity appeared to be more spread out over the year, with some species showing a spring-summer or spring-summer-fall pattern of spawning activity (e.g., *A. mitchelli*; Breder and Rosen, 1966; Peebles and Flannery, 1992; Pattillo et al., 1997); fall-winter or fall-winter-spring spawning patterns (e.g., *Pseudopleuronectes americanus*; Dovel, 1967; Klein-MacPhee, 2002c), or year-round spawning, at least in warmer portions of their ranges (e.g., *B. chrysoura* and *T. maculatus*; McHugh, 1967; Rogers et al., 1984; Pattillo et al., 1997). Most of those species are broadcast spawners in nearshore to offshore marine areas. However, variations in that general pattern of spawning areas among marine nursery species was shown by three species belonging to the genus *Menidia*. One of those, *M. peninsulae* is found along the Florida coast of the Gulf of Mexico, a second, *M. menidia* along the Atlantic coast and the third species, *M. beryllina*, is found in both areas. All spawn in the spring-summer-fall pattern, but unlike most of the other marine nursery species, all three were found to be estuarine spawners, spawning over sandy bottoms and near the bases of *Spartina* grasses (Breder and Rosen, 1966; Kneib, 1997; Pattillo et al., 1997). Larvae and juveniles of all three are nektonic and pelagic, occurring in schools in estuaries (Haedrich, 1983; Patillo et al., 1997), in some cases extending distributions upstream into fresh waters.

There are also resident FW populations of *M. beryllina* (McLane, 1955; Hubbs, 1982). *M. beryllina* was said to mature in a single year, with few individuals surviving into their second summer (Joseph and Yerger, 1956).

Among other marine nursery species, *L. xanthurus* was reported to spawn along the coasts of the Gulf of Mexico and south Atlantic in the period from October or November to March, with a peak between November and February (Barger and Williams, 1980), while *Micropogon undulatus*, with a more-or-less similar latitudinal distribution, spawned from September through May. The hatchlings of both of those species moved to inshore waters and entered estuaries, requiring 30 to 60 days for the trip, and developed into juveniles in the estuaries (Hoss et al., 1988). Populations of *B. tyrannus*, another marine nursery species with a wide distribution along the Atlantic coast, showed differing times of spawning activity correlated with locations in its geographical range. Spawning activity in waters north of Long Island occurred from May to September, between Long Island and Cape Hatteras, from March to May and again in September and October, and south of Cape Hatteras between October and March (Nelson et al., 1976). Redfish or red drum, *S. ocellata* (included here as a marine nursery species despite apparent flexibility in nursery habitats) was reported to spawn along beaches and in the vicinity of inlets and passes, with multiple spawnings. In the Gulf of Mexico spawnings were reported to occur from August to mid-November with peak activity in September and October (Peebles and Flannery, 1992; Pattillo et al., 1997). The spawning period sometimes extended from mid-September to mid-February in waters of southwest Florida. Along the Atlantic coast spawning was reported to begin in July or earlier and continue to December with a peak in September or October (Mercer, 1984a). Juvenile *S. ocellata* were found to more-or-less permanently inhabit an estuarine marsh creek for as long as 37 months in the northern Indian River Lagoon (Adams and Tremain, 2000). Numbers of individuals in that creek did vary with season, with more individuals present during winter months. Little correlation was found between abundance and ambient salinity (1 to SW) or dissolved oxygen levels (to minimal values of ca. 3.5 ppm). Juveniles of *B. chrysoura*, *C. nebulosus*, *L. xanthurus*, and *Pogonias cromis* were also regularly present in that creek.

C. nebulosus, another sciaenid of the Gulf of Mexico and lower Atlantic coast, again included

here as a marine nursery species though showing flexibility in spawning and nursery habits (Mercer, 1984b), was reported to spawn in bays and nearshore waters of the south Atlantic and Gulf of Mexico, with spawning occurring between April and October, beginning as early as late March in the Cedar Key, FL area (Moody, 1950) and with seasonal peaks in spring and summer (McMichael and Peters, 1989). The species was not known to spawn below an ambient temperature of 20 °C (Gray et al., 1991). Female *C. nebulosus* were shown to vary in spawning characteristics, comparing individuals from five estuarine systems ranging geographically from Redfish Bay, TX to Charlotte Harbor, FL (Brown-Peterson et al., 2002). The conclusion reached regarding persisting differences found among those populations in duration of spawning season, time of peak gonadosomatic index, size at sexual maturity, mean batch fecundity, and spawning frequency was that differing responses to variations in ambient salinities among estuaries was the most plausible explanation for those results. A recent analysis of mitochondrial DNA haplotypes among *C. nebulosus* populations from around the Gulf of Mexico had shown the presence of discrete subpopulations, suggesting 'isolation by distance' (Gold et al., 1999). Some authors had concluded that individuals of *C. nebulosus* remained within an estuary for their entire life history (Tabb, 1966; Brown-Peterson et al., 2002), though that does not seem to be the case for the species throughout its range.

A large fraction of those species considered to be marine transient species showed spring-summer or spring-summer-fall spawning patterns (e.g., *P. saltatrix*, Breder and Rosen, 1966; Norcross et al., 1974; Finucane et al., 1980); others showed a fall-winter, fall-winter-spring, or a winter-spring pattern (e.g., *L. rhomboides*; Caldwell, 1957; Schimmel, 1977); and some showed possible year-round spawning (e.g., *Gadus morhua*; Klein-MacPhee, 2002a). Again, similar to marine nursery species, spawning was primarily broadcast spawning in nearshore to offshore areas with newly-hatched individuals being planktonic.

While the examples above represent only a very small fraction of the 237 species considered to be involved with the 20 estuarine systems considered here, some points seemed evident: (a) there seemed to be some differences in timing of spawning activities among the three life history groups, with apparently more winter spawners among marine nursery and marine transient species than among permanent

residents, and overall, spawning periods did occur in all seasons of the year; (b) spawning activity of all/nearly all of those species persisted over a significant period of time, whether by multiple spawnings of individuals, at different times by different members of a population, or a combination of the two; (c) species with wide latitudinal distributions (e.g., *B. tyrannus*) showed different seasonality of spawning patterns among sub-populations over their range of distribution; (d) permanent resident species spawned in estuarine waters and all/almost all attach their eggs in some fashion; and (e) marine nursery species and marine transients generally spawned in nearshore to offshore areas and were broadcast spawners.

Relationships between seasonality of production in estuarine systems and use by developmental stages of a particular species were not evaluated here. Spawning patterns of migratory species, especially of marine nursery species, appear to be strongly correlated with periods of high marine planktonic primary production, generally with a late summer/early fall peak, and a winter/early spring peak, at least along the Atlantic coast from North Carolina to Florida (Turner et al., 1979; Weinstein, 1981). Plankton production provides the food base for developing zooplankton, especially copepods, on which developing fishes feed. It has also been noted that other possible advantages of winter spawning include slower development at low temperatures that would reduce demands on limited food supplies, reproducing at a time when predation pressure is at a minimum, and taking advantage of favorable currents allowing shoreward transport of the developing fishes (Miller et al., 1984). The time lag between hatching in open oceanic waters and arrival of developmental stages at estuaries would seem adaptive for entering these nursery grounds at the time when ambient temperatures are likely increasing and when primary production is also increasing in these areas (Warlen and Burke, 1990). Times of low estuarine primary production may not be limiting to developing individuals that are primarily detritus feeders, whereas individuals that feed on living algae, or small consumer organisms dependent on live algae, may not find sufficient food to survive during times of the year when primary production is low. Juvenile fishes in estuaries were said to be trophic generalists (Miller and Dunn, 1980), a conclusion drawn in that study for limited groups of marine nursery species, especially juvenile sciaenids that prey on small arthropods. In general, marine nursery species were said to be highly flexible in prey selection.

However, distribution of an appropriate spectrum of prey in time, space, and size was important to their success, as well as was the absence of competing resident species (Thorman, 1982, 1983; Thorman and Wiederholm, 1984). Analyses of trophic interactions in estuarine systems have indicated a high degree of opportunistic feeding by many/most estuarine fishes, resulting in enhanced stability in such systems (Miller and Dunn, 1980; Elliott et al., 2002). It was concluded that a broad niche breadth in feeding habits and wide environmental tolerances were required for success among juveniles of estuarine nursery species.

Thus, annual cycles of spawning are expected to be keyed, in a broad sense, to food availability in nursery areas as well as to ambient conditions, e.g., photoperiod, temperature, and salinity. Spreading spawning activity of any particular population over an extended period, even over the entire year, especially in warmer areas, would seem to reduce the possibility of loss of a year class in a particular region. That would be especially true for areas subject to unpredictable and extreme conditions of weather.

