

NOAA's Estuarine Living Marine Resources Program

*Estuarine-catadromy: a Life History Strategy
Coupling Marine and Estuarine Environments
via Coastal Inlets*

November 1995

*U.S. Department of Commerce
National Oceanic and Atmospheric Administration
National Ocean Service*

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The Strategic Environmental Assessments (SEA) Division of NOAA's Office of Ocean Resources Conservation and Assessment (ORCA) was created in response to the need for comprehensive information on the effects of human activities on the nation's coastal ocean. The SEA Division performs assessments of the estuarine and coastal environments and of the resources of the U.S. Exclusive Economic Zone (EEZ).

In June 1985, NOAA began a program to develop a comprehensive information base on the life history, relative abundance and distribution of fishes and invertebrates in estuaries throughout the nation. The Estuarine Living Marine Resources (ELMR) program has been conducted jointly by the SEA Division, the National Marine Fisheries Service (NMFS), and other agencies and institutions. Three salinity zones as defined in Volume 1 of NOAA's *National Estuarine Inventory Data Atlas* (NOAA 1985) provide the spatial framework for organizing information on species distribution and abundance within each estuary. These salinity zones are tidal fresh (0.0 to 0.5 ppt), mixing (0.5 to 25 ppt), and seawater (>25 ppt). The primary data developed for each species include spatial distribution by salinity zone, temporal distribution by month, and relative abundance by life stage, e.g., adults, spawning, juveniles, larvae, and eggs. Life history summaries and tables are also developed for each species. The nationwide ELMR data base was completed in January 1994, and includes data for 135 species found in 122 estuaries and coastal embayments. Twenty reports and reprints are available upon request, and representative ones are listed below.

Additional information on this or other programs of NOAA's SEA Division is available from:

NOAA/NOS SEA Division, N/ORCA1
1305 East-West Hwy., 9th Floor
Silver Spring, Maryland 20910
Phone (301) 713-3000
Fax (301) 713-4384

Selected reports and reprints available from NOAA's Estuarine Living Marine Resources program include:

Monaco, M.E., et al. 1990. Distribution and abundance of fishes and invertebrates in West Coast estuaries, Vol. I: Data summaries. ELMR Rep. No. 4. NOAA/NOS SEA Division, Rockville, MD. 232 p.

Emmett, R.L., et al. 1991. Distribution and abundance of fishes and invertebrates in West Coast estuaries, Vol. II: Species life history summaries. ELMR Rep. No. 8. NOAA/NOS SEA Division, Rockville, MD. 329 p.

Nelson, D.M., et al. 1991. Distribution and abundance of fishes and invertebrates in Southeast estuaries. ELMR Rep. No. 9. NOAA/NOS SEA Division, Rockville, MD. 167 p.

Monaco, M.E.; et al. 1992. Assemblages of U.S. west coast estuaries based on the distribution of fishes. *Journal of Biogeography* 19: 251-267.

Nelson, D.M., et al. 1992. Distribution and abundance of fishes and invertebrates in Gulf of Mexico estuaries, Vol. I: Data summaries. ELMR Rep. No. 10. NOAA/NOS SEA Division, Rockville, MD. 273 p.

Bulger, A.J., et al. 1993. Biologically-based salinity zones derived from a multivariate analysis. *Estuaries* 16: 311-322.

Pattillo, M.E., et al. In Prep. Distribution and abundance of fishes and invertebrates in Gulf of Mexico estuaries, Vol. II: Species life history summaries. ELMR Rep. No. 11. NOAA/NOS SEA Division, Silver Spring, MD.

Stone, S.L., et al. 1994. Distribution and abundance of fishes and invertebrates in Mid-Atlantic estuaries. ELMR Rep. No. 12. NOAA/NOS SEA Division, Silver Spring, MD. 280 p.

Jury, S.H., et al. 1994. Distribution and abundance of fishes and invertebrates in North Atlantic estuaries. ELMR Rep. No. 13. NOAA/NOS SEA Division, Silver Spring, MD. 221 p.

Bulger, A.J., et al. 1995. Estuarine-catadromy: a life history strategy coupling marine and estuarine environments via coastal inlets. ELMR Rep. No. 14. NOAA/NOS SEA Division, Silver Spring, MD. 110 p.

*Estuarine-catadromy: a Life History Strategy Coupling
Marine and Estuarine Environments via Coastal Inlets*

Arthur J. Bulger
Clark Hall
Department of Environmental Sciences
University of Virginia
Charlottesville, Virginia 22903

and

Tony A. Lowery and Mark E. Monaco
Biogeographic Characterization Branch
Strategic Environmental Assessments Division
Office of Ocean Resources Conservation and Assessment
National Ocean Service
Silver Spring, MD 20910

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Chapter 1

Characterizing the Estuarine-catadromous Life History Strategy

Arthur J. Bulger
Clark Hall
Department of Environmental Sciences
University of Virginia
Charlottesville, Virginia 22903

and

Tony A. Lowery and Mark E. Monaco
Biogeographic Characterization Branch
Strategic Environmental Assessments Division
Office of Ocean Resources Conservation and Assessment
National Ocean Service
Silver Spring, MD 20910

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Characterizing the Estuarine-catadromous Life History Strategy

Introduction

Species that spend most of their adult stage in the marine environment and spawn there, and in their early life history stages migrate to, and reside in, estuarine environments, are the focus of this report. We will refer to species employing this life history strategy as "estuarine-catadromous". This group includes species that are very important both economically and ecologically in southeastern and mid-Atlantic estuaries. In 1988 these species accounted for: 81% of the South Atlantic region's shellfish landings; 63% of the South Atlantic region's finfish landings; 54% of the Chesapeake region's shellfish landings; and 45% of the mid-Atlantic region's finfish landings (NMFS 1989). Like anadromy and catadromy, this life history pattern includes regular and predictable migrations across salinity gradients, and is often treated as a minor variant of diadromy. Yet, this life history strategy includes species that dominate commercial harvests in the southeastern region of the United States (the focal area for this report), as well as in the Mid-Atlantic and Gulf of Mexico regions.

These species must pass through inlets at least twice during their life history. The first and most critical passage occurs during early life history stages (often at less than one centimeter in total body length), with little or no capacity for self-generated movement relative to the water masses in which they travel. Since they migrate through inlets at a vulnerable life history stage where small changes in survivorship can have large effects on recruitment success, they may be especially sensitive to inlet characteristics and inlet modification that affect estuarine water circulation. After maturation, estuarine-catadromous species return through inlets to the marine environment.

Inlet physical and hydrological features affecting the recruitment of these species include tidal prism, mouth width, inlet current speeds, and flushing characteristics. It is important to remember that these species must not only traverse coastal inlets, but also find and orient to them; thus, tidal plume characteristics may also be important. Therefore, anthropogenic and natural modifications of inlets affecting these features are likely to impact the recruitment of these species either negatively or positively.

Estuarine-catadromy vs. Diadromy

The life history of each individual species is in some way unique. Nevertheless, patterns emerge following examination of the life histories of many species. This is in part because there are a finite number of life history trajectories that are successful, and in part because scientists are trained to find patterns. The search for patterns is motivated by the need to comprehend and manage a large number of facts concerning a diversity of life forms. Although the focus of this report is on estuarine-catadromous species that have a suite of common life history characteristics, there still remains considerable diversity within this group. These species spawn outside estuaries, yet their larvae migrate through inlets to estuarine nursery areas; in most cases, their juveniles migrate out of the estuary. The life history pattern of these species has received less attention than other groups (e.g., diadromous species) perhaps because it does not fit neatly into the terminology framework developed for other kinds of species which migrate across salinity gradients.

Nineteen estuarine-catadromous species in this report rely on marine habitats for maturation and spawning and use estuaries as nursery areas (Table 1). These migratory species, which are exposed to substantial variation in physical parameters (such as salinity, temperature or turbidity) during the course of their lives, stand in sharp contrast to the many relatively sedentary species that characterize some marine habitats (e.g., coral reefs), which never experience such wide variation in physical parameters. It is often assumed that the risks and costs of transit across these substantial physical gradients are balanced by enhanced recruitment (Day et al. 1989).

Review of the life histories of diadromous versus estuarine-catadromous species has led us to focus on two seemingly important differences: 1) vocabulary (there is no comparable vocabulary to describe the life history of estuarine-catadromous life history patterns); and 2) complex larval transport (estuarine-catadromous life history patterns require that larvae and small juveniles transit long distances through inlets, plus nearshore and continental shelf environments in some cases, at a relatively small size, whereas this is not usually the case—at least for anadromous species).

Diadromous terminology

A specialized terminology has been developed to describe fish species that migrate between fully fresh and saltwater, recently reviewed in McDowall (1988). Out of several sets of definitions, McDowall (1988) adopts those of Myers (1949). The most general and inclusive term in this set is *diadromous*, used to describe fishes that regularly migrate between the sea and fresh water, which recognizes diadromy as a specialized form of migration. Types of diadromous species are anadromous, catadromous and amphidromous, defined as follows.

Anadromous: diadromous species (e.g., Atlantic salmon) that spend most of their lives at sea and migrate to freshwater to spawn. This life history thus includes a spawning run of adults and a reciprocal seaward migration which may be accomplished by newly-hatched larvae through well-grown juveniles a year or more old.

Catadromous: diadromous species (e.g., American eel) that spend most of their lives in freshwater and migrate to the sea to spawn. This life history also includes a spawning run of adults and a reciprocal migration to fresh water, normally accomplished by well-grown juveniles weeks to months old, and occasionally older.

Amphidromous: diadromous species whose migrations from freshwater to the sea or vice versa are not for the purpose of breeding, but occur at some other regular phase of the life cycle. The key point for amphidromy is apparently that neither migration is followed immediately by reproduction; i.e., the timing of reproduction relative to migration is critical in the definition.

Estuarine-catadromous terminology

No fully comparable set of terms has been developed for species that regularly migrate between the sea and estuaries, but not as far as freshwater. However, McHugh (1967) provided a classification of estuarine nekton based on six groups of species, as follows: 1) freshwater species that occasionally enter brackish waters; 2) truly estuarine species that spend their entire lives in the estuary; 3) anadromous and catadromous species; 4) marine species that pay regular seasonal visits to the estuary, usually as adults; 5) marine species that use the estuary primarily as a nursery ground, usually spawning and spending much of their adult life in the sea, but often returning seasonally to the estuary; 6) adventitious visitors, which appear irregularly and have no apparent estuarine requirements.

The nineteen estuarine-catadromous species discussed in this report fall into McHugh's group 5; the lack of accepted terminology for species with this life history may have been partly responsible for their absence from, or limited treatment in, some recent reviews of marine-estuarine-freshwater migratory behavior (McKeown 1984, Dadswell et al. 1987, McDowall 1988), or even erroneous treatment (McDowall 1988), despite the substantial ecological and economic importance of some species with this life history (Miller et al. 1984). Indeed, among the least understood mechanisms of transport associated with estuaries is the one used by species that spawn offshore and subsequently enter estuarine systems as late larvae or early juveniles (Boehlert and Mundy 1988).

McHugh observed that group 5 contains the species that numerically dominate the nekton of most Atlantic estuaries in North America. In a more recent review, Day et al. (1989) reached the same conclusion. The members of this group perform complicated migrations between offshore and estuarine waters, and not uncommonly, into freshwater as well (McHugh 1967). Day et al. (1989), in a book on estuarine ecology, refer to McHugh's group 5 as "saltwater spawners"; however, this term does not differentiate these species from those that spend their entire lives in the sea. These "saltwater spawners" have often been called "estuarine dependent" marine species. These species typically spawn in nearshore coastal waters, then larvae and/or eggs are transported into estuaries on coastal currents, including tidal currents. The mechanisms of transport of the larvae of at least some species probably include various active processes, such as control of vertical position in the water column. In the estuary, larvae grow into juveniles, spending weeks to years there before moving out into adult feeding grounds at sea.

Several advantages to estuarine nursery areas over continental shelf areas have been suggested, including predator avoidance and greater food resources. However, comparison during the fall season of the sizes of juvenile spot, croaker, flounder, and menhaden (all of which use estuaries as nursery areas), with species that do not inhabit estuarine nursery areas, suggest that there is no particular individual growth advantage (Miller et al. 1984). Nevertheless, estuaries support very large numbers of juveniles of these species, and it is unclear whether other environments could support similarly high densities as found in estuarine nursery areas (Miller et al. 1984).

The widespread use of estuaries by early life history stages of so many species has led to the concept of "estuarine dependence," which implies that an estuary is required for some part of the life cycle. However, it has been stated that relatively few species are absolutely estuarine dependent (Day et al. 1989). Nevertheless, many species use estuaries as their primary nursery areas, while others use portions of the continental shelf influenced by estuaries. Even if estuarine residence is not absolutely required by these species, it may be responsible for their abundance and success.

Some species that are always described as anadromous have landlocked populations, so it might be said that the anadromous habit for these species is no more obligate than estuarine existence is for the estuarine-catadromous menhaden, for example. Examples of landlocked "diadromous" populations include striped bass (Hassler 1988), alewife and blueback herring (Bozeman et al. 1989), and pink salmon (Kwain 1987). Nevertheless, for both diadromous and estuarine-catadromous life history patterns, migration across salinity gradients is typical, whether or not dependence is an issue. The term "estuarine-catadromous" describes the life-history pattern and avoids the issue of the degree to which the species are dependent on estuaries.

Estuarine-catadromous Larval Transport

In general, oceanographic processes transport water mass layers either to and away from shore, parallel to shore, or through estuarine inlets. Non-local forcing of sea level variation due to wind events or storm surges can significantly affect estuarine currents and circulation (Norcross and Shaw 1984). Such events can have direct consequences for larval transport, as evidenced by the delivery of spot (*Leiostomus xanthurus*) cohorts to Chesapeake Bay by wind-induced current reversals (Norcross and Bodolus 1991). Interannual variation in the occurrence of favorable meteorological events probably contributes to variation in year-class strength in estuarine-dependent, as well as other, fish stocks (Miller et al. 1984, Norcross and Shaw 1984).

Norcross and Shaw (1984) point out the consequences of these oceanic processes for larval transport and survival: larvae needing estuarine nursery areas will benefit from onshore Ekman transport, and pelagic larvae will benefit from increased primary productivity associated with upwelling or convergence zones. Spawning, with consequences for larval transport, may also be associated with semi-permanent gyres occurring seasonally in relatively shallow water; these gyres

and associated currents also provide means of larval transport. Norcross and Shaw (1984) state that these gyres may be geostrophic, wind-driven, or driven by residual tidal flows (non-linear interactions of bottom topography and local tidal characteristics).

The larvae of some species cross substantial distances at sea. Because of their low vagility, and the long distances they may traverse, fish eggs and larvae arriving at favorable nursery areas must, in many cases, have been transported by ocean currents. Govoni and Pietrafesa (1994) succinctly summarize the importance of oceanographic processes by stating "larvae that are advected toward the coast and into estuaries may survive; those that are advected elsewhere may perish". While larvae may be able to select among a few water masses by moving vertically in the water column (Epifanio 1988), the processes that drive the water masses necessarily drive larval transport as well, and therefore some of the relevant ocean circulation processes will be described briefly below. The behavioral aspects in the selection of water masses by larvae are discussed in Epifanio (1988) and McCleave and Wippehauser (1987).

Ocean circulation

Currents (water masses in motion) can be categorized as either thermohaline or wind-driven (Thurman 1985). Wind-driven currents are set in motion by moving air masses, and result in horizontal and vertical movement in the surface layers of water bodies. Thermohaline circulation has a significant vertical component, and is initiated at the surface by temperature and/or salinity conditions that produce a high-density water mass which sinks below the surface layers. Thermohaline circulation is primarily responsible for mixing of deep water masses.

Horizontal Circulation: Due to the Coriolis effect, a wind-driven surface current moves at an angle to the right of the wind in the Northern Hemisphere. This surface water mass, moving in a thin layer, sets in motion another layer beneath it. The energy of the wind is passed through the water column from the surface down, with each successive layer being set in motion with a lower velocity than, and in a direction to the right of, the layer that set it in motion. The vertical structure of the water column under these circumstances is called an Ekman spiral. Theoretically, the surface current should flow at an angle of 45 degrees to the right of the direction of the wind, and the net water movement, the Ekman transport, will be at a right angle to the wind. In practice, surface currents generally move at an angle of less than 45 degrees to the right of the wind, and the Ekman transport is at an angle of less than 90 degrees to the wind. This is

particularly true in shallow coastal waters, where all water movement may be in a direction very nearly that of the wind, and the turning with increased depth is minor (Thurman 1985).

As a consequence of gyral circulation and Ekman transport, waters converge and sea level is elevated in the center of ocean basins. Gravity tends to move water down the surface slope, and the Coriolis force deflects this water to the right in the Northern Hemisphere; the net result of these two forces is a current moving around the hill of water (Thurman 1985). This geostrophic current can move water horizontally at a depth greater than that of wind-driven currents, although velocity is extremely slow, 1-4 centimeters per second (cms) (Davis 1991). Geostrophic currents also develop in the coastal ocean in response to local elevations in sea level; for example, when wind blows parallel to the coast, causing water to pile up against the coast under the influence of the Coriolis effect. This water must eventually run downslope back toward the ocean under the influence of gravity, whereupon the Coriolis effect causes it to veer to the right in the Northern Hemisphere. A second condition that causes geostrophic flow along continental margins is the runoff of large quantities of freshwater, which may pile up on top of oceanic water due to the fresher water's low density. Gravity forces the fresher water to run down slope out to sea. Local geostrophic currents may flow in the opposite direction of the dominant along-shore current, and vary in response to runoff water volume and local wind direction.

Vertical Circulation: Upwelling is a form of wind-induced vertical circulation (Thurman 1985). It occurs in the open ocean or along continental margins where surface water flow is away from the area. If surface water flows are not sufficient to conserve volume, water must come from beneath the surface to replace that which has been displaced. Coastal upwelling is common where wind conditions are such that surface waters adjacent to the continents are carried out towards open waters via Ekman transport. Upwelling waters are typically nutrient-rich and cooler than the displaced surface waters. Downwelling occurs when surface waters are blown towards the coast, and warm surface water is carried to greater depths than it would be otherwise (Davis 1991).

Offshore to nearshore transport

This section discusses mechanisms of offshore to nearshore transport of water masses and entrained eggs and larvae; these mechanisms are responsible for most offshore-to-nearshore larval transport (Boehlert and Mundy 1988, Govoni and Pietrafesa 1994, Miller et al. 1984, Norcross and Shaw 1984). The term "offshore" (i.e. mid-shelf and outer shelf (Lee

et al. 1985)) is used in the following sections to mean the water mass, generally >20 m and <100 m in depth, between the Gulf Stream and U.S. southeastern coast nearshore waters. The term "nearshore" (i.e., inner shelf (Lee et al. 1985)) generally refers to shoal water in contact with the shoreline <20 m in depth.

Generally, eggs and larvae that become entrained in nearshore water are more likely to be transported to U.S. southeastern coast estuaries than eggs and larvae entrained by the Gulf Stream (Boehlert and Mundy 1988, Miller et al. 1984, Norcross and Shaw 1984). The Gulf Stream is the dominant current for the U.S. southeastern coast. It flows roughly parallel to the shore, with its western edge in the vicinity of the 100 m isobath, from the Florida Keys to Cape Hatteras, where it is deflected eastward toward the open ocean. Therefore, the water between the Gulf Stream's western edge and the U.S. southeastern coast is the primary area from which eggs and larvae are recruited to the southeastern estuaries.

It is necessary to discuss transport throughout the water column because the eggs and larvae of estuarine-catadromous species as a group may be found from the surface to bottom layers. For example, Govoni and Pietrafesa (1994) report Atlantic menhaden were found in abundance in the surface and mid-layer waters, and Atlantic croaker and spot in the mid-layer and bottom layers off North Carolina during the winter. The eggs of white and brown shrimp are demersal, while their larvae are planktonic. The eggs of summer flounder are positively buoyant, and later larvae become demersal. Some larvae are capable of controlling their vertical position via physiological or behavioral means (Boehlert and Mundy 1988, Epifanio 1988, Forward et al. 1993, McCleave and Wippelhauser 1987); such larvae may be transported in whatever water layers are available to them in the water column. It is important to keep in mind that larvae of a single species may be in different water layers at different times (Boehlert and Mundy 1988, Epifanio 1988, Forward et al. 1993, McCleave and Wippelhauser 1987, Miller et al. 1984, Weinstein et al. 1988).

Winds of sufficient velocity, fetch, and duration set up mass movements of seawater on regional and sub-regional scales (Lee et al. 1985). Often wind-driven surface waters move (i.e., primarily wave transport) roughly parallel (e.g., <10-15 degrees to the right) with the wind (Bowden 1983, Fedorov and Ginsburg 1992). Eggs and larvae present in the surface layer are transported generally downwind. Therefore, easterly winds transport surface eggs and larvae shoreward on the U.S. East Coast, while westerly winds transport surface eggs and larvae offshore (Boehlert and Mundy 1988, Miller et al. 1984).

Because of the progressive elimination of the lower current vectors in Ekman spirals with decreasing depth (Bowden 1983, Thurman 1985), depth-averaged current vectors may be still roughly parallel to wind vectors at the 40 m isobath (Lee et al. 1985). Therefore, downwind transport of surface layer eggs and larvae is important in shallow coastal waters and sea surface layers (Boehlert and Mundy 1988, Miller et al. 1984). Once nearshore, other transport mechanisms (e.g., longshore transport, wave refraction, etc.) increase in importance (Boehlert and Mundy 1988, Norcross and Bodolus 1991). Atlantic menhaden is an example of a species for which surface transport is important (Govoni and Pietrafesa 1994).

While wind impingement of the sea surface sets up current vectors roughly parallel to the wind in the surface layers, current vectors are shifted progressively clockwise with depth, creating the Ekman spiral. A mass of sub-surface seawater is transported in a direction approximately 45 to 90 degrees right of the wind direction in deep water (Bowden 1983, Fedorov and Ginsburg 1992, Lee et al. 1985, Thurman 1985). The water volume transported can be substantial, as Ekman spirals can reach depths ≤ 100 m (Bowden 1983, Fedorov and Ginsburg 1992).

Ekman transport of offshore eggs and larvae is important in delivering eggs and larvae to the shallower nearshore waters. (Boehlert and Mundy 1988, Norcross and Bodolus 1991). Lee et al. (1985) reported shoreward Ekman transports of water (and entrained organisms) during periods of northerly winds, and offshore Ekman transports during periods of southerly winds off the southeastern U.S. coast.

Southerly winds remove water from the vicinity of the southeastern U.S. coast via Ekman transport. The departing nearshore water is replaced by shoreward movement of deeper water. This upwelling is an important mechanism for transporting eggs and larvae entrained in bottom layers to nearshore waters (Boehlert and Mundy 1988). Miller et al. (1984) observed a seasonally recurring bottom layer 1-3 m thick moving shoreward at about 5 cms off North Carolina in spring and summer. Once eggs and larvae entrained in deeper waters are transported to nearshore waters, other transport mechanisms take over (Boehlert and Mundy 1988, Norcross and Bodolus 1991). Conversely, northerly winds result in transport of demersal eggs and larvae offshore, away from the U.S. southeastern coast. Ekman transport drives water shoreward, producing downwelling, and a deeper layer of water moving offshore (Bowden 1983, Davis 1991, Fedorov and Ginsburg 1992, Lee et al. 1985).

Thermally-driven density currents can be of importance seasonally due to differential rates of cooling and warming of nearshore versus offshore waters. The larger oceanic water masses are more thermally stable than nearshore waters, resulting in density differences between the nearshore and offshore water masses. These differences drive thermohaline density currents that create some rather complex scenarios for egg and larval transport. Miller et al. (1984) have proposed a thermally and wind-driven transport mechanism that could deliver offshore water to the nearshore waters; this will be discussed further in the context of winter spawners.

Nearshore transport and estuarine inlet injection

With the delivery of eggs and larvae to nearshore waters, longshore processes become important in transporting eggs and larvae. In general, longshore transport along the southeastern U.S. coast depends on sub-regional wind and wave regimes. Eventually shore-parallel transport places eggs and larvae in the vicinity of estuarine inlets and their tidal plume dynamics (Boehlert and Mundy 1988, Norcross and Shaw 1984, Seabergh 1988, Wang 1988).

Once in the vicinity of an inlet, several mechanisms are available for the injection of organisms into estuaries (Boehlert and Mundy 1988, Miller et al. 1984, Pietrafesa and Janowitz 1988). Flood tide currents and meteorologically forced currents are probably responsible for most egg/larvae injection into estuaries. Density currents, tidal plume interactions and tidal plume reflux are probably of secondary importance. Often, egg/larvae injection results from a complex interaction of tidal pumping, meteorologic forcing, and estuarine circulation patterns. The time scales in which these mechanisms operate are hourly (tides and density driven circulation) to weekly (meteorologic forcing and floods) (Seabergh 1988, Wang 1988, Wiseman et al. 1988).

Inlet tidal currents disrupt longshore transport by taking in and exhausting massive volumes of nearshore coastal water, approximately twice daily on the southeastern U.S. coast (Gross 1987). Additionally, ebb tidal currents refract wave fields to focus and slow wave transport in the vicinity of inlets (Bearman 1989). This places positively buoyant and neutrally buoyant eggs and larvae into water that will be partially refluxed later. Likewise, flood tidal currents negatively refract and accelerate wave fields into the inlets. This enhances reflux of water in the vicinity of the inlet and, by default, the injection of entrained eggs/larvae. Therefore, in periods of faster tidal currents (e.g., spring tides, maximum ebb and flood currents) egg/larvae injection into the estuaries is enhanced.

Larval injection also occurs when meteorologic forcing elevates sea level at the mouth of an estuary. This elevation can be due to Ekman transport, onshore surface currents, barometric pressure differences, and storm surge. These events can greatly increase the injection of nearshore water, and thus any entrained eggs and larvae, as the water level in the estuary equilibrates to the elevated sea level (Bearman 1989, Miller et al. 1984, Pietrafesa and Janowitz 1988, Rogers et al., 1993). This increased volume of water in the estuary does not necessarily exit on subsequent ebb tides; it can persist until sea level outside the inlet returns to normal. Therefore, retention of eggs and larvae is enhanced (Bearman 1989, Pietrafesa and Janowitz 1988, Rogers et al. 1993).

Pietrafesa and Janowitz (1988) discussed physical oceanographic processes affecting larval transport around and through North Carolina inlets. In previous studies it had been assumed that larvae and juveniles of offshore-spawned species (including Atlantic croaker, summer and southern flounders, spot and Atlantic menhaden) entered estuaries at the bottom of the water column and used tidal flows as a primary transport mechanism up estuary to nursery areas. Pietrafesa and Janowitz (1988) showed that substantial sea level differences occurred in response to wind stress on the Sound versus the ocean side of the barrier islands in the Pamlico Sound area. For example, when the wind persisted to the north, Oregon Inlet drained or "ebbed" even on flood tides; the opposite was also true, enhancing larval transport through the inlets during winter. They concluded that, in addition to flood tides, non-local forcing (due to synoptic-scale wind events) can affect transport of larval fish through the estuary mouths through the entire water column.

Because tidal plumes are usually less dense and often different in temperature than nearshore waters, nearshore waters are drawn into the plumes by diffusive advection. This sets up density currents of nearshore water in the direction of the plume. As a result, nearshore waters are accelerated toward the inlet (Bowden 1983). Further, these density currents can accelerate, and move progressively toward the inlet, with depth (Heaps 1972). Therefore, these plume-driven density currents are most advantageous to negatively and neutrally buoyant egg/larvae transport to the vicinity of the inlet. Later, the well-placed eggs and larvae can be injected into the estuary during subsequent flood tides. These density currents are important during slack tides, but less so during ebb and flood tides, which are stronger.

Differences between the tidal plume and nearshore waters in salinity or temperature probably trigger behavioral responses that increase the likelihood of lar-

val transport through inlets into estuaries (Pietrafesa and Janowitz 1988, Rogers et al. 1993). It has been suggested that a cueing mechanism might be that larvae track warm, saline waters in winter, which enter estuaries on the flood tide. This will be discussed more fully in the following sections.

Behaviorally enhanced transport by meteorologic injection

Rogers et al. (1993) have proposed a behaviorally mediated, wind-driven mechanism for transport of brown shrimp postlarvae through inlets once they have traversed the shelf in the Gulf of Mexico. Similar interactions of behavior and cold front passage could be operative for the transport of other species and at other locations, such as on the Atlantic Coast. The hypothesis is based on the observation that brown shrimp become concentrated near inlets as they move shoreward from the spawning grounds. This could be the result of an active process (as presented in the Rogers et al. 1993 hypothesis), or a passive (physical) one. For example, several physical processes result in the accumulation of passive particles at the mouths of tidal inlets; these involve the interaction of longshore transport, the predominant wave approach, residual differences in estuarine flood and ebb plumes, and transport or drift reversals at the downstream or updrift side of tidal inlets (reviewed in Rogers et al., 1993).

The behaviorally-mediated, wind-driven transport hypothesis developed for brown shrimp in the Gulf of Mexico may be summarized as follows:

Stage I. Strong, cold northerly winds associated with atmospheric frontal passages drive chilled, low-salinity water from shallow estuarine basins into the coastal boundary layer. The postlarvae in the nearshore zone descend onto or near the bottom (as they do in the laboratory in response to cooling temperatures). This behavior would result in postlarvae congregating where cool, low-salinity water emerges from estuaries, i.e., at the mouths of passes.

Stage II. After the front passes, these shallow, less saline and cooler nearshore waters are warmed by mixing with warmer, high-salinity shelf water and by the return of southerly winds. Postlarvae then rise into the water column at night as these waters begin to return to the drained estuary; the transport of postlarvae up estuary by normal tidal flows is enhanced by wind-stress and sea-level enhanced return flow.

Stage III. The next cold front passage elicits the same behavioral response, except that the postlarvae are now further up estuary. Thus, the postlarvae resist flushing by cool-water-induced downward migration.

Stage IV. The return of southerly winds push water up the estuary as in Stage II, except postlarvae are closer to the head of the estuary at the beginning of this stage, and carried further inland.

Such wind-driven hydrologic exchanges in general have potentially substantial effects on organismal transport, and can often dominate astronomically-driven tides (reviewed in Rogers et al. 1993).

Behaviorally enhanced transport via estuarine circulation

Vertically homogeneous estuarine circulation is of common utility to eggs/larvae throughout the water column because incoming currents are roughly the same vertically (Boehlert and Mundy 1988, Epifanio 1988, Norcross and Shaw 1984, Pritchard 1952, 1955, Thurman 1985). These circulation patterns are of greatest influence during slack and neap tides. This is due to the usually unidirectional currents in the inlets during periods of elevated or depressed sea level, relative to estuarine water level (e.g., tidal waves, tidal wave troughs, meteorologic forcings, floods, etc.).

The typical pattern of circulation in a positive estuary (where combined freshwater inputs exceed evaporation (Pritchard 1952)) provides an upstream inflow of high salinity water along the bottom and outflow of fresh or brackish water over the incoming wedge of saline water (Pritchard 1952, 1955, Thurman 1985). This circulation pattern can provide passive transport into and up the estuary for demersal eggs/larvae (Boehlert and Mundy 1988, Epifanio 1988, Norcross and Shaw 1984, Pritchard 1952, 1955, Thurman 1985). This situation allows for passive upstream transport of planktonic organisms in an estuary's lower layers (Norcross and Shaw 1984). The situation can be similar in moderately stratified estuaries (Boehlert and Mundy 1988, Epifanio 1988, Norcross and Shaw 1984, Pritchard 1952, 1955, Thurman 1985).

Weinstein et al. (1988) demonstrated that spot and croaker, together with southern and summer flounder, are transported through passes to estuarine nursery areas by a mechanism called "selective tidal stream transport" (McCleave and Wippelhauser 1987). Selective tidal stream transport is a mechanism whereby organisms can maintain position in estuaries, or achieve net upstream movement by active vertical movements (Norcross and Shaw 1984, Epifanio 1988). In this behavior, organisms make a semidiurnal vertical migration in phase with the tidal flow to accomplish horizontal migration. They enter the water column while the tidal flow is in the direction of migration, and leave when it is in the opposite direction (McCleave and Wippelhauser 1987). Adults and immatures of

other species also use this mechanism, and it is also known to occur in American eel and Atlantic salmon young (McCleave and Wippelhauser 1987). Weinstein et al. (1988) also showed that spot and flounders use selective tidal stream transport within estuaries to aid in dispersal into marshes, while croaker, by remaining near the bottom at all times, accumulate in deep water at the head of the estuary. Brown, pink, and white shrimp all probably make use of selective tidal stream transport in passes (Benfield and Aldrich 1992). Miller et al. (1984) suggest that the more surface-oriented larvae, such as menhaden, might avoid ebb currents by seeking the sides of passes, where currents are slower.

Estuarine-catadromous Spawning Strategies

Three strategies

Three spawning strategies are typical of estuarine-catadromous species in the southeastern U.S. region: 1) nearshore/near-inlet spawning, usually in warm waters; 2) offshore winter spawning; and 3) offshore spawning, either year-round or in the summer. Raynie and Shaw (1994) similarly identified two fish larval assemblages traversing an inlet in the Gulf of Mexico: a warm water assemblage resulting from spawning near the tidal pass, and a cool water assemblage resulting from offshore spawning. Spawning season is especially important in the southeastern U.S. region in considering offshore spawners, because it provides information about the hydrologic climate in which the eggs and larvae are found, and hence the direction in which they may be transported. Spawning season may be of less importance in considering the transit of near-inlet spawners, since at least tidal influences are perennial in nearshore waters. The issue remains, however, that larvae of all three groups must transit inlets at very small size, and are vulnerable to the variations in hydrological regimes at ocean inlets. It should be emphasized again that small differences in survival at the larval stage may produce large differences in the later adult stock (Sinclair 1987, Boehlert and Mundy 1988).

Nearshore/near-inlet warm-water spawning: The six species (red drum, spotted seatrout, northern kingfish, black drum, weakfish and blue crab) in this group all spawn in or near inlets, or at least in nearshore waters; some may also spawn in estuaries proper on occasion or regularly. So far, less attention has been paid to the larval transport of most of these species, presumably because tidal and other nearshore processes (such as wind-driven currents) should provide ample opportunity for the young of these species to enter estuaries. (See the section containing life his-

tory summaries for these species for more information and references.)

It may be adaptive that these larvae are typically released in warmer waters. Since their transit to the estuaries is relatively short (e.g., days to weeks, except in the case of the blue crab), they can grow rapidly in warm, food-rich waters, and enter the estuaries at a size capable of some mobility.

Five of the six species in this group are finfish of the drum family, Sciaenidae. The only exception is the blue crab, which is otherwise unique for two reasons:

- 1) although the blue crab spawns near inlets, its life history appears adapted to eject larvae out onto the continental shelf for an extended period; and
- 2) relatively more attention has been paid to the transport of larval blue crabs than the other near-inlet spawners in this group.

Of the sciaenids, red drum spawn at night, primarily in nearshore waters close to channels and passes, and also in large estuaries and nearshore shelf waters. Spotted seatrout spawn at dusk in deep channels (2.5-4.5 meters) adjoining shallow sea-grass flats, along deeper edges (1.0-3.0 meters) of sea-grass flats, in shallow, nearshore shelf waters, and in higher-salinity parts of estuaries. Black drum spawn in open bays in, and possibly outside, channels and passes. Weakfish spawn in nearshore and estuarine waters. Northern kingfish apparently spawn in "outside waters, the young probably being transported passively into bays" (U.S. Fish and Wildlife Service 1978); however, judging by the small size of the larvae in bays, northern kingfish probably spawn close to estuaries, if outside them.

Blue crabs typically mate within the estuary at mesohaline to oligohaline salinities. After copulation, females migrate to the mouth of the estuary in large bay environments. Sperm is stored by females until just before spawning, when fertilization occurs. The eggs remain attached to the female's abdomen until the larvae emerge, typically on an ebb tide. Blue crab larvae hatched at the mouths of estuaries drift out to sea where they feed and grow for 30-60 days. Megalopae (postlarvae) are probably the main reinvasive stage (Smith and Knappenberger 1989).

Offshore winter spawning: These seven species (menhaden, croaker, spot, summer flounder, southern flounder, pinfish, and striped mullet) spawn offshore in winter, and would be expected to share similar larval transport mechanisms based on winter water mass movements. It may be adaptive that these larvae are released during periods of cold water temperatures, since they have longer (up to several months), and often

less direct, transits to the estuaries. Cold water temperatures may increase their chances for survival by maintaining low metabolic rates of these larvae. Thus, if food is sparse in the offshore waters, the larvae may survive longer. By the time they reach estuaries, the waters have warmed, and growth rates can increase with increases in metabolic rates and feeding. (See the section containing life history summaries for these species for more information and references.)

Larval transport of five species in this group (menhaden, croaker, spot, summer flounder and southern flounder) were considered in detail by Miller et al. (1984). These species accounted for 70% of the 1991-1992 domestic commercial landing for the East and Gulf of Mexico Coasts (NMFS 1992). The attributes of this group are: 1) after hatching near the Gulf Stream, larvae migrate shoreward during December-March; 2) larvae or small juveniles migrate through inlets and sounds to estuarine nursery areas in early spring; 3) large juveniles or subadults migrate out of juvenile nursery areas in the fall; 4) adults migrate offshore in fall or winter; 5) spawning occurs in winter (Miller et al. 1984). A few fish may spawn at the end of one year, but most do not spawn until the second year of life. The abundance of these species suggests that this life history pattern is quite successful, and Miller et al. (1984) argue that the key elements of this success are winter (versus other season) spawning, plus estuarine (versus offshore) nursery areas. Additional potential advantages of winter spawning mentioned by Miller et al. (1984) include: 1) minimal predation on larvae in winter (due to absence of summer resident predators); and 2) longer survival times on low rations (due to lower metabolic demands at low winter temperatures).

The most important aspect of winter spawning in this context is that winter currents favor shoreward transport of pelagic, offshore-spawned larvae. Nelson et al. (1977) concluded that winter winds in the region resulted in shoreward Ekman transport of water volumes containing menhaden larvae. However, both Yoder (1983) and Miller et al. (1984) discount the mechanism and conclusions presented by Nelson et al. (1977). Miller et al. (1984) proposed an alternate three-layer model of the winter current regime off North Carolina which could account for substantial shoreward larval transport. This model, which incorporates both wind-driven and thermohaline elements, is as follows. In winter, mean regional winds tend to be directed offshore. The offshore winds drive surface currents offshore. These winds will cause surface waters to move offshore in a layer 2-5 m thick at speeds of 5-15 cms. During this time of year, passing cold fronts extract a great deal of heat from shelf waters. As a result, inshore waters cool more rapidly than offshore

waters, increase in relative density and sink, by gravity, and flow offshore in a thin bottom boundary layer. Thus, a surface layer and a bottom layer are both moving offshore. As a kinematical consequence of conserving mass and volume, an intermediate (interior) layer of water moving shoreward will occur. It is likely that this layer occupies 50-70% of the water column, moves at about 3-8 cms, and brings relatively warm, salty water onshore.

Miller et al. (1984) recognize three current patterns favoring shoreward larval transport in southeastern U.S. waters: the 5-15 m thick surface layer in fall (moving at 10-20 cms); the 1-3 m thick bottom layer in spring and summer (moving at about 5 cms); and the relatively thicker intermediate layer in winter (moving at 3-8 cms). All three current patterns would be available for shoreward transport of larvae present at the appropriate time and in the right layer. Of the three, the intermediate winter layer is considered to be the most persistent, and therefore best for larval transport because it is partly density driven and thus less subject to wind-forcing. The second best time for onshore transport of larvae would be during fall in the surface layer; however, these surface currents are more responsive to wind changes. The persistent intermediate onshore layer transport is most likely to be in effect on the shelf beyond the 25 m depth contour; within the 25 m contour, conditions are more variable and may be more dominated by winds (J.M. Miller pers. comm., Norcross and Bodolus 1991).

Differences in spawning time and vertical distribution among species may explain differences in abundance and age of cohorts arriving at estuaries. Miller et al. (1984) suggested that more spot larvae relative to croaker may be delivered to estuaries because spot spawning peaks in winter during the existence of the persistent onshore intermediate layer; croaker spawning peaks earlier in the fall, when onshore transport in the surface layer may be more variable. Because menhaden are more surface-oriented than spot or croaker, some may be transported in the offshore surface current in winter. Movement of menhaden vertically between the offshore surface current and the onshore intermediate current may be responsible for the greater size (age) variability of menhaden arriving at estuaries. Miller et al. (1984) suggest that shoreward transport of all five species they considered, whether fall or winter spawned, would be enhanced by larvae actively selecting the warmest water available to them in the vertical dimension. This selection of warmer water may explain the observed precise age distribution of spot and croaker larvae along onshore-offshore transects.