Temperature and salinity relationships

Several environmental conditions could either directly or indirectly limit utilization of estuarine salt marsh systems by fishes in egg, developmental, or adult stages; however, only two major influences, temperature and salinity, were extensively considered here. Anecdotal field observations providing information on ambient temperature and/or salinity conditions, under which individuals of a particular species were collected or found to be living at a particular moment in time, were combined with information from controlled field and laboratory experiments. Coverage was incomplete, with no full elaboration over an annual cycle in a natural setting of expectations of the influences of either ambient salinity or temperature, or their interactions, on a particular species. However, the combinations of available information provide insight into ambient salinity and temperature limits and interactive circumstances, and how those might act in determining acceptable habitats. Information on age or size and degree of sexual maturity was included where available. Some environmental cues that appeared to trigger physiological and/or behavioral responses were also incorporated into the discussion.

Information on ranges of ambient salinity and temperature encountered for each of the estuarine sys-

tems listed was included here (Table 1). As would be expected, estuarine salt marsh systems located in the midregion of the evaluated latitudinal range (25°20'N to 58°30'N) showed the widest annual ranges of ambient temperatures. It had been suggested (Bulger, 1984) that there was a decrease in mean annual water temperature of 1°C/°latitude from Florida northward along the Atlantic coast of North America. There did not seem to be any predictable pattern of variations in ambient salinities among the included group of salt marshes, though it might be expected that evaporation would be greater in warmer areas, resulting in potentially higher salinities in shallow waters, especially at low tide on clear, windy days. The most extreme situation noted was in Indian River, FL impoundments, where ambient salinities ranged from 2–200, with salinities in excess of SW being produced by evaporation during periods when the impoundments were cut off from tidal exchanges (Gilmore et al., 1982). Some among the 20 systems considered here typically had variations from FW, or near to it, to a mid-range of salinities, others from mid-range salinities to normal SW or higher, but most showed at least annual variations from near FW to near SW. Temperature and salinity relationships will first be discussed separately, with further consideration of some interactions of these conditions.

Temperature

Some species with the wide latitudinal ranges do have wide thermal tolerance/habitat occupation limits, but not exclusively so. Some of these do not vary greatly from species with limited distributions in any part of the latitudinal range considered here. While temperature ranges for successful spawning of many of the marine nursery and marine transient species were frequently found to be at mid-ranges of temperatures tolerated by juvenile and adults of those species, that was not always the case. A number of northern species have been shown to spawn in winter at relatively low ambient water temperatures, while widely distributed *M. cephalus* spawn from late fall through the winter and into late spring, depending on the population.

Information was not included on water temperatures in the North River study, the most southern of included estuaries (Odum and Heald, 1972). However, annual water temperature extremes in Everglades areas near to the North River site ranged from lows of 6–7°C to highs of 35–37°C (Loftus and Kushlan, 1987). Water temperatures at the Texas locations ranged from a low of 0.21°C to a high of 34.9°C

(Gunter, 1945), with monthly mean values ranging from 13.41°C to 29.86°C. Only lowest water temperatures (<0°C) were given for the James and Hudson Bay locations (Morin et al., 1980), but stations were reported to be ice-covered through much of the year (Table 1).

Species were organized by life history categories in making comparisons of ambient temperature and salinity conditions known to be tolerated (based on laboratory analyses) or in which the species had been found to be surviving in nature (occupied). Highest ranges of environmental temperatures tolerated or occupied were generally by species from the southern end of the included range of distribution, and lowest temperatures tolerated or occupied were characteristic of species from the northern end of the distribution, as would be expected. Species with the widest ranges of distribution showed wide ranges of temperature tolerance or occupancy, especially for species with distributions extending from subtropical areas into cold temperate waters. That seemed consistent with the concept that temperature-preference relationships of fishes have evolved as functions of the amplitudes of the annual thermal cycles experienced by individuals of a particular species (Johnson and Kelsch, 1998). Those experiencing annual cycles of relatively high amplitude (e.g., temperate species) should show positive responses in thermal acclimations. Those with low amplitude in thermal cycles (e.g., cold stenotherms or tropical mesotherms) would show thermal tolerance relationships that were either independent of or negative functions of acclimation temperatures (the negative function was exhibited in *Gambusia affinis*, but an adaptive basis for this could not be rationalized; Johnson and Kelsch, 1998).

The widest tolerable/occupied temperature ranges reported for estuarine permanent resident species was for *C. variegatus*, which ranged from a low of –1.8 (Bennett and Beiting, 1997) to a high of 43°C (Harrington and Harrington, 1961). The range reported for this species in Delaware waters was 2–33°C (Warlen, 1964). In laboratory analyses individuals of *C. variegatus* exhibited a critical thermal maximum (CTM) of 45.1°C (Bennett and Beiting, 1997). At ambient temperatures below 10°C, individuals of that species have been found to burrow into the substratum, which functions to maintain their body temperatures above the freezing point of the water. *C. variegatus* was also found to have the largest physiological thermal tolerance zone of any fish that has been measured (Bennett and Beiting,

1997). *C. varietatus* was said to spawn in the temperature range 17.4–27.5°C (Florida; Harrington and Harrington, 1961). Thermal tolerance limits were found to range between –1.5–32°C for *F. heteroclitus* (Massman, 1954; Umminger, 1971a). Both of those species have extensive distributions along the Atlantic coast, with *C. variegatus* also extending along the Gulf coast. Collections of *A. xenica*, *F. confluentus*, and *F. similis* were reported from waters ranging in temperature from 7–38°C (Cedar Key, FL), all of which species have native distributions limited to southern portions of the included latitudinal range (Nordlie, 1987; Nordlie and Haney, 1998). *F. majalis* was reported taken at temperatures within the range of 7.5 to 31.7°C (Virginia; Richards and Castagna, 1970). The minimal thermal occupancy limits for most of those species would likely be lower than 7°C in areas north of where those observations were made. Another estuarine permanent resident, limited in distribution to waters of the Gulf of Mexico and the Florida peninsula, *F. grandis*, was found to spawn within the range of temperatures from 4–33°C, tolerating temperatures from 2–34.9°C in developmental and adult stages (Renfro, 1960; Pattillo, et al., 1997).

Among marine nursery species, *B. tyrannus*, a widely distributed species (Jupiter Inlet, FL to Nova Scotia; Dahlberg, 1970), was reported collected from waters varying in ambient temperatures from 0–25°C (Massman, 1954; Kendall and Reintjes, 1975). Another widely distributed species, *A. mitchelli*, was reported from waters ranging from 4.5–39.8°C (Simmons, 1957; Pattillo et al., 1997) and spawning in the range of 22–32°C. A northern species, *P. americanus*, was taken over a range of temperatures of –1.4–19.3°C (Duman and DeVries, 1974). Two other marine nursery species with more southern distributions, *L. xanthurus* and *M. undulatus* (Hoss et al., 1988), spawned at ambient temperatures ranging from 18–25°C. Larvae were found to remain in coastal waters for 30–60 days before entering estuaries where they developed into juveniles at cooler ambient water temperatures (6–14°C). *M. undulatus* was found to enter estuaries earlier than *L. xanthurus* and as a result faced colder temperatures. The lethal minimal temperature for *L. xanthurus* was 4–5°C, and varied with size, suggesting that *L. xanthurus* larvae entering estuaries during especially cold periods might be killed by lower water temperatures (Dawson, 1958).

The most widely distributed of species inhabiting estuaries of the Gulf and Atlantic coasts of North

America, based on the fraction of the total number of collection sites at which a species was taken, included *M. cephalus* (listed here as a marine nursery species), reported to have a world-wide distribution between 42°N and 42°S latitude (Thomson, 1966). Temperature limits reported for the species vary widely, based on work carried out in different geographical locations. The species was found to have an optimum of 21–24°C for spawning, and an overall tolerable range of 5–37°C for juveniles and adults (Pattillo et al., 1997). *M. cephalus* was shown to have a CTM that was significantly altered by acclimation temperature and also altered during the day, with a peak near midday (Sylvester, 1975). Upper CTM increased from 38.5°C at an acclimation temperature of 20.0°C, to 41.3°C at an acclimation temperature of 29.0°C, all at ambient salinities of 32–33, in experiments carried out in Hawaii. Thermal tolerance limits for *M. curema* were somewhat higher than for *M. cephalus* (11.8°C, Tagatz and Dudley, 1961; to 39.0°C, MagoLeccia, 1965) for this closely-related but somewhat more southern species. It had been suggested (Moore, 1974) that *M. curema* was rarely found at ambient temperatures below 20°C. It might also be expected that populations from different geographic areas of such widely-distributed species as these two species of mullets would show differing responses to environmental conditions among locations.