Other species that also spawn offshore in winter may share the larval transport mechanisms described by (Miller et al. 1984) for menhaden, croaker, spot, summer flounder and southern flounder in the southeastern U.S. region. These additional species include striped mullet and pinfish. Shoreward transport for those larvae spawned in the fall (as are some croaker larvae) is also available in the 5-15 m thick surface layer discussed above. Striped mullet and pinfish spawn primarily offshore in winter, with some spring spawning. Larvae of both species are pelagic and found near the surface. Thus, striped mullet, pinfish and menhaden may be exposed to similar transport processes.

Again, the shoreward transport mechanisms described for all of these offshore-spawned species are most likely effective on the shelf beyond the 25 m depth contour; within the 25 m contour, conditions are more variable and may be more dominated by winds and longshore processes (J.M. Miller pers. comm.; Norcross and Bodolus 1991). Once within the 25 m contour, these offshore-spawned larvae would come under the influence of coastal processes that control the transport of all estuarine-catadromous larvae close to shore and to inlets. Their transport would be influenced by coastal and tidal currents, as well as by synoptic scale wind-driven currents.

Offshore spawning, either year-round or in the summer: This group includes the pink, white and brown shrimps, as well as ladyfish, southern kingfish, and cobia. The transport processes governing the delivery of the larvae of some of these species are perhaps the least well-understood of the 19 species covered in this report. (See the section containing life history summaries for these species for more information and references.)

Mulholland (1984) provides a life history overview for penaeid shrimp. Adult penaeid shrimp live and spawn in highly saline offshore waters. The demersal eggs hatch 12-16 hours after spawning. Upon hatching, the embryos enter the larval phase of development, during which they pass through five naupliar, three protozoal, and three mysis stages. Feeding begins during the first protozoal stage when the larvae cease to live on the yolk. The planktonic larvae develop at sea, and the young shrimp enter the estuarine nursery grounds as postlarvae about 8 mm in total length. After reaching shallow inshore waters, the planktonic postlarvae settle to the bottom, usually in seagrass beds, become benthic postlarvae at about 10 mm total length, and develop into juveniles in the estuaries. The difference between postlarval and juvenile stages has not been clearly defined. The juveniles spend 2-6 months in the estuaries and gradually move toward

deeper water as they develop. At about 100 mm total length, they return to offshore waters to mature and spawn. The entire cycle is completed in about 12 months. In the Gulf of Mexico, pink shrimp are found in greater densities over calcareous mud and sand, or mixtures of shell and sand. In contrast, white and brown shrimp occur in greater densities over terrigenous silt. The importance of the vegetated shore zone of estuaries cannot be overemphasized; the young of most penaeid shrimp use these areas for feeding and protection from Florida to Texas. The size of the shrimp harvest is positively related to the area of intertidal vegetation (Turner 1977).

The penaeids (brown, pink and white shrimp) span the late winter-to-summer seasons in their transit to estuaries in the southeastern U.S. region. Wenner and Beatty (1993) found that ingress of postlarval brown, pink, and white shrimp to South Carolina marsh creeks was seasonal, and agreed with temporal patterns described for the southeastern coastal region. Peak occurrence of the three species in plankton samples was as follows: brown shrimp in February-March; white shrimp in July; and pink shrimp in August. The timing of peak arrival of postlarvae of these species may provide more information about the oceanographic climate to which they are exposed than the timing of their spawning, since most sources indicate that their spawning seasons are protracted.

Brown shrimp spawn in the South Atlantic region from North Carolina to northeast Florida during most of the year (Larson et al. 1989). Large brown shrimp postlarvae have been collected off South Carolina in late winter and early spring, suggesting that postlarvae overwinter in offshore waters in the south Atlantic region. Brown shrimp postlarvae may be transported in winter by the same oceanographic processes as those described by Miller et al. (1984) for spot, croaker, menhaden, summer flounder, and southern flounder.

Along the southeastern coast, white shrimp spawn from March to November, but mostly from April to October (Muncy 1984). In the Gulf of Mexico, pink shrimp spawn principally at water temperatures of 20-31 °C (Bielsa et al. 1983), so in the southeastern region, they are probably summer spawners. White and pink shrimp are probably subject to transport processes similar to southern kingfish and cobia.

The transit of larval southern kingfish and cobia larvae to southeastern estuaries may represent something of an anomaly. Spring and summer merge in terms of the wind influence on shelf circulation, at least in the North Carolina region of the southeast. This season is characterized by conventional Ekman coastal upwelling with an offshore flow in the surface layer (about

2-7 m thick and moving at about 10 cms), and an onshore flow in a bottom boundary layer (Miller et al. 1984). Cobia larvae are found offshore primarily in the surface layer at this time, yet they manage to reach coastal areas. Cobia usually spawn offshore from mid-June to mid-August off the coast of Virginia, and earlier off the coast of the Carolinas (mid-May off South Carolina). At least some spawning occurs 50-90 km offshore. Cobia eggs are found in waters ranging from 20 to 165 meters deep. Most are found in the upper meter of the water column in offshore waters (Ditty and Shaw 1992), yet larvae are common in Bogue Sound and New River estuaries in North Carolina, and juveniles are common in many southeastern U.S. estuaries (Nelson et al. 1991).

Southern kingfish spawn entirely or largely offshore at depths of 9-36 m usually in nearshore oceanic waters. In the South Atlantic Bight (south of Cape Fear), some spawning occurs from April to August, with peak spawning in April-June. Peak spawning may occur later in the year at higher latitudes (Smith and Wenner 1985). Whether southern kingfish eggs are pelagic or demersal is apparently not known (U.S. Fish and Wildlife Service 1978), so the water layer in which they occur, and hence the current regime to which they may be exposed, cannot be certainly stated. However, southern kingfish may spawn close enough to shore (in the vicinity of the offshore/nearshore boundary) that tidal and wind events may explain their movement to estuarine areas.

Ladyfish spawning locations are unknown, but they are believed to spawn pelagic eggs offshore throughout most of the range of the species, as judged by the locations of capture of early larvae. Spawning appears to occur throughout the year, perhaps peaking in the fall (Zale and Merrifield 1989, U.S. Fish and Wildlife Service 1978), late winter and early spring (Manooch and Raver 1984), or late spring and early summer (Zale and Merrifield 1989). Those ladyfish larvae spawned during fall or winter would have the same hydrologic transport mechanisms available to them in the region as the species in the offshore-winter spawning group.

Summary

Estuarine-catadromous species in the southeastern region appear to fall into three major categories with respect to spawning season and location, and their transport processes into two categories, nearshore versus offshore. Larvae and eggs spawned close to shore need to rely only on longshore and through-inlet processes to reach their estuarine nursery areas. While still imperfectly understood, these nearshore processes at least appear to be perennially available for larval transport. Nearshore processes are also required by the larvae in the other two species groups. It appears that there is at least a tenable hypothesis for the offshore-to-nearshore transport of larvae spawned offshore in winter in the region, embodied in the three-layer model of Miller et al. (1984). For larvae spawned offshore in other seasons, possible transport processes appear less clear; an example is larval cobia, which appear to be associated with a water mass moving away from estuarine nursery areas.

Species Life History Summaries

This section contains brief life history summaries for the 19 estuarine-catadromous species discussed in this report. The purpose of the summaries is to provide a background for understanding the most likely transport mechanisms available to larvae of these species. The early life history table indicates the state of information currently available for the transport of the eggs and larvae of the species. The format for these summaries is shown below. A few exceptions to this format occur for species that are well studied, versus those for which there is limited data on larval transport.

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Species Life History Summaries Format

Species Name

Primary references used for development of the General Life History section.

General Life History

Section on: name, family, overall distribution, east coast distribution, areas of abundance; general importance, remarks, habitat associations.

Section on: spawning location, timing, and other characteristics; age at maturity, life expectancy and fecundity; egg and hatching characteristics.

Section on: larval development, when (season, size) larvae/postlarvae/small juveniles enter estuaries.

Section on: larval transport, larval activities, associations and characteristics, hypotheses.

Larval transport

Statements and specific references on larval transport for the species.

References

Specific references used in preparing each summary are cited at the end of the summary.

Brown shrimp (*Penaeus aztecus*) Life History Summary

This general life history summary is based primarily on Pattillo et al. (In Prep.), Larsen et al. (1989), Benfield and Aldrich (1992), Wenner and Beatty (1993), and Rogers et al. (1993).

General Life History

The brown shrimp (Penaeidae) can be found from Martha's Vineyard, Massachusetts to the Florida Keys, and in the Gulf of Mexico from Apalachicola Bay to the northwestern Yucatan Peninsula; it is absent from the western coast of Florida; its maximum density occurs along the coasts of Texas, Louisiana, and Mississippi (Pattillo et al. In prep.). In the Atlantic region, brown shrimp are most abundant on the North Carolina coast, and are moderately abundant from South Carolina to Florida (Larsen et al. 1989). The species is important both commercially and ecologically (Pattillo et al. In prep.). Brown shrimp inhabit bays, estuaries, and coastal waters; the species has an annual life cycle, and all feeding life stages are omnivorous (Pattillo et al. In prep.). In estuaries, postlarvae and small juveniles are associated with shallow, low-salinity vegetated habitats, and large juveniles and sub-adults inhabit nonvegetated, deeper open water

bottoms. Juvenile brown shrimp inhabit estuarine nursery areas in the south Atlantic region from March through July, moving to larger bays as they grow. The brown shrimp nursery period in Gulf of Mexico estuaries varies slightly from region to region and from year to year, but in general occurs in March-June. Sexual differentiation typically begins at about 50 mm TL. Growth slows markedly when shrimp reach 100 mm, beyond which males grow more slowly than females. At a length of 80-120 mm, sub-adults move into coastal waters, emigrations coinciding with ebb tides and full moons. Tolerance to temperature and salinity changes with life stage. Adults can tolerate salinities ranging from 0.8 to 45 ppt (Pattillo et al. In prep., Larsen et al. 1989).

Brown shrimp spawn in offshore waters, usually at depths of 46-91m, but spawning can occur at 18-137 m (Pattillo et al. In prep.). Spawning in the south Atlantic region occurs during most of the year from North Carolina to northeast Florida (Larsen et al. 1989). Peak spawning occurs in the Gulf of Mexico from September through May, although it may occur year-round in deep water (>46 meters) (Pattillo et al. In prep.). In the northern Gulf of Mexico, there are two spawning peaks—the first from September through November, and the second (smaller) in April and June. In waters off Texas, spawning occurs at depths greater than 14 m, throughout the year at depths 64-110 m, and, in shallower waters, spawning peaks in late spring and fall. Female brown shrimp reach sexual maturity at about 140 mm. Female brown shrimp release an average of 246 thousand eggs, only 15% of which may hatch (Pattillo et al. In prep.). Eggs are demersal and non adhesive (Larsen et al. 1989). Hatching usually occurs in 24 h, but is inhibited at salinities other than 27-35 ppt, and does not occur at temperatures below 24 °C (Larsen et al. 1989, Pattillo et al. In prep.).

Planktonic larvae develop offshore through 5 naupliar, 3 protozoal, and 3 mysis stages before metamorphosis to postlarvae. Larval development takes about 11 days at 32 °C, or 17 days at 24 °C; development stops at temperatures below 24 °C. In the South Atlantic region, surface currents transport postlarvae to coastal areas during late winter and spring. Large postlarvae have been collected off South Carolina in late winter and early spring, suggesting that postlarvae overwinter in offshore waters in the south Atlantic region. Postlarvae begin to move from coastal areas into estuaries when water temperatures rise above 11 °C (Larsen et al. 1989), at about 8-14 mm TL (Pattillo et al. In prep.). They migrate to nursery areas in March through June in North Carolina, February to April in South Carolina, and March through June in Georgia and Florida. Some may immigrate during fall in northeast Florida and Georgia. Wenner and Beatty (1993)

found that ingress of postlarval brown, pink, and white shrimp to South Carolina marsh creeks was seasonal, and agreed with temporal patterns described for the southeastern coastal region. Peaks in occurrence of the three species in plankton samples were as follows: brown shrimp in February-March; white shrimp in July; and pink shrimp in August. By the time they reach their estuarine nursery, brown shrimp postlarvae are large enough to actively migrate to shallow, vegetated areas. Once in the estuary, postlarvae may use selective tidal stream transport. Postlarval and juvenile brown shrimp feed on detritus and small benthic animals. The shrimp spend about three months on the nursery grounds in the Gulf of Mexico (Pattillo et al. In prep.). Larvae can tolerate salinities ranging from only 24.1 to 36 ppt, yet postlarvae seem to have normal growth in salinities anywhere from 2 to 40 ppt, and water temperatures from 16 to 32.2 °C. Postlarvae have been collected at 13-31 °C, and juveniles at 2-38 °C (Pattillo et al. In prep.).

Brown and white shrimp have been shown to be attracted to organic components of estuarine water in their migration to nursery areas; brown, pink, and white shrimp all probably make use of selective tidal stream transport in passes (Benfield and Aldrich 1992).

Rogers et al. (1993) have proposed that brown shrimp in the Gulf of Mexico employ a behaviorally enhanced transport by meteorological injection recruitment strategy (see pages 7-8). Similar interactions of behavior and cold front passage could aid postlarval transport on the Atlantic coast as well. The hypothesis may be summarized as follows:

Larval Transport

1) "The estuarine recruitment of [brown shrimp] postlarvae occurs during a time when the strongest atmospheric cold fronts (winter storms or migrating anticyclonic circulation systems) pass through southwestern Louisiana. These low-frequency, cold air outbreaks have been shown to be responsible for significant shelf-estuarine exchanges. Such wind-driven hydrographic exchanges have potentially substantial effects of organismal transport" (Rogers et al. 1993).

2) "... brown shrimp postlarvae appear to concentrate near river mouths or entrances to bays... coastal engineering and sediment transport research have documented several processes responsible for the accumulation of passive particles at the mouths of tidal inlets. These processes involve the interaction of longshore transport, the predominant wave approach, residual differences in estuarine flood and ebb plumes, and transport or drift reversals at the downstream or updrift side of tidal inlets" (Rogers et al. 1993).

3) See also the "Recruitment enhancement hypothesis" as put forth by Rogers et al. (1993), pp. 390-391.

4) "The mechanisms by which postlarvae locate and gain access to estuarine systems have not been comprehensively examined. Once postlarvae enter coastal waters they are thought to locate estuaries by orienting along the horizontal salinity gradients which extend outward from estuaries. Transit into estuaries is thought to involve selective tidal transport synchronized by salinity differentials between tidal currents, endogenous rhythms, or hydrostatic pressure" (Benfield and Aldrich 1992).

5) "Larval stages are capable of vertical migration to control their position in the water column" (Pattillo et al. In prep.).

6) "Brown shrimp and postlarvae (10-15 mm TL) move into estuaries from February to April with incoming tides and migrate to shallow and often vegetated nursery areas" (Pattillo et al. In prep.).

7) In the south Atlantic region, surface currents transport postlarvae to coastal areas during late winter and spring; postlarvae are transported into estuaries by incoming tides (Larsen et al. 1989).

8) Brown, pink, and white shrimp all probably make use of selective tidal stream transport in passes (Benfield and Aldrich 1992).

References

Benfield, M.C., and D.V. Aldrich. 1992. Attraction of postlarval *Penaeus aztecus* Ives and *P. setiferus* (L.) (Crustacea: Decapoda: Penaeidae) to estuarine water in a laminar-flow choice chamber. *Journal of Experimental Marine Biology and Ecology*. 156:39-52.

Larsen, S.C., M.J. Van Den Avyle, and E.L. Bozeman Jr. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (South Atlantic)—brown shrimp. U.S. Fish Wildl. Serv. Biol. Rep. 82(11.90). U.S. Army Corps of Engineers, TR EL-82-4, 14 pp.

Pattillo, M.E., T.E. Czapla, D.M. Nelson, and M.E. Monaco. In Prep. Distribution and abundance of fishes and invertebrates in Gulf of Mexico estuaries, Vol II: Species life history summaries. ELMR Rep. No. 11. NOAA/NOS Strategic Environmental Assessments Division, Silver Spring, MD.

Rogers, B., R.F. Shaw, W.H. Herke, and R.H. Blanchet. 1993. Recruitment of postlarval and juvenile brown

shrimp (*Penaeus aztecus* Ives) from offshore to estuarine waters of the northwestern Gulf of Mexico. *Estuarine, Coastal, and Shelf Science* 36:377-394.

Wenner, E.L., and H.R. Beatty. 1993. Utilization of shallow estuarine habitats in South Carolina, U.S.A., by postlarval and juvenile stages of *Penaeus* spp. (Decapoda: penaeidae). *Journal of Crustacean Biology* 13(2):280-295.

Pink shrimp (*Penaeus duorarum*) Life History Summary

This general life history summary is based primarily on Benfield and Aldrich (1992), Biesla et al. (1983), Mulholland (1984), Pattillo et al. (In Prep.), Rogers et al. (1993), and Wenner and Beatty (1993),

General Life History

The pink shrimp (Penaeidae) is found from lower Chesapeake Bay to south Florida (including Bermuda) in the Atlantic Ocean, and into the Gulf of Mexico to Isla Mujeres, Mexico (Biesla et al. 1983). Maximum densities are found in the eastern and southwestern Gulf of Mexico. The species is important both commercially and ecologically. Pink shrimp are caught in commercial quantities throughout most of the geographic range of the species, and juveniles support a bait shrimp industry throughout the Gulf of Mexico (Mulholland 1984). They are omnivorous and provide food for many other species, and are an important link between marine and estuarine ecosystems (Biesla et al. 1983). The minimum survival temperature in Florida waters is about 12 °C, and in the laboratory pink shrimp voluntarily occupied temperatures as high as 38 °C (Mulholland 1984). The species is especially abundant in broad, shallow continental shelf areas, and in shallow bays and estuaries (Biesla et al. 1983). In the Gulf of Mexico, pink shrimp are found in greater densities over calcareous mud and/or sand, or mixtures of shell and sand; in contrast, white and brown shrimp occur in greater densities over terrigenous silt (Mulholland 1984). Eggs and adults are demersal, and larvae are planktonic through the postlarval stage (Pattillo et al. In prep.).

Pink shrimp spawn in offshore waters, usually at depths of 15-48 m, but also from 4 to greater than 48 m (Biesla et al. 1983). Spawning on the Tortugas shelf occurs throughout the year, shifting from shallow to deeper water in fall and winter; further north in the Tampa Bay area (Gulf Coast of Florida) the majority of spawning occurs between April and September; spawning occurs at water temperatures of 20-31 °C (Mulholland

1984). Maximum spawning occurs between 27 and 30.8 °C. Larvae are generally more abundant during spring, summer and fall than during winter, indicating seasonality in reproduction. The number of eggs released per spawn is unknown; shrimp weighing 10.1-66.8 g contain 44,000 to 534,00 developing ova (Pattillo et al. In prep.). Eggs are demersal (Biesla et al. 1983).

Planktonic larvae develop offshore through 5 naupliar, 3 protozoal, and 2-5 mysis stages before metamorphosis to postlarvae (Biesla et al. 1983). The planktonic larvae migrate vertically in the water column on a daily cycle, nearer the surface at night (Mulholland 1984). Larval development takes about 15 days at 26 °C, or 21 days at 21 °C (Biesla et al. 1983). Postlarvae have been collected at salinities of 0.5 to 42 ppt, but laboratory survival is poor below 10 ppt (Mulholland 1984). Postlarvae become benthic at about 10 mm TL.

Surface currents transport postlarvae to coastal areas (Biesla et al. 1983); some pink shrimp travel at least 278 km (Mulholland 1984). They are about 8 mm TL, and 21-28 days posthatching when they enter estuaries (Pattillo et al. In prep., Biesla et al. 1983). The abundance of immigrating postlarvae increases with increasing velocity of flood tides; most postlarvae enter Florida and Texas estuaries on flood tides (Mulholland 1984). Wenner and Beatty (1993) found that ingress of postlarval brown, pink, and white shrimp to South Carolina marsh creeks was seasonal, and agreed with temporal patterns described for the southeastern coastal region; peaks in occurrence of the three species in plankton samples were as follows: brown shrimp in February-March, white shrimp in July, and pink shrimp in August. Brown and white shrimp have been shown to be attracted to organic components of estuarine water in their migration to nursery areas; pink shrimp may be also. Brown, pink, and white shrimp all probably make use of selective tidal stream transport in passes (Benfield and Aldrich 1992).

Entry into estuaries may be facilitated by inflows after periods of low estuarine water level. Pink shrimp spend about 2-6 months in nursery areas. Pink shrimp distribution is correlated with shoal grass (*Halodule wrightii*) and the species appears to actively select this habitat as postlarvae (Pattillo et al. In prep.). They are more active during the day and burrow at night, but this pattern is influenced by the local tidal cycle. They attain a length of 95-100 mm TL prior to emigration from estuarine nursery areas to offshore waters, but also show area- and season-dependent size effects at emigration (Biesla et al. 1983). Emigration occurs year-round with peaks in fall and spring. Rogers et al. (1993) have proposed a four-stage recruitment hypothesis for brown shrimp in the Gulf of Mexico (see section on brown

shrimp). Similar interactions of behavior and cold front passage could aid postlarval transport of pink shrimp both in the Gulf of Mexico and on the Atlantic Coast as well.

Larval Transport

1) "Larval stages are capable of vertical migration to control their position in the water column" (Pattillo et al. In prep.).

2) Surface currents transport postlarvae to coastal areas (Bielsa et al. 1983).

3) Brown, pink, and white shrimp all probably make use of selective tidal stream transport in passes (Benfield and Aldrich 1992).

References

Benfield, M.C., and D.V. Aldrich. 1992. Attraction of postlarval *Penaeus aztecus* Ives and *P. setiferus* (L.) (Crustacea: Decapoda: Penaeidae) to estuarine water in a laminar-flow choice chamber. *Journal of Experimental Marine Biology and Ecology* 156:39-52.

Bielsa, L.M., W.H. Murdoch, and R. Labisky. 1983. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (south Florida)—pink shrimp. U.S. Fish Wildl. Serv. FWS/OBS-82/11.17). U.S. Army Corps of Engineers, TR EL-82-4, 21 p.

Mulholland, R. 1984. Habitat suitability index models: pink shrimp. U.S. Fish Wildl. Serv. FWS/OBS-82/10.76, 17 p.

Pattillo, M.E., T.E. Czapla, D.M. Nelson, and M.E. Monaco. In Prep. Distribution and abundance of fishes and invertebrates in Gulf of Mexico estuaries, Vol II: Species life history summaries. ELMR Rep. No. 11. NOAA/NOS Strategic Environmental Assessments Division, Silver Spring, MD.

Rogers, B., R.F. Shaw, W.H. Herke, and R.H. Blanchet. 1993. Recruitment of postlarval and juvenile brown shrimp (*Penaeus aztecus* Ives) from offshore to estuarine waters of the northwestern Gulf of Mexico. *Estuarine, Coastal, and Shelf Science* 36:377-394.

Wenner, E.L., and H.R. Beatty. 1993. Utilization of shallow estuarine habitats in South Carolina, U.S.A., by postlarval and juvenile stages of *Penaeus* spp. (Decapoda: penaeidae). *Journal of Crustacean Biology* 13(2):280-295.

White shrimp (*Penaeus setiferus*) Life History Summary

This general life history summary is based primarily on Benfield and Aldrich (1992), Gracia (1991), Muncy (1984), Pattillo et al. (In prep.), Rogers et al. (1993), and Wenner and Beatty (1993).

General Life History

The white shrimp (Penaeidae) is found from Fire Island, New York to St. Lucie Inlet, Florida on the Atlantic Coast, and in the Gulf of Mexico from Ochlocknee River to Campeche, Mexico (Pattillo et al. In prep.). In the Atlantic region, white shrimp are most abundant on the Georgia and northeast Florida coasts, and in the Louisiana, Texas, and Tabasco regions in the Gulf of Mexico. The species is important both commercially and ecologically. They are omnivorous and provide food for many other species; they are considered to be euryhaline, and have been collected in temperatures of 7-38 °C (Pattillo et al. In prep.). The development of all stages takes place in a little over a year; the average life span is 16 months in a heavily exploited population (Gracia 1991). White shrimp were the first commercially important penaeid shrimp, and overfishing probably contributed to their decline in abundance (Muncy 1984). White shrimp inhabit bays, estuaries, and coastal waters. Juvenile white, pink and brown shrimp tend to inhabit different substrates; white shrimp prefer muddy substrates (Muncy 1984). White shrimp remain about four months in estuaries, and the age of first spawning is about eight months (Gracia 1991). In estuaries, postlarvae and adults are associated with shallow, mud/sand bottoms high in organic detritus, or marsh grass in oligohaline to euhaline salinities.

White shrimp spawn year-round in the Gulf of Mexico, usually at depths of 8-31 m in offshore waters (Muncy 1984). Recruitment is therefore continuous, but periods of high and low abundance occur. Two main generations are spawned annually: the first is numerically dominant and is spawned in late spring and early summer; the second mainly occurs in autumn (Gracia 1991). There may be some spawning in estuaries. Spawning in the South Atlantic region occurs in at least 9 m of water, within 9 km from shore. Spawning in the South Atlantic region occurs from May to September (Pattillo et al. In prep.), or March to November (Muncy 1984). In general, the increase in bottom water temperatures in spring triggers spawning, and rapid decreases in temperature in fall coincide with decreased spawning. White shrimp may spawn up to four times during their lifetime, but probably only once in Carolina waters (Muncy 1984). Life expectancy is about

18 months, but individuals have lived to four years in the laboratory. Female white shrimp release about 0.5-1.0 million eggs per spawn; eggs are non adhesive and demersal (Pattillo et al. In prep.). Hatching usually occurs in 10-12 hrs.

Planktonic larvae develop offshore through 5 naupliar stages in 24-36 h; these are followed by 3 protozoal and 3 mysis stages before metamorphosis to postlarvae. Larval development takes about 10-12 days. They enter estuaries during the second postlarval stage at about 7 mm TL, 2-3 weeks posthatching, and become benthic (Muncy 1984). Postlarvae have been collected in salinities of 0.4-37.4 ppt, and temperatures of 13-31 °C (Pattillo et al. In prep.).

Larvae and postlarvae are transported by prevailing coastal and tidal currents. Postlarvae enter North and South Carolina estuaries from June through September (Muncy 1984). Wenner and Beatty (1993) found that ingress of postlarval brown, pink, and white shrimp to South Carolina marsh creeks was seasonal, and agreed with temporal patterns described for the southeastern coastal region. Peaks in occurrence of the three species in plankton samples were as follows: brown shrimp in February-March, white shrimp in July, and pink shrimp in August. The abundance of white shrimp peaks in June-August in Georgia estuaries (Muncy 1984). Brown and white shrimp have been shown to be attracted to organic components of estuarine water in their migration to nursery areas; brown, pink, and white shrimp all probably make use of selective tidal stream transport in passes (Benfield and Aldrich 1992). Postlarval abundance peaks in Georgia waters in June through August. White shrimp are more active in daylight than pink or brown shrimp; they also tend to move farther upstream into low-salinity water, as far as 160 km in Louisiana and 210 km in northeast Florida. In the South Atlantic states, white shrimp nursery areas are associated with *Spartina alterniflora* wetlands (Muncy 1984). Emigration occurs at 100-120 mm TL. Rogers et al. (1993) have proposed a four-stage recruitment hypothesis for brown shrimp in the Gulf of Mexico (see section on brown shrimp). Similar interactions of behavior and coldfront passage could aid postlarval transport of white shrimp both in the Gulf of Mexico and on the Atlantic coast as well. River discharge during the tropical storm season can have a positive or negative effect on recruitment to estuaries in the Gulf of Mexico, depending on the timing of the discharge (Gracia 1991).

Larval Transport

1) Favorable currents transport larvae and postlarvae shoreward; in Georgia, nearshore and northerly bottom currents carry postlarvae into estuaries and sounds (Muncy 1984).

2) Brown, pink, and white shrimp all probably make use of selective tidal stream transport in passes (Benfield and Aldrich 1992).

3) "The mechanisms by which postlarvae locate and gain access to estuarine systems have not been comprehensively examined. Once postlarvae enter coastal waters they are thought to locate estuaries by orienting along the horizontal salinity gradients which extend outward from estuaries. Transit into estuaries is thought to involve selective tidal transport synchronized by salinity differentials between tidal currents, endogenous rhythms, or hydrostatic pressure" (Benfield and Aldrich 1992).

References

Benfield, M.C., and D.V. Aldrich. 1992. Attraction of postlarval *Penaeus aztecus* Ives and *P. setiferus* (L.) (Crustacea: Decapoda: Penaeidae) to estuarine water in a laminar-flow choice chamber. *Journal of Experimental Marine Biology and Ecology* 156:39-52.

Gracia, A. 1991. Spawning stock-recruitment relationships of white shrimp in the southwestern Gulf of Mexico. *Transactions of the American Fisheries Society* 120(5):519-527.

Muncy, R.J. 1984. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (South Atlantic)—white shrimp. U.S. Fish Wildl. Serv. FWS/OBS-82/11.27. U.S. Army Corps of Engineers, TR EL-82-4, 19 p.

Pattillo, M.E., T.E. Czaplá, D.M. Nelson, and M.E. Monaco. In prep. Distribution and abundance of fishes and invertebrates in Gulf of Mexico estuaries, Vol. II: Species life history summaries. ELMR Rep. No. 11. NOAA/NOS Strategic Environmental Assessments Division, Silver Spring, MD.

Rogers, B., R.F. Shaw, W.H. Herke, and R.H. Blanchet. 1993. Recruitment of postlarval and juvenile brown shrimp (*Penaeus aztecus* Ives) from offshore to estuarine waters of the northwestern Gulf of Mexico. *Estuarine, Coastal, and Shelf Science* 36: 377-394.

Wenner, E.L., and H.R. Beatty. 1993. Utilization of shallow estuarine habitats in South Carolina, U.S.A., by postlarval and juvenile stages of *Penaeus* spp.

(Decapoda: penaeidae). *Journal of Crustacean Biology* 13(2):280-295.

Blue Crab (*Callinectes sapidus*) Life History Summary

This general life history summary is based largely on Day et al. (1989), Epifanio et al. (1989), Hill et al. (1989), Smith and Knappenberger (1989), and Smith et al. (1989).

General Life History

The blue crab (Portunidae) occurs in coastal waters from Massachusetts Bay to eastern South America, including the Gulf of Mexico. It supports valuable commercial and recreational fisheries throughout the mid- and south Atlantic states as well as in the Gulf of Mexico; it plays an important role in the structure and function of estuarine communities (Hill et al. 1989). Adult and juvenile blue crabs are estuarine residents and are considered nektonic or members of the "mobile benthos" (Day et al. 1989). Blue crab larvae are hatched at the mouths of estuaries and drift out to sea where they feed and grow. The large interannual variations in commercial harvest and year class strength of adult crabs may result in part from variation in the supply of prejuveniles re-entering estuaries (Smith et al. 1989). In estuaries, vegetated habitats support an order of magnitude more juvenile crabs than adjacent unvegetated marsh creeks, but the environmental cues that stimulate prejuveniles to settle in one habitat versus another are not well known (Smith and Knappenberger 1989).

Copulation takes place within the estuary at middle to low salinities; in the Chesapeake Bay region, mating occurs in May through October (Hill et al. 1989), with peak activity in late August and early September (Smith and Knappenberger 1989). After copulation, females migrate to the mouth of the estuary in large bay environments (Hill et al. 1989); this behavior may be different in lagoonal or open coast situations. Sperm is stored by females for up to several months until just before egg extrusion, when fertilization occurs (Smith and Knappenberger 1989); egg production shows a peak in May or June and again in August in the Chesapeake Bay region (Smith and Knappenberger 1989). The eggs remain attached to the female's abdomen until the larvae emerge, typically on an ebb tide. Fecundities have been estimated to be 700,000 to two million eggs (Hill et al. 1989). The duration of the egg stage is 10-17 days in the Chesapeake Bay region (Smith and Knappenberger 1989).

Larvae (zoea) are planktonic and commonly pass through seven zoeal stages. Laboratory studies indicate that zoeae survive and molt at salinities greater than 20 ppt and temperatures between 20 and 30 °C (Smith and Knappenberger 1989). Beyond the first zoeal stage, optimum salinities for larval development increase; megalopal (postlarval) development is optimal at salinities above 30 ppt (Smith and Knappenberger 1989).

Evidence indicates that blue crab larvae hatched at the mouths of estuaries drift out to sea where they feed and grow (Hill et al. 1989). First stage larvae swim toward the surface; they are positively phototactic, and negatively geotactic. The larval period lasts 30-60 days; early larval stages are present in the area of the estuary mouth, later stages further offshore (Smith and Knappenberger 1989). Because blue crab larvae remain near the surface throughout zoeal development, their transport must be controlled by near surface flow (Epifanio et al. 1989). In the Chesapeake Bay region, coastal/shelf circulation can be complex. However, waters leaving Chesapeake and Delaware Bays generally move southward in a rather confined "coastal jet" (Epifanio et al. 1989). Farther offshore, particularly during the summer months, the net flow regime results in a northerly current over the inner continental shelf (Epifanio et al. 1989, Smith and Knappenberger 1989). The larvae presumably become entrained first in the southward jet, then the northward inner shelf current (Epifanio et al. 1989). This process is estimated to take 1-2 months (Smith and Knappenberger 1989), sufficient time for the larvae to metamorphose into postlarvae (megalopae) while being retained in the region of the Bay mouth. Postlarvae are concentrated on the inner continental shelf adjacent to the Bay as well as further offshore; postlarval development takes 30 to 90 days, averaging 40 days (Smith and Knappenberger 1989).

For the blue crab life cycle to be completed, crabs must move from the inner continental shelf to the estuary proper. It is hypothesized that the megalopae are the main reinvasive stage, but juvenile reinvasion is also possible (Smith and Knappenberger 1989). One theory for reinvasion is that megalopae take advantage of landward, residual, non-tidal currents. While net flow from Chesapeake Bay is seaward, both the vertical and horizontal physical complexities of flow across the Bay mouth create reasonably predictable regions of residual inflow of water. Megalopae entrained in these residual inflows will be transported into the Bay.

A second reinvasion theory is that megalopae exploit tidally driven currents. To exploit landward tidal currents, megalopae would have to swim up in the water

column during flood tides (where they are indeed found, especially at night), and sink in the water column on ebb tides (where they are found especially during the day), to produce net landward transport. This second reinvasion mechanism has been shown to effectively transport postlarvae up the estuary in Delaware and other estuarine systems, but it has not yet been documented for Chesapeake Bay (Smith and Knappenberger 1989).

A third proposed mechanism for postlarval reinvasion centers on episodic, wind-induced water exchange events. During periods of strong and persistent easterly winds, shelf surface waters are driven into Chesapeake Bay and other east coast estuaries; these events could transport megalopae into the estuaries. Increased megalopal settlement on artificial substrates in the York River has been correlated with major inflow events (Smith and Knappenberger 1989).

Once in Chesapeake Bay, megalopae most probably utilize the tidal flood currents to move upstream and invade the shallow sub-estuaries and tributaries (Smith and Knappenberger 1989). During this journey, the megalopae eventually settle and undergo metamorphosis to the first juvenile instar. Settlement typically occurs in August through November in Chesapeake Bay, and is strongly episodic. The timing and magnitude of the settlement pulses vary from year to year, but they last a few days and appear to be correlated with maximum tide associated with the full moon.

Larval Transport

1) Surface currents, nearshore and on the inner continental shelf; wind-driven currents (Epifanio et al. 1989, Johnson and Hester 1989).

2) Tidal currents in passes (postlarvae) (Smith and Knappenberger 1989).

References

Day, J.W., Jr., C.S.S. Hall, W.M. Kemp, and A. Yanez-Arancibia. 1989. *Estuarine Ecology*. John Wiley and Sons, New York, 558 p.

Epifanio, C.E., A.K. Masse, and R.W. Garvine. 1989. Transport of blue crab larvae by surface currents off Delaware Bay, USA. *Marine Ecology Progress Series* 54:35-41.

Hill, J., D.L. Fowler, and M.J. Van Den Avyle. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Mid-Atlantic)—Blue crab. U.S. Fish Wildl. Serv. Biol. Rep. 82(11.100). U.S. Army Corps of Engineers, TR EL-82-

Johnson, D.R., and B.S. Hester. 1989. Larval transport and its association with recruitment of blue crabs to Chesapeake Bay. *Estuarine, Coastal and Shelf Science* 28:459-472.

Smith, D.E., and M. Knappenberger. 1989. Blue crab recruitment dynamics in Chesapeake Bay: A review of current knowledge. Virginia Sea Grant Publication VSG-89-01.

Smith, D. E., R.J. Orth, E. Olmi, J. van Montfrans, and R.N. Lipcius. 1989. Blue crab recruitment work shop, February 5-7, 1989: summary of activities. Virginia Sea Grant Publication.

Ladyfish (*Elops saurus*)
Life History Summary

This general life history summary is based largely on Manooch and Raver (1984), U.S. Fish and Wildlife Service (1978), and Zale and Merrifield (1989).

General Life History

The ladyfish (Elopidae) is a coastal pelagic fish found from Massachusetts and Bermuda to Brazil and throughout the Gulf of Mexico (Manooch and Raver 1984). It is uncommon north of Cape Hatteras and most common in Florida and Antilles waters; it is also found in the Indian and Western Pacific oceans (Zale and Merrifield 1989). The ladyfish supports recreational fisheries, but the flesh is considered inedible because of its boniness, and therefore does not support a commercial fishery (Zale and Merrifield 1989). Ladyfish are found in warm coastal waters as well as brackish and completely freshwaters (Manooch and Raver 1984). Adults tolerate a wide range of salinities. Adult ladyfish usually inhabit relatively open inshore and coastal habitats, but may also ascend rivers for considerable distances, although their occurrence in completely freshwater is apparently rare (Zale and Merrifield 1989). Adult ladyfish feed primarily on fish and decapod crustaceans; larvae feed primarily on zooplankton. Adults have been captured at 11-35 °C.

Adult ladyfish apparently move from inshore waters to offshore waters to spawn, and larvae are transported by currents and/or swim to inshore waters. Ladyfish spawning locations are unknown, but they are believed to spawn pelagic eggs offshore (Manooch and Raver 1984) throughout most of the range of the species (U.S. Fish and Wildlife Service 1978), as judged by the locations of capture of early larvae. Fecundity and size at sexual maturity are unknown. Eggs are undescribed;

spawning appears to occur throughout the year, perhaps peaking in the fall (Zale and Merrifield 1989, U.S. Fish and Wildlife Service 1978), late winter and early spring (Manooch and Raver 1984), or late spring and early summer (Zale and Merrifield 1989).

The larval stages include leptocephalus stages (U.S. Fish and Wildlife Service 1978). Early Stage I larvae are captured offshore only in clear, warm, saline waters (22.2-30.0 °C, 28.5-39.0 ppt). Late Stage I larvae are captured inshore. Stage II and III larvae and juveniles inhabit beaches, canals, bayous, lagoons, tidal ponds, creeks, and rivers; they live in water of a wide range of temperatures and salinities (0.0-45 ppt, 16-35 °C). Larval and juvenile ladyfish use estuaries, salt marshes, and mangroves as nurseries; reduction of these habitats is likely to impact the fishery (Zale and Merrifield 1989).

Larval Transport

No information in references. Hypothetical, probably similar to mechanisms for other species that spawn offshore at relevant seasons off the southeastern U.S. coast.

References

Manooch, C.S., and D. Raver. 1984. Fishes of the southeastern United States. North Carolina State Museum of Natural History, Raleigh, NC, 362 p.

U.S. Fish and Wildlife Service. 1978. Development of fishes of the Mid-Atlantic Bight. Biological Services Program, Fish and Wildlife Service, U.S. Dept. of the Interior. FWS/OBS-78/12, vols. 1-6.

U.S. Fish Wildl. Serv. 1978. Biol. Rep. 82(11.104). U.S. Army Corps of Engineers, TR EL-82-4, 17 p.

Zale, A.V., and S.G. Merrifield. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (South Florida)—ladyfish and tarpon.

Atlantic menhaden (*Brevoortia tyrannus*) Life History Summary

This general life history summary is based largely on Grosslein and Azarovitz (1982), Manooch and Raver (1984), Miller et al. (1984), Norcross and Bodolus (1991), and Rogers and Van Den Avyle (1989).

General Life History

The Atlantic menhaden (Clupeidae) is an abundant, euryhaline, coastal pelagic fish, which, together with the Gulf menhaden, constitutes the largest commercial fishery by weight, and about eighth largest in value, in the United States. It is also a significant food source for several important commercial and sport fish species. It is used almost exclusively for fish meal and other additives to livestock feed, and for the oil extracted from the flesh, which has a variety of uses (Grosslein and Azarovitz 1982). Its large biomass indicates that it is extremely important in coastal ecosystems. It occurs along the Atlantic Coast from Nova Scotia to Florida, and is replaced by the Gulf menhaden along the coast of the Gulf of Mexico (Rogers and Van Den Avyle 1989). Dense schooling is a characteristic behavior, with 50 to 200 thousand fish in a school (Manooch and Raver 1984). Spotter aircraft are used to locate these large schools, which are harvested with purse seines. Larval menhaden feed on individual zooplankton, and juveniles and adult menhaden are filter feeders on primarily phytoplankton (Rogers and Van Den Avyle 1989). Marked seasonal migrations are made each year: slowly northward as waters warm in April and May; and southward in early autumn. From May to October, most of the adult population is within 8 km of the coast, usually in water less than 20 m deep (Grosslein and Azarovitz 1982).