Larvae of *P. saltatrix*, a marine transient, were taken in tows made in the Gulf of Mexico at temperatures of 23.9 and 25.7°C (salinity 36.10, Barger et al., 1978). Minimal acceptable temperature for *P. saltatrix* spawning was said to be 18.0°C (salinity 26.6) on the east coast of the U.S. (Norcross, et al., 1974), and the species was shown to spawn over the temperature range of 18–26.3°C, with later life stages tolerating temperatures from 11.9–29.8°C (Pattillo et al., 1997). *G. bosci*, was taken in waters ranging in temperature from 0.5–33.2°C (Dahlberg and Conyers, 1973), while adults of *Caranx hippos* occupied a more limited thermal range of 15–38°C (Pattillo et al., 1997). Another marine transient identified in estuaries from Georgia to Massachusetts, *P. dentatus*, was found to survive an ambient temperature of 2°C for up to 8 days, with greater mortality among smaller than larger individuals (Malloy and Targett, 1991). They could survive indefinitely at an ambient temperature of 3°C. Salinities of 10–30 had no significant influence on survival, but a small interaction of temperature and salinity was found in growth rate, with higher growth rates at elevated temperatures and salinities.

The ranges of water temperatures at which freshwater transients were collected were similar to those of species belonging to other life history groups. *G. holbrooki* was reported collected at ambient temperatures ranging from 7–38 °C (Nordlie and Mirandi, 1996), and *Dorosoma cepedianum* was taken at temperatures ranging from 8.8–30.5 °C (Gunter, 1945; Renfro, 1960; Tagatz, 1967), with *G. holbrooki*, being a southern species, while *D. cepedianum* has a distribution extending as far north as the St. Lawrence river (Eddy, 1957), so would be expected to occupy waters at temperatures down to $\cong 0$ °C in the northern part of its range.

Data were not included on thermal tolerances/occupancies for diadromous species, but anadromous species from colder areas, e.g., James and Hudson Bays, would encounter temperatures of $\cong 0$ °C through significant periods of the year (Morin et al., 1980). Populations of *S. salar*, an anadromous species, had lower thermal limits for growth from a series of colder Norwegian rivers than did populations from warmer rivers. Such differences led to differences in sizes at smolt-parr transformation and differences in sex ratios among populations (Jensen and Johnsen, 1985). *A. rostrata*, a catadromous species with a distribution along coasts of the Gulf of Mexico and Atlantic of North America (Eddy, 1957), would be expected to have wide thermal tolerance limits, from freezing or near freezing temperatures, likely into the 30s.

Salinity

Fish that enter and remain for any significant period of time in salt marsh systems encounter fluctuations in ambient salinity, potentially over wide ranges in many situations. Generally those habitats also may simultaneously fluctuate in ambient temperature levels and in other ambient conditions. The more extensive coverage of responses to environmental salinities was consistent with conclusions drawn in many studies that salinity is one of the prime environmental factors, directly and indirectly involved in determining patterns of species associations in estuarine salt marsh systems (e.g., Gunter, 1961; Kinne, 1964, 1966, 1967; McHugh, 1967; Hoff and Ibara, 1977; Weinstein et al., 1980; Haedrich, 1983; Whitfield, 1983, 1999; Rogers et al., 1984; Thorman and Wiederholm, 1984; Cyrus and Blaber, 1992). An accepted generalization has been that young of coastal species of invertebrates and fishes often show greater tolerance of reduced salinities than do adults of the same species (Gunter, 1961). That was based on the presence of young, but

not adults, of many marine species in salt marshes. Questions asked here of individuals of species that occur in salt marsh systems focused on ranges of ambient salinities tolerated; possible changes in tolerances in different ontogenetic stages; interactions with ambient temperature and/or with other environmental conditions; and possible roles played by prior salinity environments in determining present responses and tolerances.

Salinity tolerance or salinity occupation patterns of representative groups of all five life history classes were included in this discussion. Species chosen as examples for discussion of salinity tolerance limits from among those considered to be permanent residents of estuarine salt marshes included: several members of the family Fundulidae (*A. xenica*; *F. confluentus*, *F. grandis*, *F. heteroclitus*, *F. majalis* and *F. similis* [or *F. majalis similis*]; and *L. parva*), two members of the Cyprinodontidae (*C. variegatus* and *F. carpio*), and one member of the Poeciliidae (*P. latipinna*). The widest salinity range over which any of these species had been found to be surviving in nature was FW – 167 for *C. variegatus*, based on field observations (Gilmore et al., 1982). Prior to that, individuals had been found surviving in a tidepool in which the salinity had risen to 142 (Simpson and Gunter, 1956). Individuals of *C. variegatus* have been acclimated in the laboratory to a salinity of 125, with some individuals kept alive to a salinity of 135 in long-term studies (Nordlie, 1985, 2000a). This species also has freshwater populations (Kaill, 1967).

Salinity tolerance limits for *Fundulus* species, including *F. confluentus*, *F. grandis*, *F. heteroclitus*, *F. majalis*, and *F. similis*, all of which are considered permanent estuarine residents, range from FW (or very near to it) to salinities of at least 100 (based on a combination of field observations and laboratory experimental work (Massman, 1954; Renfro, 1960; Joseph and Saksena, 1966; Schmelz, 1970; Dahlberg, 1972; Griffith, 1974; Pattillo et al., 1997; Nordlie, 2000a, b). The first two species have distributions limited to the Gulf of Mexico and the lower Atlantic coast, while the third has a wide distribution from north Florida to Maine along the Atlantic coast, and the fourth (including *F. similis*) is distributed around the Gulf of Mexico and up the Atlantic coast to New Hampshire (Relyea, 1983). *F. heteroclitus* larvae obtained by hormone-induced spawning and hatched in water with a salinity of 25.3 at a temperature of 21 ± 2 °C, were found to have a salinity tolerance range extending from 0.39 at the lower end to >100 at

the upper end of the range (Joseph and Saksena, 1966). They were unable to acclimate individuals to a salinity as low as 0.16. Other species included in this group not known to tolerate (based on laboratory studies) or occupy (field observations) waters ranging to salinities as high as 100, included *L. parva* (FW – 80, Dunson and Travis, 1991), *F. carpio* (0.5–90, Nordlie and Walsh, 1989), and *P. latipinna*. *P. latipinna*, a resident around the Gulf of Mexico and south Atlantic coast, also has extensive FW populations (Rosen and Bailey, 1963). Individuals from FW populations of the species were found to tolerate a range of ambient salinities from FW to 70, while individuals from brackish waters tolerated a range from FW to 80 (temperature of $20 \pm 1^\circ\text{C}$; Nordlie et al., 1992).

Species included in the marine nursery category generally showed wide ranges of salinity tolerances, but only one was reported to extend to a salinity as high as 100, *M. beryllina* (FW – 120, Simmons, 1957; Renfro, 1960; Copeland, 1967; Hubbs, 1982). *M. cephalus* was reported to be found occupying waters with salinities ranging to 90 (South Africa, Wallace, 1975), and adults of the species were regularly found in FW situations (Kilby, 1955; Tagatz and Dudley, 1961; Nordlie et al., 1982; Blaber, 1987). Other species included in the group known to occupy waters with wide ranges of salinity included *A. hepsetus* and *A. mitchelli* (FW to 75–80, Simmons, 1957), *B. patronus* (FW – 54.3, Renfro, 1960), and *T. maculatus* (FW – 50, Simmons, 1957). Some marine nursery species show narrow ranges compared to others in the group. Examples of species with narrow salinity ranges included *Selene vomer* (collected at 8.6–45.2, Roessler, 1970) and *Diapterus olisthostomus* (0.7–31.3, Dahlberg, 1972). However, it should be expected that the latter species occupies and tolerates waters with salinities as least as high as SW ($\cong 35$). Developmental stages of *B. tyrannus* (Massman, 1954), another marine nursery species, were said to be 'euryhaline', but this capability was found to be increasingly lost with development.