Menhaden spawn during all months of the year (Rogers and Van Den Avyle 1989), but not in all locations in each month (Manooch and Raver 1984). Peak spawning off the southeastern United States occurs in October to March off the coasts of Virginia and the Carolinas. A few individuals mature at one year, most by age two, and all by age three (Rogers and Van Den Avyle 1989). Menhaden may live as long as 8-12 years, but there is heavy fishing mortality from age one onward (Rogers and Van Den Avyle 1989). There is very large interannual variation in juvenile abundance. Fecundities are estimated to be 38 to 631 thousand eggs per female (Rogers and Van Den Avyle 1989). The eggs are pelagic; hatching occurs in 2.5-2.9 days at 15.5 °C in the laboratory (Rogers and Van Den Avyle 1989).

The larvae are transported by currents, and perhaps by swimming to estuarine nursery areas. Larvae metamorphose into juveniles in the low salinity portions of estuaries; no metamorphic larvae or prejuveniles have been found at sea (Grosslein and Azarovitz 1982). Juveniles gradually move down the estuary where they remain until autumn, when they move out into the ocean.

Larval transport of menhaden, croaker, spot, summer flounder and southern flounder was considered in detail by Miller et al. (1984). The attributes of this group are: 1) after hatching near the Gulf Stream, larvae migrate shoreward during December-March; 2) larvae or small juveniles migrate through inlets and sounds to estuarine nursery areas in early spring; 3) large juveniles or sub-adults migrate out of juvenile nursery areas in the fall; 4) adults migrate offshore in fall or winter; 5) spawning occurs in winter. The abundance of these species suggests that this life history pattern is quite successful, and Miller et al. (1984) argue that the key elements of this success are winter (versus other season) spawning, plus estuarine (versus offshore) nursery areas.

The most important aspect of winter spawning in this context is that winter currents favor shoreward transport of pelagic, offshore-spawned larvae. Miller et al. (1984) propose a three-layer model of the winter current regime off North Carolina which could account for substantial shoreward larval transport. This model incorporates an intermediate (interior) layer of water moving shoreward. It is likely that this layer occupies 50-70% of the water column, moves at about 3-8 cms, and brings relatively warm, salty water onshore. This intermediate winter layer is persistent, and therefore best for larval transport because it is partly density driven, thus less subject to wind-forcing. The persistent intermediate onshore layer transport is most likely to be in effect on the shelf beyond the 25 m depth contour; within the 25 m contour, conditions are more variable and may be more dominated by winds (J.M. Miller, pers. comm., Norcross and Bodolus 1991).

Differences in spawning time and vertical distribution among species may explain differences in abundance and age of cohorts arriving at estuaries. Movement of menhaden vertically between the offshore surface current and the onshore intermediate current may be responsible for the greater size (age) variability of menhaden versus spot or croaker arriving at estuaries.

Miller et al. (1984) suggest that shoreward transport of all five species they considered, whether fall or winter spawned, would be enhanced by larvae actively selecting the warmest water available to them in the vertical dimension.

Larval Transport

1) Onshore currents: wind-induced surface currents in the fall; in winter, onshore intermediate layer (resulting from surface wind-induced offshore currents plus bottom density-driven offshore currents) (Miller et al. 1984).

2) Through inlets: tidal flood; selective tidal stream transport (Miller et al. 1984); currents resulting from winter storms (Pietrafesa and Janowitz 1988).

3) Tide may be an important mechanism in gathering larvae at inlets and transporting larvae through inlets (Pietrafesa and Janowitz 1988).

4) Within estuaries: selective tidal stream transport (Weinstein 1988).

References

Grosslein, M.D., and T.H. Azarovitz. 1982. Fish distribution. Marine Ecosystems Analysis Program, New York Bight Atlas Monograph 15. New York Sea Grant Institute, Albany, NY, 182 p.

Manooch, C.S., and D. Raver. 1984. Fishes of the southeastern United States. North Carolina State Museum of Natural History, Raleigh, NC, 362 p.

Miller, J.M., J.P. Reed, and L.J. Pietrafesa. 1984. Patterns, mechanisms and approaches to the study of migrations of estuarine-dependent fish larvae and juveniles. *In*: McCleave, J.D., G.P. Arnold, J.J. Dodson and W.H. Neill (eds.) Mechanisms of migration in fishes. Plenum Press, NY, pp. 209-225.

Norcross, B.L., and D.A. Bodolus. 1991. Hypothetical northern spawning limit and larval transport of spot. *In* Hoyt, R. D. (ed.), Larval fish recruitment and research in the Americas. NOAA Tech. Rep. NMFS 95, pp. 77-88.

Pietrafesa, L.J., and G. S. Janowitz. 1988. Physical oceanographic processes affecting larval transport around and through North Carolina inlets. American Fisheries Society Symposium 3:34-50.

Rogers, S.G., and M.J. Van Den Avyle. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Mid-Atlantic)—Atlantic menhaden. U.S. Fish Wildl. Serv. Biol. Rep. 82(11.108). U.S. Army Corps of Engineers, TR EL-82-4, 23 p.

Weinstein, M.P. (ed.). 1988. Larval fish and shellfish transport through inlets. American Fisheries Society

Symposium 3. American Fisheries Society, Bethesda, MD, 165 p.

Cobia (*Rachycentron canadum*)

Life History Summary

This general life history summary is based largely on Ditty and Shaw (1992), Shaffer and Nakamura (1989), Nelson et al. (1991), and U.S. Fish and Wildlife Service (1978).

General Life History

Cobia (Rachycentridae) are mainly coastal and continental shelf pelagic fish, with a circumtropical and subtropical distribution, with the exception of the central and eastern Pacific and Mediterranean Sea (Shaffer and Nakamura 1989); they are also found seasonally in temperate waters. In the western Atlantic, they are found from Massachusetts and Bermuda to the Rio de la Plata, Argentina (Shaffer and Nakamura 1989). Cobia are carnivorous fish that feed primarily on crustaceans, and also on other benthic invertebrates and fish (Shaffer and Nakamura 1989). They are considered to have low abundance and low recruitment throughout their range (Ditty and Shaw 1992, Shaffer and Nakamura 1989).

Commercial catches are usually incidental, occasionally targeted; the main recreational fishery is in the United States. Cobia are highly prized by sportsmen (Ditty and Shaw 1992), where recreational landings exceed commercial landings by more than tenfold (Shaffer and Nakamura 1989). Adults may reach a length of 2 m and weight of 68 kg. Cobia often associate with larger rays, sharks and sea turtles, and are attracted to boats, buoys and floating debris (Shaffer and Nakamura 1989). Early juvenile stages move into coastal and estuarine waters with relatively high salinities. Adults occasionally enter estuaries; for example, cobia enter Chesapeake Bay in late May or early June, and leave by mid-October (tagging studies revealed that the same individuals returned to the bay every summer). They have been taken in waters of 22.5-44.5 ppt salinity (Shaffer and Nakamura 1989).

Cobia are solitary, or found in groups of 2-8 fish. There is evidence that adult cobia make seasonal migrations that coincide with changes in water temperature and spawning activity. Their distribution is thought to be greatly affected by temperature; they have been taken in waters of 16.8-32.0 °C (Shaffer and Nakamura 1989); they do not appear in the Chesapeake until temperatures reach 19 °C. In the laboratory, 90 day-old cobia ceased feeding when the temperature was lowered to 18.3 °C (Shaffer and Nakamura 1989). Adult

cobia exhibit a north-south/inshore-offshore pattern along the coast of the southeastern United States, and in the Gulf of Mexico, cobia winter in the Florida Keys and move north and west along the coast in the spring.

Spawning takes place during the day (Ditty and Shaw 1992), usually offshore (U.S. Fish and Wildlife Service 1978), but also in estuarine waters (Ditty and Shaw 1992). Cobia form spawning aggregations (Shaffer and Nakamura 1989); spawning takes place from mid-June to mid-August off the coast of Virginia (Shaffer and Nakamura 1989), and occurs earlier in the year off the coast of the Carolinas (as early as mid-May off South Carolina). Spawning may occur in the Gulf of Mexico as early as March, with young cobia being common in May, June and July off Texas; possible spawning of cobia has been observed in the Gulf in August, about 48 km offshore, in waters estimated to be 82-165 m deep (Ditty and Shaw 1992). At least some spawning occurs 50-90 km offshore. Male cobia mature at an earlier age and a smaller size (second year, 51.8 cm fork length [FL], 1.14 kg) than do females (third year, 69.6 cm FL, 3.27 kg), and cobia are known to live 10 to 15 years (Shaffer and Nakamura 1989). Fecundities of females 100-125 cm FL is estimated to be 1.9-5.4 million eggs (Shaffer and Nakamura 1989). Fecundity of an eight-year-old female was estimated to be 6-7 million eggs. Throughout the Gulf of Mexico, most larvae are collected in June-September. Peak spawning of cobia in Puerto Rican waters apparently occurs in August. Cobia spawn during the day, and eggs are found in the upper meter of the water column in waters ranging from 20 to 165 meters deep, warmer than 20 °C, and 19-35 ppt salinity. Cobia eggs and larvae are planktonic (Shaffer and Nakamura 1989). Most are found in the upper meter of the water column in offshore waters (Ditty and Shaw 1992), although larvae are common in Bogue Sound and New River estuaries in North Carolina, and juveniles are common in many southeast U.S. estuaries (Nelson et al. 1991). In the laboratory, naturally spawned cobia eggs collected in the field had the highest hatching rate at 33-35 ppt and at 26.5 °C (Shaffer and Nakamura 1989). Cobia eggs are estimated to hatch in 24 h at 29 °C (Ditty and Shaw 1992). On the Atlantic coast, eggs have been collected in coastal waters 20-49 m deep, near the edge of the Florida Current, in the Gulf Stream, and rarely in lower Chesapeake Bay and North Carolina estuaries.

Day-one hatchlings are about 2.5-3.0 mm long (Ditty and Shaw 1992). Day-5 larvae have absorbed the yolk sac, are 4-5 mm long, and begin active feeding. By the tenth day, larvae are 5-10 mm long and capable of active, prolonged swimming. Shaffer and Nakamura (1989) provide a table of average length of cobia aged from 1-131 days which may be helpful in

interpreting capture information. Nineteen-day-old cobia averaged 12.1 mm (range: 10.0-15.5 mm), 24-day old cobia averaged 24.2 mm (range: 19.0-33.0 mm) and 59-day-old cobia averaged 98.2 mm (range: 69-120 mm). Larvae 13-15 mm in length have been taken 40-64 km offshore in the Gulf of Mexico, whereas larger individuals (45-140 mm) have been taken most frequently inshore. Larvae 14-23 mm long were taken at night at the surface 925 km off Delaware. However, eggs and small larvae were taken together in the Crystal River estuary in Florida in waters 28.1-29.7 °C and 30.4-34.1 ppt.

Larval Transport

No information in references. Cobia primarily spawn in the summer, so summer current systems might be responsible for transport, plus swimming.

References

Ditty, J.G., and R.F. Shaw. 1992. Larval development, distribution and ecology of cobia *Rachycentron canadum* (Family: Rachycentridae) in the northern Gulf of Mexico. Fishery Bulletin 90:668-677.

Nelson, D.M., E.A. Irlandi, L.R. Settle, M.E. Monaco, and L.C. Costen-Clements. 1991. Distribution and abundance of fishes and invertebrates in southeast estuaries. ELMR Rep. No. 9. NOAA/NOS Strategic Environmental Assessments Division, Rockville, MD, 177 p.

Shaffer, R.V., and E.L. Nakamura. 1989. Synopsis of biological data on the cobia *Rachycentron canadum* (Pisces: Rachycentridae). NOAA Tech. Rep. NMFS 82, 21 p.

U.S. Fish and Wildlife Service. 1978. Development of fishes of the Mid-Atlantic Bight. Biological Services Program, Fish and Wildlife Service, U.S. Dept. of the Interior. FWS/OBS-78/12, vols. 1-6.

Pinfish (*Lagodon rhomboides*)
Life History Summary

This general life history summary is based largely on Manooch and Raver (1984), Miller et al. (1984), Norcross and Bodolus (1991), Pietrafesa and Janowitz (1988), and U.S. Fish and Wildlife Service (1978).

General Life History

The pinfish (Sparidae) is an abundant groundfish that inhabits coastal waters from Cape Cod to Yucatan, Mexico, including the Gulf of Mexico, Bermuda and the Bahamas (Manooch and Raver 1984). Pinfish are both euryhaline and eurythermal, and may be found at depths of a few centimeters to 73 meters, usually occurring close to vegetation or other cover. Adults are usually found in open waters, as opposed to estuaries; youngest larvae offshore, and juveniles in estuaries or in transit. Pinfish are essentially non-schooling, with the probable exception of offshore spawning aggregations. Pinfish are omnivorous and feed primarily during the day.

Spawning occurs offshore, probably near the surface (U.S. Fish and Wildlife Service 1978), from about mid-October through March with maximum spawning off the southeastern U.S. during December and January. Sexual maturity may be attained at one year, but most initially reproduce when older. Pinfish probably live longer than seven years. Eggs and larvae are pelagic. Hatching takes about 48 h at 18 °C and 34 ppt salinity. Fecundities are estimated as 7-90 thousand eggs per female.

Larval Transport

No information in references; hypothetical.

Since this species spawns in winter in this region, mechanisms of larval transport available to them would probably be the same as those postulated for other winter spawners, such as spot, croaker, menhaden, summer and southern flounders (Miller et al. 1984, Pietrafesa and Janowitz 1988). These mechanisms are as follows:

1) Onshore currents: wind-induced surface currents in the fall; in winter, onshore intermediate layer (resulting from surface wind-induced offshore currents, plus bottom density-driven offshore currents) (Miller et al. 1984).

2) Through inlets: tidal flood; selective tidal stream transport (Miller et al. 1984); currents resulting from winter storms (Pietrafesa and Janowitz 1988).

3) Tide may be an important mechanism in gathering larvae at inlets and transporting larvae through inlets (Pietrafesa and Janowitz 1988).

References

Manooch, C.S., and D. Raver. 1984. Fishes of the southeastern United States. North Carolina State Museum of Natural History, Raleigh, NC, 362 p.

Miller, J.M., J.P. Reed, and L.J. Pietrafesa. 1984. Patterns, mechanisms and approaches to the study of migrations of estuarine-dependent fish larvae and juveniles. *In*: McCleave, J.D., G.P. Arnold, J.J. Dodson and W.H. Neill (eds.). Mechanisms of migration in fishes. Plenum Press, NY. pp. 209-225.

Norcross, B.L., and D.A. Bodolus. 1991. Hypothetical northern spawning limit and larval transport of spot. *In* Hoyt, R.D. (ed.), Larval fish recruitment and research in the Americas. NOAA Tech. Rep. NMFS 95, pp. 77-88.

Pietrafesa, L.J., and G.S. Janowitz. 1988. Physical oceanographic processes affecting larval transport around and through North Carolina inlets. American Fisheries Society Symposium 3:34-50.

U.S. Fish and Wildlife Service. 1978. Development of fishes of the Mid-Atlantic Bight. Biological Services Program, Fish and Wildlife Service, U.S. Dept. of the Interior. FWS/OBS-78/12, Vols. 1-6.

Spotted seatrout (*Cynoscion nebulosus*)
Life History Summary

This general life history summary is based largely on Banks et al. (1991), Manooch and Raver (1984), Pattillo et al. (In prep.), Peebles and Tolley (1988), and U.S. Fish and Wildlife Service (1978).

General Life History

The spotted seatrout (Sciaenidae) is a coastal groundfish that inhabits waters on the eastern coast of the United States from Cape Cod, Massachusetts, south to Campeche, Mexico (Banks et al. 1991, Pattillo et al. In prep.). They are most abundant in Florida and the Gulf states and are rare north of Delaware Bay. They are an important component of the recreational and commercial fisheries of the southeastern United States; most of the commercial catch is incidental (as opposed to targeted) and far exceeded by the sport catch (Pattillo et al. In prep.). All life stages are euryhaline (Manooch and Raver 1984). Larval to adult stages

are often associated with seagrasses, which appear to be the primary habitat for juveniles and adults; this is an inshore, demersal species, which migrates very short distances (Pattillo et al. In prep.). Larvae feed primarily on zooplankton, juveniles on benthic invertebrates, and adults on fish. Adults are euryhaline and can tolerate salinities ranging from 0.2-70.0 ppt, and seem to prefer temperatures of 15-26 °C (Pattillo et al. In prep.).

Spawning occurs in the summer months at dusk in deep channels (2.5-4.5 meters) adjoining shallow seagrass flats, along deeper edges (1.0-3.0 meters) of seagrass flats, in shallow, nearshore shelf waters, and in higher-salinity parts of estuaries (Peebles and Tolley 1988, Pattillo et al. In prep., U.S. Fish and Wildlife Service 1978). The spawning season is protracted and variable in the Gulf of Mexico, but generally occurs in March through October (Banks et al. 1991, U.S. Fish and Wildlife Service 1978). Spawning may occur throughout the year in southern Florida and Mexican waters. In the mid-Atlantic states, spawning occurs in spring and summer, peaking in April-May. The approximate ranges of temperature and salinity for spawning are 24-30 °C and 18.5-36 ppt (Pattillo et al. In prep.). Spotted seatrout mature between their first and third year of life, and live as long as 15 years. Size at maturity and growth rates vary among estuaries. Males are much smaller than females at maturity. Adults weigh up to 10 pounds and grow to approximately 30 inches (Manooch and Raver 1984). Spotted seatrout are multiple spawners at intervals as short as four days, and female seatrout produce from 15,000 to 1.1 million eggs per batch; they may produce as many as 10 million eggs per spawning season (Pattillo et al. In prep.). Eggs are pelagic (>30 ppt) or demersal (<25 ppt), depending on salinity (Pattillo et al. In prep.). Hatching occurs in 16-20 h at 25 °C; the best hatching rates in one study occurred at 15-25 ppt, and in another at 19-38 ppt at 28 °C (Pattillo et al. In prep.).

Larvae at hatching are about 1.5 mm SL. Spotted seatrout are among the most euryhaline sciaenid larvae (Banks et al. 1991). Larvae feed primarily on zooplankton.

Larval Transport

1) Spotted seatrout probably use selective tidal stream transport in the Gulf of Mexico (Raynie and Shaw 1994).

References

Banks, M.A., G.J. Holt, and J.M. Wakeman. 1991. Age-linked changes in salinity tolerance of larval spotted

seatrout (*Cynoscion nebulosus*, Cuvier). *Journal of Fish Biology* 39:505-514.

Manooch, C.S., and D. Raver. 1984. Fishes of the southeastern United States. North Carolina State Museum of Natural History, Raleigh, NC, 362 p.

Pattillo, M.E., T.E. Czaplak, D.M. Nelson, and M.E. Monaco. In prep. Distribution and abundance of fishes and invertebrates in Gulf of Mexico estuaries, Vol. II: Species life history summaries. ELMR Rep. No. 11. NOAA/NOS Strategic Environmental Assessments Division, Silver Spring, MD.

Peebles, E.B., and S.G. Tolley. 1988. Distribution, growth, and mortality of larval spotted seatrout, *Cynoscion nebulosus*: a comparison between two adjacent estuarine areas of southwest Florida. *Bulletin of Marine Science* 42(3):397-410.

Raynie, R.C., and R.F. Shaw. 1994. Ichthyoplankton abundance along a recruitment corridor from offshore spawning to estuarine nursery ground. *Estuarine, Coastal and Shelf Science* 39:421-450.

U.S. Fish and Wildlife Service. 1978. Development of fishes of the Mid-Atlantic Bight. Biological Services Program, Fish and Wildlife Service, U.S. Dept. of the Interior. FWS/OBS-78/12, Vols. 1-6.

Weakfish (*Cynoscion regalis*) Life History Summary

This general life history summary is based largely on Grosslein and Azarovitz (1982), Manooch and Raver (1984), and Mercer (1989).

General Life History

The weakfish (Sciaenidae) is an abundant coastal euryhaline groundfish occurring from Massachusetts Bay to southern Florida, occasionally straying to Nova Scotia and the eastern Gulf of Mexico; it is most abundant from North Carolina to Rhode Island (Mercer

1989). Feeding occurs throughout the water column (Grosslein and Azarovitz 1982) primarily on shrimps, anchovies and clupeid fishes. Foraging activity peaks during periods of low light intensity. Adults have been collected at 7-32 ppt (Mercer 1989). Weakfish are highly prized by recreational fishermen and also support local commercial fisheries; wide fluctuations in commercial landings have been attributed to overfishing and habitat loss (Mercer 1989). Weakfish are considered an important link between estuarine and marine ecosystems. Adult weakfish migrate seasonally between inshore and offshore waters (Manooch and Raver 1984). Weakfish younger than age four migrate south along the coast in fall and winter; older fish move south and offshore in autumn, and return to inshore northern grounds in the spring (Grosslein and Azarovitz 1982). The largest fish travel fastest and migrate furthest, move inshore first in the spring, and tend to congregate in the northern part of the range. Some adults may remain in inshore waters throughout the winter from North Carolina southward. In northern areas, a greater proportion of adults spend the summer in ocean waters rather than in estuaries.

Spawning occurs in nearshore and estuarine waters after the spring inshore migration (Mercer 1989, U.S. Fish and Wildlife Service 1978). In North Carolina, spawning occurs from March to September with peak activity from April to June; in the Delaware Bay to New York area the season extends from May to mid-July (Mercer 1989). In the New York Bight area, two spawning peaks occur: larger fish in mid-May and smaller fish in June (Mercer 1989). Both males and females reach sexual maturity between one and two years of age; North Carolina fish mature at a smaller size than more northerly fish (Mercer 1989). Weakfish grow rapidly and live as long as nine years. Fecundities are estimated to be between 286,000 and two million eggs per female. Hatching occurs in 36-40 h at 20-21 °C; laboratory hatching was optimal at 18-24 °C (Mercer 1989).

Eggs and larvae have been collected in Delaware Bay at 12-31 ppt (Mercer 1989). Weakfish larvae are usually collected in nearshore waters, but also as far as 70 km offshore; weakfish larvae are 1.5-1.75 mm TL at hatching and become demersal at 8 mm (Mercer 1989). The use of estuarine areas by juvenile weakfish is well-documented (Mercer 1989).

Larval Transport

No information in references. Hypothetical: tidal, coastal, storm currents.

References

- Grosslein, M.D., and T.H. Azarovitz. 1982. Fish distribution. Marine Ecosystems Analysis Program, New York Bight Atlas Monograph 15. New York Sea Grant Institute, Albany, NY, 182 p.
- Manooch, C.S., and D. Raver. 1984. Fishes of the southeastern United States. North Carolina State Museum of Natural History, Raleigh, NC, 362 p.
- Mercer, L.P. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Mid-Atlantic)—weakfish. U.S. Fish Wildl. Serv. Biol. Rep. 82(11.109). U.S. Army Corps of Engineers, TR EL-82-4, 17 p.

Spot (*Leiostomus xanthurus*) **Life History Summary**

This general life history summary is based largely on Flores-Coto and Warlen (1993), Manooch and Raver (1984), Miller et al. (1984), Norcross and Bodolus (1991), Pattillo et al. (In prep.), Pietrafesa and Janowitz (1988), and Phillips et al. (1989).

General Life History

Spot (Sciaenidae) is an abundant, euryhaline groundfish that inhabits coastal waters from the Gulf of Maine to the Bay of Campeche, Mexico (Pattillo et al. In prep., Phillips et al. 1989). The area of greatest abundance, and the center of the commercial fishery on the Atlantic coast, extends from Chesapeake Bay to South Carolina. They are usually found in depths less than 100 m (Norcross and Bodolus 1991). Spot support valuable commercial and sport fisheries; their very large biomass in estuaries indicates that they are important in the structure and function of these ecosystems (Phillips et al. 1989). Spot occur in shallow inshore waters in the summer, then spawn offshore on the mid- to outer continental shelf (Norcross and Bodolus 1991), and inshore of the Gulf Stream, in the fall and winter (Manooch and Raver 1984); spawning may be closer inshore at the beginning and end of the season. There are very few spot captured in the Middle-Atlantic Bight in spring, and spot from these northern areas may share a common wintering ground south of Cape Hatteras with southern spot (Norcross and Bodolus 1991). Adults feed largely on benthic copepods and polychaetes, with other benthic invertebrates of secondary importance in the diet (Phillips et al. 1989).

The spawning season is protracted, occurring in the fall, winter and spring (Norcross and Bodolus 1991,

Flores-Coto and Warlen 1993). It begins as early as September and ends as late as May, depending on location; the season extends from October through March off the coasts of North and South Carolina. Off the coast of North Carolina, peak spawning occurs in December and January, and 75-90 km offshore (Phillips et al. 1989). Sexual maturity is first attained at age 2-3 years. Few spot live as long as five years (Pattillo et al. In prep.). Fecundities are estimated to be between 30-60 thousand eggs per female (Phillips et al. 1989). Although spawning in nature has not been observed, laboratory studies show that spawning takes place between 17.5 and 25.0 °C; rarely is there water as warm as this in the Middle-Atlantic Bight in winter, so the area near Cape Hatteras has been hypothesized as the northern spawning limit (Norcross and Bodolus 1991). Incubation takes 48 hours at 20 °C (Phillips et al. 1989).

Eggs and early larvae are planktonic and pelagic (Pattillo et al. In prep.). Larvae are 1.5-1.7 mm TL at hatching (Phillips et al. 1989), and are subject to transport by currents and wind (Pattillo et al. In prep.). This means that the pelagic larvae recruiting to Chesapeake Bay 1-3 months after spawning must be transported as much as 250 km. Although physical processes that might be responsible for larval transport can be hypothesized, precise mechanisms are still unknown. Strong northerly offshore winds are common in the southern Middle-Atlantic Bight in winter, but there are episodes of southerly winds from January onward. These short-term reversals of the seasonal wind patterns could cause current reversals and serve as a transport mechanism for spot recruiting to Chesapeake Bay. Episodes of southerly winds have in fact preceded the appearance of spot cohorts in Chesapeake Bay; the duration and frequency of southerly wind events during the months when larvae are in transit could be related to spot year-class strength (Norcross and Bodolus 1991). Larvae collected south of Cape Hatteras in nearshore and estuarine waters of North Carolina suggest that spawning takes place some 90 km offshore (Flores-Coto and Warlen 1993) beyond the 30 m isobath, and that transit time to the estuary takes about 82 days (Flores-Coto and Warlen 1993); other estimates of transit time are 60-90 days. During transit, spot larvae grow rapidly, but are still small enough to require exogenous means of transport. Spot, as well as other offshore-spawned, estuarine-dependent fish, may accumulate and grow in nearshore waters prior to estuarine recruitment (Flores-Coto and Warlen 1993). Tides may be an important mechanism controlling larval gathering (Pietrafesa and Janowitz 1988). Once inside the estuary, larvae move toward freshwater and use the upper reaches of estuaries as nurseries. They return to more saline areas as they grow older. Severe winters with low tempera-

tures have been known to cause extensive mortalities in estuarine populations of juveniles (Pattillo et al. In prep.). Larvae feed on zooplankton (Phillips et al. 1989).

Larval transport of menhaden, croaker, spot, summer flounder and southern flounder were considered in detail by Miller et al. (1984). The attributes of this group are: 1) after hatching near the Gulf Stream, larvae migrate shoreward during December-March; 2) larvae or small juveniles migrate through inlets and sounds to estuarine nursery areas in early spring; 3) large juveniles or sub-adults migrate out of juvenile nursery areas in the fall; 4) adults migrate offshore in fall or winter; 5) spawning occurs in winter. The abundance of these species suggests that this life history pattern is quite successful, and Miller et al. (1984) argue that the key elements of this success are winter (versus other season) spawning, plus estuarine (versus offshore) nursery areas.

The most important aspect of winter spawning in this context is that winter currents favor shoreward transport of pelagic, offshore-spawned larvae. Miller et al. (1984) propose a three-layer model of the winter current regime off North Carolina which could account for substantial shoreward larval transport. This model incorporates an intermediate (interior) layer of water moving shoreward. It is likely that this layer occupies 50-70% of the water column, moves at about 3-8 cms, and brings relatively warm, salty water onshore. This intermediate winter layer is persistent, and therefore best for larval transport because it is partly density-driven and thus less subject to wind-forcing. The persistent intermediate onshore layer transport is most likely to be in effect on the shelf beyond the 25 m depth contour; within the 25 m contour, conditions are more variable and may be more dominated by winds (J.M. Miller, pers. comm., Norcross and Bodolus 1991).

Variability in spawning time and vertical distribution among species may explain differences in abundance and age of cohorts arriving at estuaries. Miller et al. (1984) suggest that more spot larvae relative to croaker may be delivered to estuaries because spot spawning peaks in winter during the existence of the persistent onshore intermediate layer; croaker spawning peaks earlier in the fall, when onshore transport in the surface layer may be more variable.

Miller et al. (1984) suggest that shoreward transport of menhaden, croaker, spot, summer flounder and southern flounder, whether fall or winter spawned, would be enhanced by larvae actively selecting the warmest water available in the vertical dimension; this selection may be the explanation for the observed precise age distribution of spot and croaker larvae along

onshore-offshore transects.

Larval Transport

1) Precise larval transport mechanisms remain unknown (Flores-Coto and Warlen 1993).

2) Eggs and larvae of spot are pelagic, and thus subject to transport by surface, wind-driven currents. Since prevailing winter winds are not favorable for surface onshore transport of spot south of Cape Hatteras (Yoder 1983), short-term (ca. four days) reversals of seasonal wind direction are hypothesized as important in spot transport across the shelf; Ekman transport may be less important (Norcross and Bodolus 1991).

3) Tide may be an important mechanism in gathering larvae at, and transporting them through, inlets (Pietrafesa and Janowitz 1988).

4) Onshore currents: wind-induced surface currents in the fall; in winter, onshore intermediate layer (resulting from surface wind-induced offshore currents, plus bottom density-driven offshore currents) (Miller et al. 1984).

5) Through inlets: tidal flood; selective tidal stream transport (Miller et al. 1984); currents resulting from winter storms (Pietrafesa and Janowitz 1988).

6) Within estuaries: selective tidal stream transport (Weinstein 1988).

References

Flores-Coto, C., and S.M. Warlen. 1993. Spawning time, growth, and recruitment of larval spot *Leiostomus xanthurus* into a North Carolina estuary. *Fishery Bulletin*, U.S. 91:8-22.

Manooch, C.S., and D. Raver. 1984. Fishes of the southeastern United States. North Carolina State Museum of Natural History, Raleigh, NC, 362 p.

Miller, J.M., J.P. Reed, and L.J. Pietrafesa. 1984. Patterns, mechanisms and approaches to the study of migrations of estuarine-dependent fish larvae and juveniles. In: McCleave, J. D., G. P. Arnold, J. J. Dodson, and W. H. Neill (eds.), *Mechanisms of migration in fishes*. Plenum Press, NY, pp. 209-225.

Norcross, B.L., and D.A. Bodolus. 1991. Hypothetical northern spawning limit and larval transport of spot. In Hoyt, R.D. (ed.), *Larval fish recruitment and research in the Americas*. NOAA Tech. Rep. NMFS 95, pp. 77-88.

Patillo, M.E., T.E. Czaplak, D.M. Nelson, and M.E. Monaco. In prep. Distribution and abundance of fishes and invertebrates in Gulf of Mexico estuaries, Vol. II: Species life history summaries. ELMR Rep. No. 11. NOAA/NOS Strategic Environmental Assessments Division, Silver Spring, MD.

Phillips, J.M., M.T. Huish, J.H. Kerby, and D.P. Moran. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Mid-Atlantic)—spot. U.S. Fish Wildl. Serv. Biol. Rep. 82(11.98). U.S. Army Corps of Engineers, TR EL-82-4, 13 p.

Pietrafesa, L.J., and G.S. Janowitz. 1988. Physical oceanographic processes affecting larval transport around and through North Carolina inlets. *American Fisheries Society Symposium* 3:34-50.

Weinstein, M.P. (ed.) 1988. Larval fish and shellfish transport through inlets. *American Fisheries Society Symposium* 3. American Fisheries Society, Bethesda, MD, 165 p.

Yoder, J.A. 1983. Statistical analysis of the distribution of fish eggs and larvae on the southeastern U.S. continental shelf with comments on oceanographic processes that may affect larval survival. *Estuarine, Coastal and Shelf Science* 17: 637-650.

Southern kingfish (*Menticirrhus americanus*) Life History Summary

This life history is based primarily on Harding and Chittenden (1987), Manooch and Raver (1984), Smith and Wenner (1985), and, U.S. Fish and Wildlife Service (1978).

General Life History

The southern kingfish (Sciaenidae) is a coastal groundfish found from New York to Argentina (Harding and Chittenden 1987), including the West Indies. It is common from Chesapeake Bay to Ft. Pierce, Florida, and is usually found in depths up to 36 m (rarely to 67 m), but is most abundant in less than 5 m depth. Southern kingfish are demersal and found over a wide range of bottom types, but are most common over clear sandy bottoms near mouths of coastal sounds. It is the most abundant of the three species of kingfish (genus *Menticirrhus*) occurring in the nearshore waters of the South Atlantic Bight from Cape Fear, North Carolina, to Cape Canaveral, Florida.

Kingfish are important in regional commercial and recreational fisheries, but most fisherman do not distin-

guish among the three species (Smith and Wenner 1985). Commercial landings in the South Atlantic Bight are primarily by-catches of the penaeid shrimp trawl fishery, but some are also taken with haul seines and gill nets. The weight of the commercial catch is estimated to be about twice that of the recreational fishery. The occurrence and abundance of this species in the South Atlantic Bight is highest in summer and fall and lowest in winter. In the South Atlantic Bight, this species was formerly assumed to move from estuarine and nearshore waters (<9 m deep) when temperatures dropped below 10 °C, into deeper (11-55 m), warmer offshore waters, but this does not now appear to be the case; Smith and Wenner (1985) interpret recent collection data to indicate a general (but not universal) winter movement of southern kingfish to the inshore, southern portion of the South Atlantic Bight. Adults are found in water temperatures ranging from 7.8-30.0 °C and salinities from 6.4-41.0 ppt, but are most common above 24 ppt. The species occurs at depths of less than 5-27 m (Harding and Chittenden 1987). Juveniles have been taken at salinities of 1.9-35.1 ppt and temperatures of 10.0-32.5 °C. Newly-hatched larvae are carried into nursery areas by currents and winds (Manooch and Raver 1984), and juveniles remain in these nursery areas for months, feeding on worms, shrimps, crabs, amphipods, and fish, while also having natural shelter from predators.

Whether southern kingfish eggs and larvae are pelagic or demersal is apparently not known, so the water layer in which they occur, and hence the current regime to which they may be exposed, cannot be certainly stated. However, southern kingfish may spawn close enough to shore that tidal and wind events may explain their movement to estuarine areas.

Larval Transport

- 1) "Currents probably transport pelagic eggs and larvae 'downstream' to nurseries in the northwest Gulf from spawning grounds located 'upstream' in or toward the north central Gulf" (Harding and Chittenden 1987).
- 2) "Newly hatched larvae are carried into estuarine nursery areas by currents and winds..." (Manooch and Raver 1984).
- 3) "[Larvae]...may be transported far up tidal rivers by high salinity bottom currents during first few weeks of life, then actively move to higher salinity areas as fish grow" (U.S. Fish and Wildlife Service 1978).

References

Harding, S.M., and M.E. Chittenden, Jr. 1987. Reproduction, movements and population dynamics of the southern kingfish, *Menticirrhus americanus*, in the northwestern Gulf of Mexico. NOAA Tech. Rep. NMFS 49, 21 p.

Manooch, C.S., and D. Raver. 1984. Fishes of the southeastern United States. North Carolina State Museum of Natural History, Raleigh, NC, 362 p.

Smith, J.W., and C.A. Wenner. 1985. Biology of the southern kingfish in the South Atlantic Bight. Transactions of the American Fisheries Society 114:356-366.

U.S. Fish and Wildlife Service. 1978. Development of fishes of the Mid-Atlantic Bight. Biological Services Program, Fish and Wildlife Service, U.S. Dept. of the Interior. FWS/OBS-78/12, Vols. 1-6.

Northern kingfish (*Menticirrhus saxatilis*) Life History Summary

This general life history summary is based primarily on Manooch and Raver (1984) and U.S. Fish and Wildlife Service (1978).

General Life History

The northern kingfish (Sciaenidae) is a coastal groundfish found from Maine to south Florida and the Yucatan, but it is most common between Cape Cod and Cape Hatteras (Manooch and Raver 1984). Few adults are taken from South Carolina to Texas, but juveniles appear regularly on beaches each year. This species prefers sandy bottoms just outside surf and sandy channels near inlets, and forms large schools in coastal waters, occasionally entering estuaries. They commonly occur at depths of 7-45 meters, and are taken at temperatures of 7.8-35.8 C. They are found May-October in the Gulf of Maine, April-October in the New York area, May-October on Virginia's eastern shore, and September-October off Ocean City, Maryland. They are taken in South Carolina only in the warmer months when temperatures are above 20 C. They spawn in spring and summer, in April and May and possibly longer off North and South Carolina; peak spawning occurs in the New York area in June and continues to September. Spawning occurs in June through August in the Gulf of Maine and in the New Jersey area. The eggs are pelagic and are apparently spawned in "outside waters, the young probably being transported passively into bays" (U.S. Fish and Wildlife Service 1978). The eggs hatch in 46-50 h in waters of 20-21 C.

"Newly hatched larvae are carried into nursery areas by currents and winds" (Manooch and Raver 1984). Larvae hatch at about 2.0-2.5 mm long. Larvae 2.6-6.0 mm long have been found in Narragansett Bay in June-August at 21.1-23.2 C. Larvae 1.9-4.5 mm have been found on Long Island beaches in late June-July. The larval stage is completed by 5 mm in length.

Larval Transport

1) "Apparently spawn in outside waters, the young probably being transported passively into bays" (U.S. Fish and Wildlife Service 1978).

2) "Newly hatched larvae are carried into estuarine nursery areas by currents and winds..." (Manooch and Raver 1984).

References

Manooch, C.S., and D. Raver. 1984. Fishes of the southeastern United States. North Carolina State Museum of Natural History, Raleigh, NC, 362 p.

U.S. Fish and Wildlife Service. 1978. Development of fishes of the Mid-Atlantic Bight. Biological Services Program, Fish and Wildlife Service, U.S. Dept. of the Interior. FWS/OBS-78/12, Vols. 1-6.

Atlantic croaker (*Micropogonias undulatus*) life History Summary

This general life history summary is based largely on Grosslein and Azarovitz (1982), Manooch and Raver (1984), Miller et al. (1984), Norcross and Austin (1988), Pattillo et al. (In prep.), Pietrafesa and Janowitz (1988), and Weinstein et al. (1988).

General Life History

The Atlantic croaker (Sciaenidae) is a euryhaline groundfish that inhabits coastal waters of less than 50 m depth from the Gulf of Maine to Argentina, including the Gulf of Mexico, but is seldom found north of New Jersey (Grosslein and Azarovitz 1982). It is most common on the Atlantic coast from Chesapeake Bay to South Carolina. Croaker support important commercial and recreational fisheries (Pattillo et al. In prep.). Croaker occur in bays, sounds and estuaries in late spring and summer, then migrate offshore and southward toward winter spawning grounds largely off Chesapeake Bay (Norcross and Austin 1988). Their distribution and seasonal movements are thus similar to spot. Temperature is the dominant factor control-

ling croaker abundance and migration times (Norcross and Austin 1988, Grosslein and Azarovitz 1982). The distribution of croaker is linked to the distribution of warm bottom waters. The occurrence of croaker is bounded by the 16 °C isotherm (Norcross and Austin 1988). Sexually mature adults start to leave estuaries in July-September, moving southward along the shore, then offshore. By November, most adults and older juveniles in South Carolina waters have moved offshore; young of the previous year re-enter sounds and rivers in early spring when water temperatures reach 16 °C. Abundance of juvenile croaker in certain years has been attributed to warm winters, and mass mortalities of young have been observed in very cold winters (Grosslein and Azarovitz 1982). The distribution of warm bottom water varies interannually, and is likely to affect the timing and location of spawning, therefore shifting the distribution of larvae (Norcross and Austin 1988). Adult croaker are opportunistic bottom-feeding carnivores (Pattillo et al. In prep.).