Eggs of *M. cephalus* were found to hatch over the salinity range of 10–55 (Lee and Menu, 1981), but larvae did not survive at salinities of either 10 or 55. An optimal salinity range for hatching of 30–40 at ambient temperatures in the range of 22.0 – 25°C was suggested, while in another study an optimal salinity range for hatching of *M. cephalus* eggs was suggested to be somewhat lower, 17–35 (Mires et al., 1975). In a third study, optimal conditions for hatching of *M. cephalus* eggs were found to be at ambient salin-

ities in the range from 32–34, and at ambient temperatures between 22.8 – 23.5°C (Sylvester et al., 1975). Best survival of *M. cephalus* eggs was in the salinity range 30–32. Minimal egg survival occurred in the salinity range 26–28 when incubated at temperatures in the range 19.5 – 20.5°C . Also, a significant decrease in egg survival was noted at dissolved oxygen concentrations <5.0 ppm, and for larvae, concentrations of <5.4 ppm (Sylvester et al., 1975). No differences were detected in survival of newly-hatched *M. cephalus* kept in salinities of 17–18, 22–23, 27–28, or 32–35 (25.3 – 25.9°C) in short-term experiments (15 days), but individuals in 22–23 salinity group grew most rapidly of the experimental groups (Murashige, et al., 1991). In long-term experiments (50 days) no significant differences were found among salinity groups in either survival or growth rates (22.2 – 26.0°C).

Prejuvenile individuals of *M. cephalus* at sizes averaging ca. 20 mm (SL), typically enter estuarine waters where they remain until reaching a size of ≥ 55 mm (SL), at which time they may move to deeper waters (Kilby, 1955; Major, 1977; Nordlie et al., 1982; Blaber, 1987). Small individuals found in salt marshes were noted to be intolerant of FW (Nordlie et al., 1982; Rogers et al., 1984), while adults are extremely euryhaline (Hedgpeth, 1967; Wallace, 1975; Blaber, 1987). Lower and upper lethal thermal limits were altered by salinity environments in *M. cephalus* (Sylvester et al., 1974). Again, we might expect differences in responses to salinities among geographically separated populations of such a widely distributed species.

C. nebulosus, another marine nursery species, has been reported from waters ranging in salinity from 0.2 to 75 (Simmons, 1957; Pattillo et al., 1997). Ranges of salinities tolerated by its eggs were observed to vary among studies: 15 to 21 (Saucier and Baltz, 1993); peak for Florida, 30–35 (Tabb, 1966); under laboratory conditions, 25 to 30 (Arnold et al., 1976); from 19 to 38 (Simmons, 1957; Pattillo et al., 1997). Salinities of 20 to 28 were found to be optimal for growth, maturation, spawning, and survival of larvae for the species (Wohlschlag and Wakeman, 1978). Both upper and lower salinity tolerance limits showed an age-linked pattern among larvae from *C. nebulosus* eggs hatched at salinities of 24 and 32, as well as in larvae of the species acclimated to hypersaline and to brackish waters (Banks et al., 1991). Minimal range of salinity tolerance was found in 3-day-old larvae (6.4 – 42.5), increasing to a maximal range at day 9 (last day tested, 1.9 – 49.8). While larvae hatched at

32 in those experiments showed an acclimation to hyposaline conditions, no acclimation to hypersaline conditions was apparent.

Known salinity tolerances or observed salinity occupancies of marine transient species presented here were generally more limited than those of marine nursery species, though some species showed extended ranges of salinity occupation including *L. rhomboides* (2–75, Simmons, 1957; Hedgpeth, 1967) and *Lutjanus griseus* (juveniles FW – 66.6, adults FW to 47.7, Pattillo et al., 1997). Species included in this group with known limited ranges of salinity tolerance or occupancy included such species as, *Carcharhinus leucas* (FW – SW, Pattillo et al., 1997), *Opisthonema oglinum* (FW – SW, Tagatz, 1967), and *P. saltatrix* (adults 7.0–36.5, Pattillo et al., 1997). Among other species generally regarded as marine transients, both juveniles and adults of *Megalops atlantica* (Pattillo et al., 1997), were found to be 'euryhaline', and individuals of *Elops saurus* were reported to survive over the salinity range from 0.1 to 75, and were found to spawn from brackish to hypersaline waters (Dahlberg, 1972; Simmons, 1957). Adults of *P. saltatrix* were found to inhabit waters of salinities ranging from 7.0 to 36.5, while their eggs survived the range from 26.6 to 34.9, larvae from 26.7 to 38, and juveniles from 8.0 to 36.2. Adults were noted to prefer the salinity range from 26.6 to 34.9 (Pattillo et al., 1997). All of these species seemed to show a high degree of euryhalinity, at least in some life stages, based on these limited sets of data, but there appeared to be significantly varying patterns of ontogenetic changes in salinity tolerances among species. A large fraction of species included in this group are capable of occupying waters of salinities significantly lower than SW, suggesting that those species, while possibly unable to enter estuarine systems at times of high FW input, can enter when salinities are not severely reduced.

Diadromous species would all be expected to tolerate salinities ranging from FW at least to SW, but not necessarily tolerate that full range in all life stages. Ontogenetic change in salinity tolerances was exhibited in the anadromous *A. sapidissima*, in which developing individuals previously inhabiting FW areas of estuarine systems apparently lost their ability to osmoregulate in FW as the temperature dropped in the fall (Zydlewski and McCormick, 1997). *D. maculatus*, an amphidromous species, was shown to have wide salinity tolerances, at least in the adult stage (FW – 75, Nordlie and Haney, 1993).

That species spawns in brackish waters, with newly-hatched individuals beginning development there or in nearshore marine waters, with individuals returning to the estuary as development continues, and gradually moving upstream to FW areas where adults generally remain except during spawning periods (McLane, 1955; Nordlie, 1979, 1981; Flores-Coto and Garcia, 1982; Teixeira, 1994; Winemiller and Ponwith, 1998).

Few freshwater transients were known to enter or remain in waters as concentrated as that of SW. Exceptions were *D. cepedianum*, larger juveniles of which were taken from waters of 41.3 (Renfro, 1960), and *Jordanella floridae*, adults of which were found to indefinitely tolerate salinities as high as 80 (Nordlie and Walsh, 1989). The latter species was not reported from any of the 20 included estuarine systems, but is a common species in both hard fresh waters and brackish waters along the Florida coast (Kilby, 1955; Brockmann, 1974; Loftus and Kushlan, 1987; Nordlie and Walsh, 1989). Most typical FW species that enter estuaries do so in dilute areas and/or at times of high FW discharge. Known upper salinity tolerance/occupancy limits of a large fraction of such species populations have been found to be no higher than that of normal SW, or significantly lower (e.g., 25 in *G. holbrooki*, Nordlie and Mirandi, 1996). A more typical stenohaline FW species that occurs in upper regions of estuaries fed by rivers, *Cottus cognatus*, was reported from waters no more saline than 1.0 (Morin et al., 1980).

Species that cannot tolerate high salinities for extended periods have been found in such situations for short periods, while species known to be unable to tolerate FW indefinitely have also been found to enter such waters for short periods of time. It has been generally assumed that such occurrences of either sort were in areas where movement to a more favorable salinity regime was easily possible. Those patterns described in this section represent examples of variations in salinity habitats and/or tolerances, of preferred salinity ranges with respect to selected spawning areas, subsequent environments where development takes place, or of salinities of adult habitats. While anecdotal information does not provide exact answers, such information helps generate a basis of understanding of the general distributions of those species able to make use of estuarine salt marsh habitats. Existing information suggests that there is no common pattern of salinity response among such species, but there are some critical salinity ranges

and also some critical periods in the typical life cycle with respect to salinity responses (Nordlie and Haney, 1998). As might be expected, the species with the widest ranges of salinity tolerances/occupancy are those that most regularly face such environmental variations, species that are permanent residents or marine nursery species in estuarine salt marsh habitats (Nordlie, 2000b).

Temperature x salinity, and other environmental interactions

Influence of environmental salinity on resistance to high temperature in 10 species of teleosts found in Texas estuaries included six species of fundulids, *A. xenica*, *F. chrysotus*, *F. grandis*, *F. pulverus*, *F. similis*, and *L. parva*, and the cyprinodontid *C. variegatus* (Strawn and Dunn, 1967), which were found to be more resistant to high temperatures than were the poeciliids, *G. affinis* and *P. latipinna*, or the centrarchid *Lepomis symmetricus*. The centrarchid was found to be the least resistant to elevated temperatures of the 10 species. Salinities at which all of these species showed highest heat resistance were near to concentrations isosmotic to their blood plasma. A similar phenomenon was demonstrated in *F. diaphanus* and *F. heteroclitus* (Garside and Jordan, 1968). Again, the upper lethal temperature for both species was found to be highest at an ambient salinity near to the isosmotic level for the blood of each species.