The spawning season is protracted and occurs in the fall, winter and spring months. Spawning takes place offshore in the vicinity of the edge of the Gulf Stream. North of Cape Hatteras croakers spawn from August or September through December. South of Hatteras, spawning occurs from September through January-March. Peak spawning occurs in October and November. Croaker occurring north of Cape Hatteras mature at two years of age, while those south of Cape Hatteras mature at one year; maximum life span is seven years (Pattillo et al. In prep.). Fecundities are estimated to be 27,000 to 1.7 million eggs per female (Pattillo et al. In prep., Manooch and Raver 1984). Spawning in the laboratory takes place at temperatures greater than 19 °C. Hatching time is 29-32 h at 23 °C and 26-30 h at 25 °C (Pattillo et al. In prep.).

The pelagic, planktonic eggs and larvae passively drift. Recently spawned larvae have been collected at depths of 15-115 m, and 20-200 km from shore. Most small larvae have been collected near midshelf about 65-125 km from shore. Larvae at hatching are 1.3-2.0 mm TL. Later larval stages and early juveniles actively swim towards estuarine nursery areas; transit time from hatching to arrival at estuaries is 60-90 days. Larvae feed on zooplankton. Larval recruitment to estuaries occurs from October through May, peaking between November and February. After spending 6-8 months in the estuary, offshore emigration begins in late March or early April (Pattillo et al. In prep.).

Larval transport of menhaden, croaker, spot, summer flounder and southern flounder was considered in detail by Miller et al. (1984). The attributes of this group are: 1) after hatching near the Gulf Stream, larvae migrate shoreward during December-March; 2) larvae

or small juveniles migrate through inlets and sounds to estuarine nursery areas in early spring; 3) large juveniles or sub-adults migrate out of juvenile nursery areas in the fall; 4) adults migrate offshore in fall or winter; 5) spawning occurs in winter (Miller et al. 1984). The abundance of these species suggests that this life history pattern is quite successful, and Miller et al. (1984) argue that the key elements of this success are winter (versus other season) spawning, plus estuarine (versus offshore) nursery areas.

The most important aspect of winter spawning in this context is that winter currents favor shoreward transport of pelagic, offshore-spawned larvae. Miller et al. (1984) propose a three-layer model of the winter current regime off North Carolina which could account for substantial shoreward larval transport. This model incorporates an intermediate (interior) layer of water moving shoreward. It is likely that this layer occupies 50-70% of the water column, moves at about 3-8 cms, and brings relatively warm, salty water onshore. This intermediate winter layer is persistent, and therefore best for larval transport because it is partly density driven, thus less subject to wind-forcing. The persistent intermediate onshore layer transport is most likely to be in effect on the shelf beyond the 25 m depth contour; within the 25 m contour, conditions are more variable and may be more dominated by winds (J.M. Miller pers. comm., Norcross and Bodolus 1991).

Variability in spawning time and vertical distribution among species may explain differences in abundance and age of cohorts arriving at estuaries. Miller et al. (1984) suggest that more spot larvae relative to croaker may be delivered to estuaries because spot spawning peaks in winter during the existence of the persistent onshore intermediate layer; croaker spawning peaks earlier in the fall, when onshore transport in the surface layer may be more variable. Because menhaden are more surface-oriented than spot or croaker, some may be transported in the offshore surface current in winter. Movement of menhaden vertically between the offshore surface current and the onshore intermediate current may be responsible for the greater size (age) variability of menhaden arriving at estuaries.

Miller et al. (1984) suggest that shoreward transport of menhaden, croaker, spot, summer flounder and southern flounder, whether fall or winter spawned, would be enhanced by larvae actively selecting the warmest water available to them in the vertical dimension; this selection may be the explanation for the observed precise age distribution of spot and croaker larvae along onshore-offshore transects.

Larval Transport

1) Onshore currents: wind-induced surface currents in the fall; in winter, onshore intermediate layer (resulting from surface wind-induced offshore currents plus bottom density-driven offshore currents) (Miller et al. 1984).

2) Through inlets: tidal flood; selective tidal stream transport (Miller et al. 1984); currents resulting from winter storms (Pietrafesa and Janowitz 1988).

3) Tide may be an important mechanism in gathering larvae at, and transporting them through, inlets (Pietrafesa and Janowitz 1988).

4) Within estuaries: selective tidal stream transport (Weinstein 1988).

References

Grosslein, M.D., and T.H. Azarovitz. 1982. Fish distribution. Marine Ecosystems Analysis Program, New York Bight Atlas Monograph 15. New York Sea Grant Institute, Albany, NY, 182 p.

Manooch, C.S., and D. Raver. 1984. Fishes of the southeastern United States. North Carolina State Museum of Natural History, Raleigh, NC, 362 p.

Miller, J.M., J.P. Reed, and L.J. Pietrafesa. 1984. Patterns, mechanisms and approaches to the study of migrations of estuarine-dependent fish larvae and juveniles. In McCleave J.D., G.P. Arnold, J.J. Dodson and W.H. Neill (eds.) Mechanisms of migration in fishes. Plenum Press, NY, pp. 209-225.

Norcross, B.L., and D.A. Bodolus. 1991. Hypothetical northern spawning limit and larval transport of spot. In Hoyt, R.D. (ed.), Larval fish recruitment and research in the Americas. NOAA Technical Rep. NMFS 95, pp. 77-88.

Norcross, B.L., and H.M. Austin. 1988. Middle-Atlantic Bight meridional wind component effect on bottom waters and spawning distribution of Atlantic croaker. Continental Shelf Research 8(1):69-88.

Pattillo, M.E., T.E. Czaplak, D.M. Nelson, and M.E. Monaco. In prep. Distribution and abundance of fishes and invertebrates in Gulf of Mexico estuaries, Vol. II: Species life history summaries. ELMR Rep. No. 11. NOAA/NOS Strategic Environmental Assessments Division, Silver Spring, MD.

Pietrafesa, L.J., and G.S. Janowitz. 1988. Physical oceanographic processes affecting larval transport

around and through North Carolina inlets. American Fisheries Society Symposium 3:34-50.

Weinstein, M.P. (ed.). 1988. Larval fish and shellfish transport through inlets. American Fisheries Society Symposium 3. American Fisheries Society, Bethesda, MD, 165 p.

Black drum (*Pogonias cromis*) Life History Summary

This general life history summary is based on Cowan et al. (1992), Manooch and Raver (1984), Pattillo et al. (In prep.), and U.S. Fish and Wildlife Service (1978).

General Life History

The black drum (Sciaenidae) is a schooling groundfish found in coastal waters from Massachusetts to Argentina. They are common throughout the Gulf of Mexico, especially in Texas waters. In Atlantic waters, they are common from Chesapeake Bay to Florida. The black drum is the largest sciaenid on the Atlantic coast (Manooch and Raver 1984), with a maximum weight of 66.3 kg. The black drum is considered to have poor flesh quality, especially in large individuals, thus the smaller individuals are more valuable. The largest commercial catch is in the Gulf of Mexico (Pattillo et al. In prep.). Black drum live from 35 to 40 years, with the record age being documented at 58 years. This long life span indicates a very low natural mortality, which probably means little surplus production is available for commercial fishery yield. Adults and juveniles are euryhaline and eurythermal, commonly found in waters at salinities 9-26 ppt but ranging from 0 to 80 ppt, and at temperatures from 3-35 °C. Eggs, larvae and adults are marine and estuarine. Adult black drum and juveniles are benthic feeders; pharyngeal teeth are well-developed by 200 mm standard length (SL) and permit drum to feed on hard-bodied prey such as crustaceans and bivalves; they also feed on annelids and fish. The preferred habitats of juveniles up to three months of age are turbid, unvegetated marshes, tidal ditches and creeks. They remain in shallow bay and shore areas until they are about 100 mm long, when they move into deeper bay areas; most remain inshore until sexual maturity. They are found in salinities of 0-35 ppt and temperatures of 8.3-35.2 °C. Black drum typically remain in estuaries for their first year of life.

Spawning occurs in open bays in, and possibly outside, channels and passes (U.S. Fish and Wildlife Service 1978). In the Gulf of Mexico, black drum spawn from February to mid-April (90% of known spawning

occurs in February-March), occasionally with a secondary peak in the fall. Black drum are seasonal residents of lower Chesapeake Bay and spawn there from April to June, especially in May. Recent work suggests that Chesapeake Bay may be the northern limit of black drum spawning, and that the season is restricted to 3-4 weeks in May (Cowan et al. 1992). Spawning occurs in troughs 9-18 m deep near the mouth of Chesapeake Bay, and, in the Gulf of Mexico, at 20-27 m depth, and during periods of rising temperature in the spring. Adults return to estuaries after spawning. Laboratory spawning has occurred at 21 °C and 28-31 ppt (Pattillo et al. In prep.). By the end of the first year, juveniles can reach 140 to 180 mm SL, and by sexual maturity (the end of the second year) females are 275 to 320 mm total length (TL) in Texas waters. Florida females mature at 5-6 years of age, and at 650-699 mm. Other studies estimate sexual maturity at 4-5 years. Fecundity has been reported to be from 1.09 to 6 million eggs. Eggs hatch in about 24 h at 20 °C. In the laboratory, spawned eggs hatched successfully at salinities of 8.8-34 ppt, with highest survival at 23-34 ppt. Eggs and larvae develop successfully at water temperatures of 18 to 20 °C.

Eggs and larvae are pelagic, and transported into estuaries and rivers primarily by tidal currents (Pattillo et al. In prep.). Larvae are 1.9-2.4 mm TL at hatching, and have been collected at salinities of 0-36 ppt and temperatures of 11-22 °C. Black drum larvae feed on zooplankton (Pattillo et al. In prep.).

Larval Transport

- 1) "Larvae are pelagic, being transported to the estuaries from passes by tidal currents" (Pattillo et al. In prep.)
- 2) "Tides may also influence the amount of spawning activity or successful recruitment" (Pattillo et al. In prep.)
- 3) "Larvae—after hatching, apparently carried into upper reaches of bays and tidal creeks by tidal currents..." (U.S. Fish and Wildlife Service 1978).

References

- Cowan, J.H. Jr., R.S. Birdsong, E.D. Houde, J.S. Priest, W.S. Sharp, and G.B. Mateja. 1992. Enclosure experiments on survival and growth of black drum eggs and larvae in lower Chesapeake Bay. *Estuaries* 15(3):392-402.
- Manooch, C.S., and D. Raver. 1984. Fishes of the southeastern United States. North Carolina State Mu-

seum of Natural History, Raleigh, NC, 362 p.

Pattillo, M.E., T.E. Czaplak, D.M. Nelson, and M.E. Monaco. In prep. Distribution and abundance of fishes and invertebrates in Gulf of Mexico estuaries, Vol. II: Species Life History Summaries. ELMR Rep. No. 11. NOAA/NOS Strategic Environmental Assessments Division, Silver Spring, MD.

U.S. Fish and Wildlife Service. 1978. Development of fishes of the Mid-Atlantic Bight. Biological Services Program, Fish and Wildlife Service, U.S. Dept. of the Interior. FWS/OBS-78/12, Vols. 1-6.

Red drum (*Sciaenops ocellatus*) Life History Summary

This general life history summary is based largely on Comyns et al. (1991), Lyczkowski-Schultz and Steen (1991), Manooch and Raver (1984), Murphy and Taylor (1990), and Pattillo et al. (In prep.).

General Life History

Red drum (*Sciaenidae*) are found in coastal and estuarine waters (usually <22 m deep; Murphy and Taylor 1990) from Massachusetts to Key West, Florida and in the Gulf of Mexico from Florida south to Tuxpan, Mexico (Manooch and Raver 1984). The species is euryhaline, but all life stages are sensitive to high salinities combined with high temperatures (Pattillo et al. In prep.). Centers of abundance are Chesapeake Bay, North Carolina, and the Gulf of Mexico. The species exhibits large random movements (Pattillo et al. In prep.). The red drum is highly prized as a food fish by both commercial and sports fishermen, and is one of the most sought-after species in the Gulf of Mexico (Pattillo et al. In prep.). Overfishing and the loss of estuarine nursery habitat are thought to have a serious impact on red drum populations (Pattillo et al. In prep.). During their fourth or fifth year, red drum adults either join schools of migratory adults, or become free-ranging in deeper waters for the remainder of their life. The fishery is largely composed of young fish; the size of the harvest is heavily dependent on recent recruitment (Pattillo et al. In prep.). The species feeds on a wide variety of prey both on the bottom and in the water column (Pattillo et al. In prep.).

Red drum spawn at night (Comyns et al. 1991), primarily in nearshore waters close to channels and passes, and also in large estuaries and nearshore shelf waters (Murphy and Taylor 1990, U.S. Fish and Wildlife Service 1983). Spawning peaks on both the Atlantic and Gulf coasts of Florida in September and Octo-

ber (Murphy and Taylor 1990). Unlike most northern Gulf sciaenids, red drum have a restricted spawning season (Comyns et al. 1991). Spawning in Texas waters takes place in October-February. In Louisiana, Mississippi, and Alabama waters, spawning takes place in August through late October, peaking in September. Spawning takes place in North Carolina waters in the fall. The average salinity of waters where spawning takes place is 28 ppt, at temperatures of 21-24 °C. The lower limit for spawning in this species is 20 °C. Spawning peaks are associated with new or full moons. Red drum grow rapidly until age 4-5 years, when growth slows (Murphy and Taylor 1990). Captive fish spawn repeatedly, producing about one million small, buoyant eggs per batch (Pattillo et al. In prep.). Sexual maturation is reached by age 3-6 in females, and mean fecundity of mature females is 2.128×10^6 (range: $2-16 \times 10^6$) eggs per batch (Comyns et al. 1991). Males mature at 1-3 years, at smaller sizes than females (Murphy and Taylor 1990). The average size of adults is 800-850 mm SL (Pattillo et al. In prep.). Fish can live up to about age 35 (Murphy and Taylor 1990). The largest weight on record is 94.69 kg. Eggs hatch in 19-20 h at 24 °C and in 28 ppt salinity, and in 22 h at 23 °C and 36 ppt. Eggs from hatchery spawns develop into feeding larvae at salinities from 10 to 40 ppt at 25 °C.

Newly-hatched larvae (1.74 mm mean SL) are negatively buoyant; eggs, larvae and early juveniles are planktonic and pelagic (Pattillo et al. In prep.). Larvae 1.7-5.0 mm are more concentrated at the surface during the day than at night in both nearshore and offshore waters (Lyczkowski-Schultz and Steen 1991). After hatching, larvae and postlarvae are carried by tidal currents and winds into the shallow inside waters of bays and estuaries (Pattillo et al. In prep.). They remain in the estuarine nursery ground for at least 6-8 months, and utilize grass and mudflats for feeding as juveniles and sub-adults.

Larval Transport

- 1) Wind driven currents (Manooch and Raver 1984).
- 2) "After hatching, larvae and postlarvae are carried by tidal currents into the shallow inside waters of bays and estuaries" (Pattillo et al. In prep.).

References

Comyns, B.H., J. Lyczkowski-Schultz, D.L. Neiland, and C.A. Wilson. 1991. Reproduction of red drum, *Sciaenops ocellatus*, in the north-central Gulf of Mexico: seasonality and spawner biomass. In Hoyt, R.D. (ed.), Larval fish recruitment and research in the Americas. NOAA Tech. Rep. NMFS 95, pp. 17-26.

Lyczkowski-Schultz, J., and J.P. Steen. 1991. Diel vertical distribution of red drum *Sciaenops ocellatus* larvae in the north-central Gulf of Mexico. Fishery Bulletin 89:631-641.

Manooch, C.S., and D. Raver. 1984. Fishes of the southeastern United States. North Carolina State Museum of Natural History, Raleigh, N.C., 362 p.

Murphy, M.D., and R.G. Taylor. 1990. Reproduction, growth, and mortality of red drum *Sciaenops ocellatus* in Florida waters. Fishery Bulletin 88:531-542.

Pattillo, M.E., T.E. Czaplak, D.M. Nelson, and M.E. Monaco. In prep. Distribution and abundance of fishes and invertebrates in Gulf of Mexico estuaries, Vol. II: Species life history summaries. ELMR Rep. No. 11. NOAA/NOS Strategic Environmental Assessments Division, Silver Spring, MD.

Striped mullet (*Mugil cephalus*) Life History Summary

This life history is based largely on Collins and Stender (1989), Manooch and Raver (1984), Miller et al. (1984), Pattillo et al. (In prep.), Pietrafesa and Janowitz (1988), and Walsh et al. (1991).

General Life History

The striped mullet (Mugilidae) is distributed worldwide between latitudes of 42° N and 42° S; in the western Atlantic Ocean it is present from Cape Cod to Brazil (Manooch and Raver 1984), but is rare or absent from equatorial areas. It occasionally enters fresh water. Prejuveniles, juveniles and adults form schools ranging from a few individuals to several hundred. It is perhaps the most widespread and abundant inshore teleost (Collins and Stender 1989). Striped mullet is important both ecologically and commercially; in some areas it is considered a valued food fish. Mullet comprise one of the most important fisheries of the southern United States (Pattillo et al. In prep.). All life stages are pelagic (Pattillo et al. In prep.). Larvae are somewhat stenohaline, but salinity tolerance increases with growth; adults and juvenile striped mullet are hardy, eurythermal and euryhaline. Larvae are carnivorous; prejuveniles change to omnivory. Adult mullet feed on algae and detrital organic matter, consumed along with large amounts of sand and mud, and opportunistically feed on animal matter, especially in the fall when more protein may be required for gonadal development.

Spawning occurs primarily in winter, with some spring spawning (Collins and Stender 1989), and takes place in deep, offshore water (U.S. Fish and Wildlife Service 1978) in and near the South-Atlantic Bight (from Cape Fear to Cape Canaveral), often seaward of 20 fathoms depth. Spawning in the Gulf of Mexico has been observed at 60-80 km offshore. In the South-Atlantic Bight, spawning has been described as occurring from October to February (peaking in December), or from November to April (peaking in January-February). Adults become sexually mature at one to three years (Pattillo et al. In prep.). The weight of spawning females ranges from 600 to 1400 g. Fecundity varies with size; 13-inch fish release 45 thousand eggs, while a 22-inch fish may produce up to four million eggs. A second source estimates fecundity ranges as 0.76 to 7.2 million eggs per female (Pattillo et al. In prep.). The life span is up to seven years for males and eight for females (Pattillo et al. In prep.). After spawning, adults return to inshore habitats. Normal hatching of striped mullet eggs occurred in the laboratory in water temperatures ranging from 20-30 °C and salinities of 15-45 ppt, although ideal hatching conditions (93.5%) are 25.5 °C and 36.3 ppt; median hatching times are 65-73 h at 20 °C, 48-50 h at 22 °C, 36-38 h at 24 °C, and 25-27 h at 32 °C (Walsh et al. 1991). Salinities of 15-45 ppt did not affect hatching times at the same temperature. Eggs are nonadhesive and only positively buoyant in waters with salinities greater than 30 ppt; if aeration or currents are inadequate, eggs at lower salinities will sink to the bottom and die (Walsh et al. 1991).

Larvae are an average of 2.65 mm TL at hatching (Pattillo et al. In prep.). The yolk is absorbed by day 5, when feeding commences at 24 °C. In the South Atlantic Bight, striped mullet larvae have been taken from January to May, with the greatest occurrence in January and February. Larval mullet have been taken over a wide range of depths, but are strongly associated with the surface; they have been taken in significantly greater numbers at night, which Collins and Stender (1989) attributed to diurnal net avoidance, rather than diel vertical movements, because of their absence in nearly all of the subsurface collections. Mullet larvae move shoreward as they grow, although the exact mechanism of movement has not been established (it has been assumed that they are carried with surface currents and winds). Larvae are planktonic until 10-12 days posthatching, when they are capable of sustained swimming (Pattillo et al. In prep.). Pigmentation of the body (silvering) is complete by day 25 at 24 °C when larvae are about 11 mm TL. This marks the end of the larval stage, and the next stage of development is called the prejuvenile stage or the "querimana" stage. The duration of this stage is temperature dependent, and lasts 30-90 days; its size range is 11-52

mm TL. Mullet move inshore to estuarine nursery areas, arriving when they are about 15-32 mm TL (larvae 16-20 mm in standard length are 40-45 days old). The prejuvenile stage terminates when the third anal fin ray changes to a hard spine. Juvenile mullet have a size range of 44-200 mm TL. Nursery areas are thought to be secondary and tertiary bays, where they remain for at least 6-8 months.

Larval Transport

1) "Fertilized pelagic eggs hatch as they are transported by winds and surface currents" (Manooch and Raver 1984).

Since this species spawns in winter in the southeastern U.S., mechanisms of larval transport available to them would probably be the same as those postulated for other winter spawners, such as spot, croaker, menhaden, summer and southern flounders (Miller et al. 1984, Pietrafesa and Janowitz 1988). These mechanisms are as follows:

1) Onshore currents: wind-induced surface currents in the fall; in winter, onshore intermediate layer (resulting from surface wind-induced offshore currents plus bottom density-driven offshore currents) (Miller et al. 1984).