Changes in daily photoperiod produced changes in salinity selections and migrations to waters of greater or lesser salinity in *G. aculeatus* (Baggerman, 1957), and a similar photoperiod effect on salinity selection was demonstrated in *F. grandis* (Spieler et al., 1976). However, changes in water temperatures, except during the postspawning period, were found to be stronger cues to altering preferred salinities than was daily photoperiod in *F. grandis* (Miller et al., 1983). Responses in lower thermal tolerance limits and in blood serum osmotic concentrations following acclimation to ambient temperatures near freezing were compared between *F. grandis* and *F. heteroclitus* (Umminger, 1969a, b, 1971a). *F. grandis* ranges from the Laguna de Tamiahua, Mexico, roughly to the mouth of the St. Johns river in north Florida (Relyea, 1983). The southern limit of distribution of *F. heteroclitus* overlaps slightly with that of *F. grandis*, and extends northward along the Atlantic coast to Port au Port, Newfoundland (Leim and Scott, 1966). In accli-

mation studies, individuals of *F. grandis* were found to survive acclimation to 4°C, but not -1.5°C (7-day experimental period, ambient salinities of 27 and 33), conditions tolerated by individuals of *F. heteroclitus*. Both species were found to show significant increases in serum osmotic concentrations at temperatures near freezing. No similar increases in serum osmotic concentration were demonstrated (Umminger, 1970) in individuals of *F. heteroclitus* acclimated to temperatures of 11, 4, and 0.1°C in FW, though there are FW populations of that species (Denoncourt et al., 1978; Samaritan and Schmidt, 1982). Also, a daily rhythm in the critical thermal maximum was demonstrated in *F. heteroclitus* (Bulger, 1984). That rhythm was apparently keyed by photoperiod, but persisted for at least 30 days in total darkness. The period of highest maximal thermal tolerance was found to be at noon when the ambient temperature was near its daily peak.

Metabolic rate in juvenile *T. maculatus* was found to be lowest at a salinity of 7 compared with rates in FW and at 15 (Peterson-Curtis, 1997). It was concluded that salinity intolerance in this species did not drive juvenile summer migrations to waters of low salinities, but rather resulted in selection for occupying salinities that were energetically less costly at existing ambient temperatures.

A triggering in synthesis of antifreeze glycopeptides (AFGP) by reductions in daily photoperiod was demonstrated in *P. americanus* (Fletcher, 1981), a process shown to protect individuals of the species from freezing at subzero water temperatures. It was later shown (Fletcher and King, 1987) that the production of AFGP in *G. morhua* was triggered by reductions in water temperatures to levels of <1°C. It was suggested that differences in life histories of the two species resulted in evolving two different triggering systems, *G. morhua* being a widely-ranging species that might not encounter subfreezing water temperatures at predictable times, while *P. americanus* with a more localized home range, would encounter such temperatures at predictable times in a normal annual cycle. Other analyses (Fletcher and Smith, 1980) had demonstrated significant permanent differences in the timing of synthesis of plasma protein antifreeze components between Nova Scotia and Newfoundland populations of *P. americanus*. *M. scorpiodes*, a circumpolar species, showed a change in serum osmotic concentration from 392 mOsm \cdot l $^{-1}$ in July (12–17°C) to 440 mOsm \cdot l $^{-1}$ in October in the Izembek lagoon on the Bering Sea where

winter temperatures dropped to -1.43°C to -1.75°C . *G. aculeatus*, another lagoon resident in the summer, did not show a similar adjustment in plasma osmotic concentration, migrating to fresh waters during the winter (Smith and Paulson, 1977).

Generalizing from a number of studies it was found that plasma osmotic concentration increased in a number of species from colder latitudes at acclimation temperatures within a few degrees \pm of 0°C , but not at higher temperatures (Burton, 1986). Plasma Na^{+} , K^{+} , Cl^{-} , and osmotic concentrations in *M. cephalus* were evaluated following acclimation at 5°C intervals over the range of ambient temperatures from 10 to 30°C in SW (Nordlie, 1976). Consistent increases in Na^{+} , Cl^{-} , and total osmotic concentrations were found over that temperature range, while there were no significant changes in plasma K^{+} . The acclimation temperature range was considered to be analogous to a typical range for that species over its wide geographical distribution in seas of both north and south temperate zones. The pattern of response was considered to be more typical of a FW teleost fish than of a marine species (Umminger, 1971b). However, there seemed to be no clear and consistent relationship between acclimation temperature, plasma osmotic concentration, plasma Na^{+} or Cl^{-} , based on published information on freshwater teleost species (Burton, 1986).

Nonindigenous species in salt marshes

Introduction and establishment of nonindigenous fish species in estuarine systems has been more limited compared with that in fresh waters, though there are well-known successful introductions of species that occur in estuaries. A number of species of salmonid fishes have been introduced in various areas, perhaps among the best known of which are of *S. trutta* from Europe to North America, as well as to other continents, and of *Oncorhynchus mykiss* from western to eastern North America, as well as to many other parts of the world (Courtenay et al., 1991). Some populations of both of those species are anadromous. In another successful introduction, striped bass, *M. saxatilis*, native to the Atlantic coast of North America were established on the Pacific coast (Scofield and Bryant, 1926). There have been widespread introductions of *G. affinis*, *G. holbrooki*, and *P. latipinna* (Courtenay and Meffe, 1989), all of which may occur in estuaries, to other regions for mosquito control, not necessarily effectively so, and sometimes

producing unexpected problems (e.g., Howe et al., 1997; Fuller et al., 1999).

Examples of generally unintentional translocations have involved *L. parva*, a small estuarine permanent resident species that is widely distributed along the east coast of North America, and which also has FW populations (Table 2). That species was reported to have established populations in the states of California, Nevada, New Jersey, New Mexico, Oregon, Texas, and Utah. Where the origins of introduced individuals were known, most apparently occurred as individuals or their fertilized eggs accompanied introductions of other species of fishes, of oysters, or were in ballast waters (Fuller et al., 1999).

Florida has had a large number of new species introduced into its waters recently, including a large number of species of cichlids (Fuller et al., 1999). The most widely distributed of those nonindigenous cichlids in Florida waters was said to be *Oreochromis aureus*, first reported to be reproducing in estuarine waters in Tampa Bay and connected waters (Courtenay et al., 1986; Fuller et al., 1999). At least two other cichlid species, *Sarotherodon melanotheron*, a plankton/benthos feeder (Faunce, 2000), and *Cichlasoma urophthalmus*, said to be a voracious predator (Fuller et al., 1999), have been found to reproduce in mangrove systems. *S. melanotheron* was first documented to be established in brackish and fresh waters of eastern Hillsborough Bay and adjoining waters, and later in ditches and saline waters of the Banana and Indian river lagoons of east Florida (Fuller et al., 1999). It was found to successfully reproduce in a seasonally impounded mangrove system associated with the Indian River lagoon, at ambient temperatures above 24°C (months of April through October, Faunce, 2000). *C. urophthalmus* was noted to spawn at salinities of 26 and 10 (1984 and 1985, respectively) in Snook creek in south Florida (Loftus, 1987), and was reported to reproduce in mangrove systems of south Florida where growth and survival of the young were more influenced by water levels and salinity than by ambient temperature (Faunce and Lorenz, 2000). A fourth cichlid, *O. mossambicus*, has the potential to inhabit estuarine areas (Courtenay et al., 1974), as it was considered to be a hardy species, very tolerant of elevated salinities (Dial and Wainwright, 1983), but said not to survive temperatures below ca. 10°C , so at present is limited to warmer regions (Fuller et al., 1999).

Another small but voracious predator species introduced into south Florida that became established in

mangrove swamps, as well as in fresh waters, was *Belonesox belizanus*, a livebearing poeciliid (Fuller et al., 1999). That species has been reported to reproduce in salinities at least as high as 35 (Turner and Snelson, 1984).

Answers to questions of how widespread such successful introductions have been or may become and what the impacts of those species might be on the indigenous faunas are presently unknown. Certainly such introductions do add to the potential for significant alterations in the biotas, organization, and production of estuarine salt marsh systems.

Profile of estuarine salt marsh resident fishes – eastern North America

A summary of characteristics, ecological, behavioral, physiological, and ontogenetic, was made of species that were considered to be permanent residents in estuarine salt marsh systems, to determine what similarities existed among species in those characteristics. While all of the various kinds of available information could not be included in discussions presented here, selecting those aspects incorporated in this paper led to the following points.

1. There are few species that can be considered permanent residents of estuarine salt marshes (spend their entire lives in the salt marsh, going through every life stage in this habitat), but among those, a large fraction are latitudinally widely distributed.
2. Spawning periods of these species are variable in duration, generally extending over several months, and can be almost any time during the year, or extend throughout the year in warmer areas, sometimes involving multiple spawnings.
3. Adult individuals of salt marsh residents show tolerances to wide variations in ambient salinity, usually from FW or near to it, to salinities of 80 or higher. Few marine nursery species or marine transients show such broad salinity tolerances.
4. Eggs, fry, and juveniles of salt marsh resident species are generally capable of surviving and developing over a wide range of ambient salinities, in many cases from FW, or near to it, to hypersaline concentrations.
5. While a few salt marsh resident species do frequent nearshore marine waters, they do not typically extend distribution to open marine waters.
6. There appear to be some species that qualify as permanent residents of salt marsh estuaries

in some situations or localities, that are typical marine nursery species, or even marine transient species in other locations. Also, some permanent residents of salt marsh estuaries have established FW populations in some areas. Examples include (among others) *C. variegatus*, *F. confluentus*, *F. grandis*, *F. heteroclitus*, *L. parva*, and *P. latipinna*.

7. Thermal tolerance limits are incompletely known for most salt marsh resident teleosts, but it appears that there is no common pattern among such species, as known thermal limits vary considerably from species to species, with some having limited ranges of thermal tolerances at either warm or cold temperatures, while other species showing similar latitudinal ranges in distributions have wide limits in temperature response. However, species showing widest latitudinal distributions generally exhibited the widest temperature limits.

Others have reached many similar conclusions (e.g., Dando, 1984; Thorman, 1986b), that few species of fishes are resident, but those that are, are numerous, are small in size, nest-building, brood-caring, and more-or-less generalists in food habits and habitat utilization. There are a number of other characteristics of permanent residents species of estuarine salt marshes that have been developed from other data, but which were not based on aspects of estuarine life discussed here. Three of the major points included: species with the widest ranges of salinity tolerances are the most ubiquitous among salinity habitats that may range from FW to extremely hypersaline; physiological responses to ambient salinity provide only “coarse tuning” in determining habitat occupation in salt marshes and adjacent waters; and variations in physiological limits with respect to ambient salinity and temperature do not appear to directly reflect the closeness of phylogenetic relationships among fishes (Nordlie and Haney, 1998; Nordlie, 2000a, b).

Fishes of estuaries of western Europe

Two recent extensive analyses of fish inhabitants of western European estuarine locations were available for comparison with information from eastern North America. Estuaries at 17 locations along the coast of western Europe extending geographically from 38°40'N latitude (Tagus, Portugal) to 59°10'N latitude, (Oslofjord, Norway, Elliott and Dewailly, 1995) were included in the earlier of these works. The second of the analyses (Pihl et al., 2002) was

more extensive, including information on 25 estuarine locations ranging from 36°N latitude (Bay of Cádiz and Guadalquivir, Spain) to 60°N latitude (NW Åland, Sweden), an analysis with a broader geographic range that combined additional information along with that from some of the estuaries evaluated in the previously mentioned study. The group of 25 locations was subdivided into three zoogeographic areas: Baltic/Skagerrak (5 locations); Atlantic/Boreal (18 locations); and Mediterranean (2 locations).

The total number of species of fishes reported from the group of 17 estuaries was 186, belonging to 69 families (Elliott and Dewailly, 1995), including some species from deeper waters, as well as a number of freshwater species. The mean number of species per location in that study was 45.8. A similar evaluation was made for the more extensive group of 25 estuarine locations that yielded a total of 255 species representing 79 families. The mean number of species taken per estuarine location for the latter group was 56.7, but collections were carried out over a wider range of habitat types (Pihl et al., 2002). In the present study of estuaries of eastern North America the average number of species per estuarine location was 42.5 (44.8 including stations with higher salinities, Table 1), roughly similar to the values for the 17 estuarine locations, but appreciably lower than that of the 25 European estuaries.

Families represented by greatest numbers of species (those with five or more species) in the more extensive analysis included: Cyprinidae (26); Gobiidae (20); Sparidae (18); Gadidae, Labridae, and Soleidae (10 each); Syngnathidae (8); Salmonidae and Pleuronectidae (7 each); Clupeidae, Phycidae, Mugilidae, and Blenniidae (6 each); and Rajidae, Cottidae, and Triglidae (5 each). The large number of cyprinids suggests that collections were made well up into river headwater as few of these species are euryhaline. Six of these families were common to both the estuaries included here from eastern North America and western Europe: Clupeidae, Salmonidae, Gadidae, Phycidae, Gobiidae, and Cottidae.

An analysis similar to that done on latitudinal variations in numbers of species over latitude and in life history grouping carried out for estuaries of eastern North America was done for species of the 25 western European estuaries. Regressions were run, first regressing total numbers of species found in each of the 25 estuaries on latitude. No significant relationship was found here ($Y = 41.061 + 0.321X$, $p = 0.5735$). The results of that analysis were quite similar

to those reported here for the estuaries of eastern North America, though one set of those species numbers did show a marginally significant negative relationship to increasing latitude. When a large number of estuarine systems, located over a wide geographical range, is included, without standardization in times of collections, in techniques, or in collecting efforts, it is not unexpected that numbers of species collected per system might show significant variation (Elliott and Dewailly, 1995). Next, percentages of permanent residents were regressed on latitude for the group of 25 estuaries, with no significant relationship found ($Y = 15.255 + 0.137X$, $p = 0.4036$). However, percentage of marine migrants, a combination of marine juveniles, marine adventitious, and marine seasonal species ($= MN + MT$ species for North American estuaries) showed a (weak) significant negative relationship to latitude for the series of 25 estuaries ($Y = 99.200 - 0.960X$, $p = 0.0495$). Again, as for North American estuaries, marine nursery (MN) species (marine juveniles in the European study) were primarily responsible for the significant negative relationship between the marine migrant group and latitude ($Y = 46.607 - 0.580X$, $p = 0.0088$). Neither the percentage of freshwater transients (FT) ($Y = -26.328 + 0.829X$, $p = 0.0561$), nor of diadromous species (D) ($Y = 12.049 - 0.010X$, $p = 0.9527$) showed a significant relationship to latitude, though the freshwater group showed a weak trend with increasing latitude. The lack of a relationship between the percentage of permanent residents and latitude, and of a negative relationship between marine migrants and latitude is consistent with findings for eastern North America. However, in the case of North America, there appeared to be a replacement of marine migrants by diadromous species.

Fishes common to estuaries of eastern North America and western Europe

Families that were found to be represented in both the estuarine systems of eastern North America (predominantly estuarine salt marsh systems) that were also represented in estuarine systems of western Europe (in none of these were collections primarily from salt marshes, though 15 of the 25 systems were indicated to include some areas of salt marsh, and four of the systems, Westerschelde, Seine, Tagus, and Ebro, were indicated to include more than 20% salt marsh in the estuarine area, Pihl et al., 2002). A total of 80 families was reported from the included estuaries of eastern

North America and 79 were reported from the 25 estuaries of western Europe (Pihl et al., 2002). The most speciose of families found in estuaries on the two continents are compared in Table 4.

Overall, 22 species were found to be common to both continents from the collections reported here. These species were *P. marinus*, *Clupea harengus*, *Sardinella aurita*, *S. salar*, *G. morhua*, *Lota lota*, *Pollachius virens*, *F. heteroclitus**, *G. affinis**, *G. holbrooki**, *G. aculeatus*, *P. pungitius*, *Micropterus salmoides**, *P. saltatrix*, *M. cephalus*, *P. gunnellus*, *Scomber scombrus*, *M. quadricornis*, *M. scorpius*, *Cyclopterus lumpus*, *Hippoglossoides platessoides*, and *S. spengleri*. Those indicated by * are North American species now inhabiting European waters. *S. spengleri* reported from European estuaries may be a related species, *S. marmoratus* (Robins and Ray, 1986). *P. saltatrix* and *M. cephalus* are both widely distributed in temperate waters, with *P. saltatrix* extending into tropical waters (Robins and Ray, 1986). *C. harengus* is found in both the north Atlantic and north Pacific, and *G. aculeatus* and *P. pungitius* have circumpolar distributions (Robins and Ray, 1986). Other species reported from estuaries of western Europe that are not indigenous to some of the estuaries in which they were collected and which are also present in North American waters, though not reported in the collections given here, include *Carassius auratus*, *C. carassius* (known at least from Texas waters, Fuller et al., 1999), *Ctenopharyngodon idella*, and *Cyprinus carpio*, all cyprinids. In addition, *O. mykiss* was reported from several of the European estuaries, though, surprisingly considering its present wide distribution, was not reported from any of those of eastern North America.

Comparisons of life history groupings among continents

Assignments of species to life history groupings (ecological guilds) is not always an easy task, and thus varies considerably among studies of estuarine/salt marsh systems. An extensive analysis was published for South Africa (Wallace et al., 1984) in which seven categories were utilized. These were: I, dependent on estuaries during entire life cycle; II(a), dependent on estuaries during juvenile phase of life cycle; II(b), dependent on estuaries during migration between rivers and the sea; III, largely, but not entirely, dependent on estuaries during juvenile phase of life cycle; IV, benefits from, but only partially dependent

on estuarine nursery areas; V, stray into estuaries from the sea, not dependent on estuaries; and VI, miscellaneous species not dependent on estuaries. Category I corresponds to permanent residents (PR) as used in the present paper, and category II(a) corresponds to marine nursery species (MN), while II(b) includes species designated here as diadromous (D). Categories III, IV, and V all appear to include those considered here as marine transients (MT), and category VI appeared to include those considered here to be freshwater transients (FT), but perhaps not exclusively so. The total number of species included in the South African analysis was 206, of which 8, or 3.9%, were considered to be permanent residents (I) and 22, or 10.7%, were considered estuarine-dependent nursery species (IIa). Both values were lower than in the present analysis (PR) 9.3%, and MN(17.7%), while for the western European estuaries values for those groups were (ER) 14.6% and 16.6%, and (MJ), 11.4% and 12.2%, for the 17 estuaries (Elliott and Dewailly, 1995) and 25 estuaries, respectively (Pihl et al., 2002). The combination of groups III, IV, and V (MT) totaled 147 species, or 71.4% of the total, with diadromous (D) totaling 4, or 1.9% of the total, and the 25 miscellaneous species included in group VI making up 12.1% of the total (assumed to include the FT group) for the South African estuaries. Among the North American estuaries the MT group constituted 52.3% of the species, while for the western European estuaries, combining marine adventitious and marine seasonal species, a grouping roughly comparable to the present MT grouping, included 50.9% and 47.4% for the studies of 17 and of 25 estuaries, respectively. Diadromous species (D) for estuaries of eastern North America constituted 5.5%, while for western Europe, 6.5% and 5.3%, for the 17 and 25 estuaries, respectively, and freshwater transients (FT) made up 15.2% of the eastern North American species, and 16.8% and 18.6% of species from the 17 and 25 estuaries, respectively, of western Europe. Thus, the MT group (marine seasonal + marine adventitious for western Europe or categories III + IV + V for South Africa) category consistently made up the largest percentage of species found in estuaries, with MN species second for eastern North America, but FT apparently second for western Europe and South Africa, and the third largest species group among estuaries of eastern North America. Estuarine residents made up the third group among western European estuaries, while marine nursery/juvenile species (IIa) were the third group among South African estuaries. Permanent

residents (PR) were only the fourth largest species group among North American and South African estuaries, with marine nursery species (referred to as MJ) fourth among estuaries of western Europe. Diadromous species made up the smallest component in percentages of species among all estuarine groups. Inclusions of species as permanent residents (estuarine residents) versus inclusion as marine nursery species (marine juveniles), or as marine nursery species versus marine transients (marine adventitious species, etc.) are somewhat arbitrary decisions, and may result in some variations as noted here among studies. For example, the observed variations in percentage representation may reveal real differences in numbers of typical freshwater species that show some euryhaline capabilities, or simply reflect the inclusion of freshwater species in collections from freshwater reaches of riverine estuaries. Freshwater transient species did appear to constitute a modestly large component of the estuarine fish faunas in all of these analyses. It is suggested that if an analysis were based on biomass, or on number of individuals per species, the diadromous component might be larger, especially in more northern estuaries (and a large component in estuaries of northwestern North America and eastern Asia).

Another interesting comparison of relative abundances of species by life history categories (ecological guilds) in an estuarine system is found in the long-term analysis of species taken in the estuarine system of Ria de Aveiro, Portugal (Pombo et al., 2002). The study illustrates the vagaries in presence of many species among years. Species were grouped as ER-estuarine resident; MJ-marine juvenile; MS-marine seasonal; MA-marine adventitious; CA-diadromous; and FW-freshwater, categories that correspond loosely to those used here when MS and MA are combined, summing to the equivalent of marine transient (MT). Representation by categories for the year 2000 showed ER, 18.0%; MJ, 14.8%; MS, 14.8%; MA, 34.4% (MS and MA combined, 49.2%); CA, 13.1%; and FW, 4.9%. Data were presented for changes in species representation over the period from 1912 to 2000. Species representations during that period varied as follows: ER-18 to 29.5% (lowest 1912, highest 2000); MJ-11.5 to 24.6% (lowest 1915, highest 1997); MS and MA combined-32.8 to 49.2% (lowest 1997, highest 1912 and 1915); CA-9.8 to 18.0% (lowest 1981 and 1999, highest 2000); and FW-0 to 11.5% (lowest 1999, highest 1981). This system has been significantly influenced over time by anthropogenic activ-

ities, including pollution and dredging. However, it was concluded that despite such activities, the system continued to support a very similar fish community throughout the century, though with a decrease in the fraction of marine adventitious species and an increase in that of estuarine residents. There have been significant variations over time in the total number of species taken in the estuary in a particular year, ranging from a low of 38 species in 2000 to a high of 55 species in 1988. Marine transients make up the largest group of species found in most estuarine systems, with marine nursery species or permanent residents, second. Percentages of diadromous species are generally quite small, with the freshwater transients varying considerably, perhaps partially associated with the numbers actually included by authors. Relative values for European estuarine fish faunas show the same general trends as did analyses of estuarine faunas of eastern North America and of South African estuaries. It seems obvious from this extensive analysis that comparisons either over time within an estuarine system, or at any particular time among estuarine systems, when life history categories (ecological guilds) are used, must be interpreted with caution, as variations may reflect the vagaries of nature, results of human intervention in the system, or differences in collection devices and extent of effort.

Fish families common to estuaries on four continents

Comparisons were made of the families of "estuarine" fishes common to a limited series of temperate zone estuaries of the four continents of Australia, Africa, Europe, and North America. Using the present sets of data for eastern North America and those for western Europe, and incorporating information for temperate South Africa and Southwestern Australia (Potter et al., 1990), it was found that there were nine families in common represented in estuaries considered on the four continents: Clupeidae, Atherinidae, Mugilidae, Gobiidae, Engraulidae, Sparidae, Hemirhamphidae, Pomatomidae, and Blenniidae (Table 5). All of these families were considered to be primarily marine, with some species occurring in or limited to brackish and/or fresh waters (Nelson, 1994). Among the species reported from North American estuaries that belonged to one of these nine families, 21/45 were marine transients and 13/45 were marine nursery species. The remaining species included four permanent resident species (all belonging to the Gobiidae), four diadromous species (all belonging to

Table 5. Common families of estuaries on four continents

Family	Western Australia	South Africa	North America	Western Europe
Clupeidae	X	X	X	X
Atherinidae	X	X	X	X
Terapontidae	X			
Mugilidae	X	X	X	X
Gobiidae	X	X	X	X
Engraulidae	X	X	X	X
Tetraodontidae	X		X	X
Apogonidae	X			
Sillaginidae	X			
Gerreidae	X		X	
Plotosidae	X			
Sparidae	X	X	X	X
Arripidae	X			
Hemirhamphidae (Exocoetidae)	X	X	X	X
Pomatomidae	X	X	X	X
Carangidae		X	X	X
Platycephalidae	X	X		
Monodactylidae		X		
Soleidae		X		X
Haemulidae		X		
Ambassidae		X		
Sciaenidae		X	X	X
Ariidae		X	X	
Clinidae		X		
Syngnathidae		X	X	X
Cichlidae		X	(X)	
Blenniidae	X	X	X	X
Galaxiidae		X		

Families common to all, 8; common to Australia, South Africa and North America only, 1; common to South Africa, North America and Europe only, 2; common to Australia, South Africa and Europe only, 0; common to Australia, Europe and North America only, 1; common to Australia and North America only, 1; common to South Africa and North America only, 2; common to Australia and Europe only, 0; common to South Africa and Europe only, 1. Species common to all four continents, 2: *Mugil cephalus* and *Pomatomus saltatrix*. Note: (X) for Cichlidae indicates several nonindigenous species. Information on fishes in estuaries of temperate South African and Western Australia from Potter et al. (1990).

the Clupeidae), and three freshwater transients (all belonging to the Clupeidae). None of these families was represented exclusively by permanent resident, diadromous, or freshwater transient species. Only two species were common to the evaluated estuarine systems on these four continents, *M. cephalus* and *P. saltatrix*, considered here to be marine nursery and a marine transient species, respectively.

Applications

It is well established that many fishes, as well as some invertebrates, of great economic importance in commercial fisheries are among those that utilize estuaries/estuarine salt marshes at some point in their life cycles (e.g., Gunter, 1967; McHugh, 1967; Haedrich, 1983; Wallace et al., 1984; Lenanton and Potter, 1987; Potter et al., 1990; Blaber, 1997, 2000; Elliott and Hemingway, 2002). Despite their acknowledged economic importance, estuarine systems are being negatively altered by a multitude of human activities (e.g., Gunter et al., 1974; Bennett, 1994; Lathrop et al., 2000; Dybas, 2003), potentially eliminating species dependent on these areas for completion of their development. Conflicting demands for use of such areas and their inherent resources are often resolved by decision makers bowing to what appears to be the most economically advantageous position. Unfortunately, regulations that would protect the integrity of such areas are often difficult to enforce, inadequate, or lacking, at least in part due to a paucity of appropriate information on potential consequences of various perturbations, especially since these systems also integrate conditions of adjacent watersheds and contributing rivers, as well as of adjacent marine waters.

It seems essential to continue to gather accurate, quantitative information on all aspects of estuaries related to normal structure and function of these systems. This should include standardizing techniques, to the extent possible, to permit better comparisons among systems and areas, and conducting studies of longer duration and across wider geographical areas to determine normal fluctuations through time and space, thus, strengthening arguments about the general nature and applicability of results. Without yardsticks representing normal organization and operation, it is difficult to determine what are abnormal/undesirable conditions.

One significant problem in acquiring baseline information that could be used in making a case for protection of an estuarine area arises with respect to deciding what components of the biota of the system should be included, and what, in addition to identifications, should be determined. Just attempting to produce a checklist of all of the resident and transient species would be an overwhelming task. One of several approaches to gathering useful information is that of choosing particular taxonomic groups, or particular species, often fishes, as indicators of

ecosystem integrity or 'health' (e.g., Karr, 1981; Elliott et al., 1988; Oberdorff and Hughes, 1992; Paller et al., 1996; Elliott and Hemmingway, 2002; Whitfield and Elliott, 2002). It has been argued that resident organisms may better reflect various environmental perturbations over time than sequential samplings of individual physical and chemical parameters. Sensitive members of the biota integrate effects of environmental alterations or events and may reflect resulting stresses: by their elimination from the biota, at least in particular habitats; by reductions in their numbers, in biomass, in growth rates, or in replacement by other species; in development of pathological conditions; in bioaccumulation of chemical pollutants; as well as other possibilities. Choices of appropriate groups or species for development of such indices, if they are to be effective, must be based on a knowledge of the roles played by the chosen group or species in their environment. This must include characteristics of that environment such as reproductive areas, foods and feeding areas, and areas of other special needs, local and regional, for various stages in the life cycle of the organism. Also, ontogenetic patterns of tolerance limits to potentially stressful environmental conditions such as severe fluctuations in temperature, salinity, or dissolved oxygen concentrations, among others, are essential parts of such species characteristics. Species may be chosen based on information that indicates that they reflect particular sensitivity or insensitivity to key environment perturbations. Making such selections involves more challenging requirements when dealing with estuarine fishes, only a small fraction of which may be permanent residents. Other fishes that utilize the estuarine environment for only a part, but an essential one, in the life cycle, include both marine juveniles that use the estuary as a nursery area, and diadromous species that must, at least, pass through the estuary to reach their spawning areas, whether freshwater or marine. Also, temporary inhabitants include marine and freshwater transients that have no specific requirement for being in the estuary, but may take advantage of various resources in such areas. Transients, especially marine transients, typically are the most abundant species found in temperate estuaries. While permanent resident species are the most logical choice to reflect long-term responses to certain kinds of stresses/alterations, members of any one of these life history groups may be useful as indicator species in particular situations.

No one approach can answer all possible kinds of questions regarding potential outcomes of natural or anthropogenic impacts on such systems. However, only with appropriate information available can useful tools be developed so critical environmental monitoring can be carried out and effective management strategies be planned and implemented. Starting with common agreement on what the limits of the systems are that are being studied (Elliott and McLusky, 2002), and designing studies whose results can stand the rigors of review of fellow scientists, of economists who apply cost/benefit analyses, of political policy makers, of resource managers, of our court systems, and of the general public, it should be possible to continue to help make progress in protecting/effectively managing such systems to the betterment of nature as well as of humankind.

Summary/conclusions

- (1) A total of 237 species of fishes representing 80 families was found to be associated with 20 estuarine systems (from published material), most of which included salt marshes, located on the Gulf of Mexico and Atlantic coasts of North America. Those estuaries ranged geographically from southern Texas and southern Florida, to Prince Edward Island and James and Hudson Bays.
- (2) Families with the highest species richness (at least 10 species each) included Clupeidae (15), Sciaenidae (13), Gobiidae (12), and Fundulidae (10, but two not truly estuarine).
- (3) Most widely-distributed species were *F. majalis* (including *F. similis* or *F. m. similis*), *C. variegatus*, *M. cephalus*, *A. mitchelli*, *M. beryllina*, *B. chrysoura*, *L. xanthurus*, *G. bosci*, *M. menidia*, *F. heteroclitus*, *A. rostrata*, *L. parva*, *A. hepsetus*, *S. marina* and *L. rhomboides*, all of which were reported from 10 or more of the 20 locations.
- (4) The highest reported species richness was in Georgia salt marshes.
- (5) Representation of species by life history groups showed 9.3% permanent residents, 17.7% marine nursery species, 52.3% marine transients, 15.2% freshwater transients, and 5.5% diadromous species.
- (6) Information from the present analyses further supported the idea of Cape Cod being a zoo-

- geographic boundary between fish faunas of warmer and cooler areas.
- (7) A regression of fractions of permanent resident fishes on latitude showed no significant trend, while a significant negative relationship was found between marine migratory (MN + MT) species and latitude. Further analyses suggested that this reduction in marine migrants was partially compensated for by an increase in diadromous (here anadromous) species with increasing latitude.
 - (8) Distributions of a number of species or subspecies of fishes associated with estuarine salt marshes originate or terminate along coasts of the Florida peninsula, both western and eastern sides, as well as the southern tip. Areas of transition seem widely distributed around the peninsula.
 - (9) In general, fishes associated with estuaries have lengthy periods of reproduction, including some with repeated spawnings by individuals, or of spawnings at different times by different populations, especially populations of some widely-distributed species that show geographic differences in spawning times.
 - (10) Variations in temperature tolerances among the species considered here were related to geographic distributions, rather than to life history patterns.
 - (11) Permanent residents species showed the widest ranges of salinity tolerances or in ranges of ambient salinity of habitats occupied among species associated with estuaries. Marine nursery species were second in this regard.
 - (12) Nonindigenous species, including some that are able to reside in estuarine habitats, have been widely introduced throughout the world. Recent introductions in Florida have included a number of species of cichlids that have established estuarine populations.
 - (13) Profiles of estuarine/salt marsh permanent resident species were developed from information on life history characteristics and environmental tolerances of eastern North American species.
 - (14) A study of a group of 17 estuarine systems located along the west coast of Europe reported a total of 186 species representing 69 families, and a larger study that included 25 estuaries of western Europe reported 255 species of fishes belonging to 79 families.
 - (15) There was significant similarity in fish families and species represented among inhabitants, comparing western European and eastern North American estuarine systems.
 - (16) Life history groupings (ecological guilds) among these species showed the largest fraction to be marine transient species (MT for North America, marine adventitious + marine seasonal visitors for western Europe), and a similar grouping (categories III, IV and V) among a group of South African estuaries. These were followed by marine nursery species (MN), with freshwater transients (FT) third, and permanent residents (PR) fourth for North American estuaries. The order among European estuaries was freshwater transients second, estuarine residents third, and marine juveniles fourth, while the order among South African estuaries was freshwater transients (VI), category VI second, marine nursery species (category IIa) third, and estuarine residents (I) fourth. Diadromous species (D for North America, CA for Europe, and IIb for South Africa) constituted the fifth category among all three groups of estuaries.
 - (17) Some of the variations found in comparing life history categories across continents may reveal differences in collecting techniques, in seasonal variations within and among estuaries, and in criteria used in assigning a species to a particular life history group.
 - (18) Comparing data included here for eastern North America and western Europe, with data for estuaries of South Africa and southwestern Australia, showed nine families represented in all of these estuarine faunas. The largest numbers of species among these nine families for eastern North American estuaries included here, were considered to be either marine transients (MT) or marine nursery (MN) species.

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