2) Through inlets: tidal flood; selective tidal stream transport (Miller et al. 1984); currents resulting from winter storms (Pietrafesa and Janowitz 1988).

3) Tide may be an important mechanism in gathering larvae at inlets and transporting larvae through inlets (Pietrafesa and Janowitz 1988).

However, the close association of mullet with the surface may argue against transport in the onshore intermediate layer.

References

Collins, M.R., and B.W. Sender. 1989. Larval striped mullet (*Mugil cephalus*) and white mullet (*Mugil curema*) off the southeastern United States. *Bulletin of Marine Science* 45(3): 580-589.

Manooch, C.S., and D. Raver. 1984. *Fishes of the southeastern United States*. North Carolina State Museum of Natural History, Raleigh, NC, 362 p.

Miller, J.M., J.P. Reed, and L.J. Pietrafesa. 1984. Patterns, mechanisms and approaches to the study of migrations of estuarine-dependent fish larvae and juveniles. In: McCleave, J.D., G.P. Arnold, J.J. Dodson, and W.H. Neill (eds.), *Mechanisms of migration in*

fishes. Plenum Press, NY, pp. 209-225.

Pattillo, M.E., T.E. Czaplak, D.M. Nelson, and M.E. Monaco. In prep. Distribution and abundance of fishes and invertebrates in Gulf of Mexico estuaries, Vol. II: Species life history summaries. ELMR Rep. No. 11. NOAA/NOS Strategic Environmental Assessments Division, Silver Spring, MD.

Pietrafesa, L.J., and G.S. Janowitz. 1988. Physical oceanographic processes affecting larval transport around and through North Carolina inlets. *American Fisheries Society Symposium* 3:34-50.

U.S. Fish and Wildlife Service. 1978. Development of fishes of the Mid-Atlantic Bight. Biological Services Program, Fish and Wildlife Service, U.S. Dept. of the Interior. FWS/OBS-78/12, Vols. 1-6.

Walsh, W.A., C. Swanson, and C.S. Lee. 1991. Combined effects of temperature and salinity on embryonic development and hatching of striped mullet, *Mugil cephalus*. *Aquaculture* 97:281-289.

Summer flounder (*Paralichthys dentatus*) Life History Summary

This general life history summary is based largely on Able et al. (1990), Grimes et al. (1989), Grosslein and Azarovitz (1982), Manooch and Raver (1984), Miller et al. (1984), Norcross and Bodolus (1991), Pietrafesa and Janowitz (1988), and Weinstein et al. (1988).

General Life History

The summer flounder (Bothidae) is a groundfish distributed from Nova Scotia to Florida, but is most abundant from Massachusetts to North Carolina; it supports important commercial and recreational fisheries (Grimes et al. 1989). The species inhabits shallow coastal and estuarine waters in spring and summer, and moves offshore to waters 40-200 m deep in winter, where spawning occurs. Summer flounder tagged in autumn in New Jersey inshore waters were distributed throughout the Middle-Atlantic Bight, suggesting homogeneity in the Middle-Atlantic Bight population (Grosslein and Azarovitz 1982). The population north of Cape Hatteras is genetically distinct from that of the south, and may differ in migration and reproductive behavior. Adults feed on fish and crustaceans both on the bottom and in the water column. They are more active in daylight (Grimes et al. 1989).

Spawning takes place at sea in fall and winter (Grosslein and Azarovitz 1982, United States Fish and Wildlife Service 1978), starting in mid-September be-

tween southern New England and New Jersey, and by October takes place as far south as Chesapeake Bay. By mid-December, most spawning in the Middle Atlantic Bight has ceased. South of Cape Hatteras spawning begins as early as November and ends by February. Spawning takes place near the bottom in shelf waters 30-200 m deep (Grimes et al. 1989). Sexual maturity is attained in the second or third year of life (Grimes et al. 1989). Females live longer (up to 10 years) and grow larger than males. Fecundities are estimated to be from 0.5 million to 3.5 million eggs per female. The eggs are buoyant. The heaviest concentrations of eggs and larvae are found between Long Island and Cape Hatteras; the greatest number of eggs are found within 46 km of shore, and larvae are most abundant between 22 and 83 km from shore. Eggs are most abundant in the water column where bottom temperatures are 12-19 °C. Incubation time in the laboratory was nine days at 5 °C and 2-3 days at 21 °C; notochord length at hatching is about 3 mm (Grimes et al. 1989).

The larvae are transported towards coastal and estuarine nursery areas by currents (Grimes et al. 1989, Manooch and Raver 1984). After the pelagic larvae metamorphose, they are capable swimmers and become demersal; they then migrate toward shore and enter estuaries. Juveniles spend the summer months in estuarine areas. Juveniles in southern waters overwinter in bays and sounds; in northern waters, some juveniles move offshore, whereas others remain inshore.

Larval transport of menhaden, croaker, spot, summer flounder and southern flounder was considered in detail by Miller et al. (1984). The attributes of this group are: 1) after hatching near the Gulf Stream, larvae migrate shoreward during December-March; 2) larvae or small juveniles migrate through inlets and sounds to estuarine nursery areas in early spring; 3) large juveniles or subadults migrate out of juvenile nursery areas in the fall; 4) adults migrate offshore in fall or winter; 5) spawning occurs in winter. The abundance of these species suggests that this life history pattern is quite successful, and Miller et al. (1984) argue that the key elements of this success are winter (versus other season) spawning, plus estuarine (versus offshore) nursery areas.

The most important aspect of winter spawning in this context is that winter currents favor shoreward transport of pelagic, offshore-spawned larvae. Miller et al. (1984) propose a three-layer model of the winter current regime off North Carolina which could account for substantial shoreward larval transport. This model incorporates an intermediate (interior) layer of water moving shoreward. It is likely that this layer occupies

50-70% of the water column, moves at about 3-8 cms, and brings relatively warm, salty water onshore. This intermediate winter layer is persistent and therefore best for larval transport because it is partly density driven, thus less subject to wind-forcing. The persistent intermediate onshore layer transport is most likely to be in effect on the shelf beyond the 25 m depth contour; within the 25 m contour, conditions are more variable and may be more dominated by winds (J.M. Miller, pers. comm., Norcross and Bodolus 1991).

Miller et al. (1984) suggest that shoreward transport of all five species they considered, whether fall or winter spawned, would be enhanced by larvae actively selecting the warmest water available to them in the vertical dimension.

Larval Transport

1) Onshore currents: wind-induced surface currents in the fall; in winter, onshore intermediate layer (resulting from surface wind-induced offshore currents plus bottom density-driven offshore currents) (Miller et al. 1984).

2) Through inlets: tidal flood; selective tidal stream transport (Miller et al. 1984); currents resulting from winter storms (Pietrafesa and Janowitz 1988).

3) Tide may be an important mechanism in gathering larvae at inlets and transporting larvae through inlets (Pietrafesa and Janowitz 1988).

4) Within estuaries: selective tidal stream transport (Weinstein 1988).

5) "Larvae of summer flounder are transported to estuarine nursery areas by currents" (Grimes et al. 1989).

References

Able, K.W., R.E. Matheson, W.W. Wallace, M.P. Fahay, and G. Shepherd. 1990. Patterns of summer flounder *Paralichthys dentatus* early life history in the mid-Atlantic Bight and New Jersey Estuaries. Fishery Bulletin 88:1-12.

Grimes, B.H., M.T. Huish, J.H. Kirby, and D. Moran. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Mid-Atlantic)—summer and winter flounder. U.S. Fish Wildl. Serv. Biol. Rep. 82(11.112). U.S. Army Corps of Engineers, TR EL-82-4, 18 p.

Grosslein, M.D., and T.H. Azarovitz. 1982. Fish distribution. Marine Ecosystems Analysis Program, New York Bight Atlas Monograph 15. New York Sea Grant

Institute, Albany NY, 182 p.

Manooch, C.S., and D. Raver. 1984. Fishes of the southeastern United States. North Carolina State Museum of Natural History, Raleigh, NC, 362 p.

Miller, J.M., J.P. Reed, and L.J. Pietrafesa. 1984. Patterns, mechanisms and approaches to the study of migrations of estuarine-dependent fish larvae and juveniles. *In*: McCleave, J.D., G.P. Arnold, J.J. Dodson, and W.H. Neill (eds.). Mechanisms of migration in fishes. Plenum Press, NY, pp. 209-225.

Norcross, B.L., and D.A. Bodolus. 1991. Hypothetical northern spawning limit and larval transport of spot. *In* Hoyt, R.D. (ed.), Larval fish recruitment and research in the Americas. NOAA Technical Rep. NMFS 95, pp. 77-88.

Pietrafesa, L.J., and G.S. Janowitz. 1988. Physical oceanographic processes affecting larval transport around and through North Carolina inlets. American Fisheries Society Symposium 3:34-50.

Weinstein, M.P. (ed.). 1988. Larval fish and shellfish transport through inlets. American Fisheries Society Symposium 3. American Fisheries Society, Bethesda, MD, 165 p.

Southern flounder (*Paralichthys lethostigma*) Life History Summary

This general life history summary is based largely on Burke et al. (1991), Manooch and Raver (1984), Miller et al. (1984), Pattillo et al. (In prep.), and Pietrafesa and Janowitz (1988).

General Life History

The southern flounder (Bothidae) is a groundfish with a discontinuous distribution from Albemarle Sound, North Carolina, to the Loxahatchee River, Florida, and in the Gulf of Mexico from the Caloosahatchee River, Florida, to northern Mexico. It supports valuable commercial fisheries (in some regions, the harvest of summer, southern, and Gulf flounders are recorded as "*Paralichthys* spp." and not distinguished) and recreational fisheries, and is a dominant predator in some estuaries. The species is both eurythermal and euryhaline, inhabiting environments with the widest range of salinities of any flounder in the region. Adults and juveniles are demersal and more active at night, and feed on fish, shrimp, crabs and polychaetes. Adults migrate from estuaries to spawn in deeper water offshore in fall and winter (Pattillo et al. In prep.).

Spawning takes place at sea in fall and winter, after sexually mature fish, at two years of age and older, move out of estuaries and bays from October through December. Like summer flounder, spot, menhaden and croaker, spawning in southern flounder occurs in the vicinity of the edge of the Gulf Stream. Females appear to live longer and grow larger than males (Manooch and Raver 1984). Maximum life span is 5-10 years. One study reported an average of 9,230 eggs per spawn (13 spawns); eggs are planktonic, and float near the surface (Pattillo et al. In prep.).

The larvae are planktonic and found throughout the water column. The larvae are transported towards coastal and estuarine nursery areas by currents. Larvae feed on zooplankton. After the pelagic larvae metamorphose (starting at 8-11 mm at 40-46 days old), they are capable swimmers and become demersal; transformation is complete by 50 days. They then migrate toward shore and enter estuaries. Optimal growth in early postlarvae occurs at higher salinities, while advanced postlarvae grow better at salinities of 5-15 ppt. In North Carolina, larvae immigrated to estuaries from the end of November to mid-April, with peak immigration in February or March; flounders entering the estuarine system were transforming larvae (Burke et al. 1991).

Larval transport of menhaden, croaker, spot, summer flounder and southern flounder was considered in detail by Miller et al. (1984). The attributes of this group are: 1) after hatching near the Gulf Stream, larvae migrate shoreward during December-March; 2) larvae or small juveniles migrate through inlets and sounds to estuarine nursery areas in early spring; 3) large juveniles or subadults migrate out of juvenile nursery areas in the fall; 4) adults migrate offshore in fall or winter; 5) spawning occurs in winter. The abundance of these species suggests that this life history pattern is quite successful, and Miller et al. (1984) argue that the key elements of this success are winter (versus other season) spawning, plus estuarine (versus offshore) nursery areas.

The most important aspect of winter spawning in this context is that winter currents favor shoreward transport of pelagic, offshore-spawned larvae. Miller et al. (1984) propose a three-layer model of the winter current regime off North Carolina which could account for substantial shoreward larval transport. This model incorporates an intermediate (interior) layer of water moving shoreward. It is likely that this layer occupies 50-70% of the water column, moves at about 3-8 cms, and brings relatively warm, salty water onshore. This intermediate winter layer is persistent, thus best for larval transport because it is partly density driven and therefore less subject to wind-forcing. The persistent

intermediate onshore layer transport is most likely to be in effect on the shelf beyond the 25 m depth contour; within the 25 m contour, conditions are more variable and may be more dominated by winds (J.M. Miller, pers. comm., Norcross and Bodolus 1991).

Miller et al. (1984) suggest that shoreward transport of all five species they considered, whether fall or winter spawned, would be enhanced by larvae actively selecting the warmest water available in the vertical dimension.

Larval Transport

1) Onshore currents: wind-induced surface currents in the fall; in winter, onshore intermediate layer (resulting from surface wind-induced offshore currents plus bottom density-driven offshore currents) (Miller et al. 1984).

2) Through inlets: tidal flood; selective tidal stream transport (Miller et al. 1984); currents resulting from winter storms (Pietrafesa and Janowitz 1988).

3) Tide may be an important mechanism in gathering larvae at, and then transporting through, inlets (Pietrafesa and Janowitz 1988).

4) Within estuaries: selective tidal stream transport (Weinstein 1988).

References

Burke, J.S., J.M. Miller, and D.E. Hoss. 1991. Immigration and settlement pattern of *Paralichthys dentatus* and *P. lethostigma* in an estuarine nursery ground, North Carolina, U.S.A. Netherlands Journal of Sea Research 27(3/4):395-405.

Manooch, C.S., and D. Raver. 1984. Fishes of the southeastern United States. North Carolina State Museum of Natural History, Raleigh, NC, 362 p.

Miller, J.M., J.P. Reed, and L.J. Pietrafesa. 1984. Patterns, mechanisms and approaches to the study of migrations of estuarine-dependent fish larvae and juveniles. In: McCleave, J. D., G. P. Arnold, J. J. Dodson and W. H. Neill (eds.) Mechanisms of migration in fishes. Plenum Press, NY, pp. 209-225.

Norcross, B.L., and D.A. Bodolus. 1991. Hypothetical northern spawning limit and larval transport of spot. In Hoyt, R.D. (ed.), Larval fish recruitment and research in the Americas. NOAA Technical Rep. NMFS 95, pp. 77-88.

Pattillo, M.E., T.E., Czaplá, D.M. Nelson, and M.E. Monaco. In prep. Distribution and abundance of fishes and invertebrates in Gulf of Mexico estuaries, Vol. II: Species life history summaries. ELMR Rep. No. 11. NOAA/NOS Strategic Environmental Assessments Division, Silver Spring, MD.

Pietrafesa, L.J., and G.S. Janowitz. 1988. Physical oceanographic processes affecting larval transport around and through North Carolina inlets. American Fisheries Society Symposium 3:34:50.

Weinstein, M.P. (ed.). 1988. Larval fish and shellfish transport through inlets. American Fisheries Society Symposium 3. American Fisheries Society, Bethesda, MD, 165 p.

Life History Table

This section includes tabular information on larval transport for the 19 estuarine-catadromous species discussed in this report. Its purpose is to facilitate comparison of transport mechanisms available to larvae of these species and to identify information gaps. The column labels are defined in the Glossary.

The two headers divide the columns into "Through Inlets" and general "Transport Mechanisms" categories, the two rows refer to larvae or eggs. Three columns ("Active Vertical" and "Active Horizontal")

refer to the dimensions in which larvae can control their movement, or the absence of control ("Passive"), through inlets. General "Transport Mechanisms" that may be marked include "Ekman Transport," Storm Events," "Swimming," "Geostrophic Currents," "Coastal Currents," and "Tidal Currents"; these are defined in the text and Glossary. The last column, "Reliability," indicates an evaluation of the content and quality of material pertaining to larval transport published for this species, shown as H (highly certain), M (moderately certain), or R (reasonable inference).

Species/life stage	Through Inlets			Transport Mechanisms						Reliability
	Active Vertical	Active Horizontal	Passive	Ekman Transport	Storm Events (2-3 days)	Swimming	Geostrophic Currents	Coastal Currents	Tidal Currents	
brown shrimp eggs				*						R
brown shrimp larvae	*	*	*	*	*	*	*	*	*	R
pink shrimp eggs				*						M
pink shrimp larvae	*	*			*	*	*	*	*	M
white shrimp eggs										H
white shrimp larvae	*	*	*			*	*	*	*	H
blue crab eggs			*	*	*		*	*	*	R
blue crab larvae	*	*		*	*	*		*	*	R
ladyfish eggs				*				*		H
ladyfish larvae	*	*		*	*	*	*	*	*	H
Atlantic menhaden eggs			*		*			*		R
Atlantic menhaden larvae	*	*		*	*	*	*	*	*	R
cobia eggs			*	*						H
cobia larvae	*	*	*	*		*		*	*	H
pinfish eggs				*				*		H
pinfish larvae	*			*	*	*	*	*	*	H

Life History Table-continued.

Species/life stage	Through Inlets			Transport Mechanisms						Reliability
	Active Vertical	Active Horizontal	Passive	Ekman Transport	Storm Events (2-3 days)	Swimming	Geostrophic Currents	Coastal Currents	Tidal Currents	
spotted seatrout eggs			*					*	*	H
spotted seatrout larvae	*		*		*	*	*	*	*	H
weakfish eggs			*					*	*	H
weakfish larvae	*	*	*		*		*	*	*	H
spot eggs				*				*		R
spot larvae	*		*	*	*		*	*	*	R
southern kingfish eggs										H
southern kingfish larvae			*					*	*	H
northern kingfish eggs			*					*	*	M
northern kingfish larvae			*					*	*	M
Atlantic croaker eggs				*	*			*	*	R
Atlantic croaker larvae	*	*	*	*	*	*	*	*	*	R
black drum eggs			*						*	R
black drum larvae			*						*	R
red drum eggs			*					*	*	R
red drum larvae			*		*		*	*	*	R
striped mullet eggs				*				*		M
striped mullet larvae	*	*		*	*	*	*	*	*	M
summer flounder eggs				*	*			*		R
summer flounder larvae	*	*		*	*	*	*	*	*	R
southern flounder eggs				*				*		R
southern flounder larvae	*	*	*	*	*	*	*	*	*	R

GLOSSARY

ACTIVE HORIZONTAL—Refers to organisms which have some control of horizontal position in the water column.

ACTIVE VERTICAL—Refers to organisms which have some control of vertical position in the water column.

AMPHIDROMOUS—Diadromous fishes whose migration from fresh water to seawater or vice-versa is not immediately followed by breeding, but occurs regularly at some other stage of the life cycle.

Amphidromy occurs in two distinct forms: marine amphidromy, in which spawning is marine and the larvae/juveniles are temporarily in fresh water before returning to the sea to grow to maturity; and freshwater amphidromy, in which spawning occurs in freshwater and the larvae/juveniles are temporarily marine before returning to freshwater to grow to maturity.

ANADROMOUS—Fishes which spend most of their lives in seawater and which migrate to freshwater to spawn.

CATADROMOUS—Fishes which spend most of their lives in fresh water and which migrate to seawater to spawn; the key distinction is a return to seawater to breed by mature adults.

COASTAL CURRENTS—Wind-driven, thermohaline, or geostrophic currents in coastal waters.

DIADROMOUS—Applied to fish which migrate between fresh and salt water. This is a general and inclusive term; see anadromous, catadromous, and amphidromous, which are exclusive, specialized forms of diadromy.

EGG—Reproductive cell of female animals; ovum.

EKMAN SPIRAL—Theoretical model to explain the vertical structure of currents that result from a steady wind dragging over an ocean of unlimited depth and extent, and of uniform viscosity. In the northern hemisphere, the surface layer of the water would flow at an angle of 45 degrees to the right of the wind direction. Water at increasing depths would drift in directions to the right until, at about 100 m depth, the water would move opposite to the wind. The velocity of the water decreases with depth throughout the spiral. In the northern hemisphere, net water transport is at 90 degrees to the right of the wind ties; these penetrate variously into estuaries.

EKMAN TRANSPORT—Net water transport resulting from EKMAN SPIRAL.

ENTRAINMENT—Process by which organisms (chiefly eggs and larvae in this context) are captured and moved by currents.

ESTUARINE RESIDENT—Applied to organisms which spawn and complete their life cycles in estuaries, although they may at times be found outside estuaries. They generally have wide salinity and temperature tolerances; examples are hogchoker, mummichog, some sea catfishes and oyster.

ESTUARINE-CATADROMOUS—Refers to species that spend most of their adult stage in the marine environment and spawn there, and in their early life history stages migrate to, and reside in, estuarine environments.

ESTUARINE/MARINE—Applied to organisms found in estuaries primarily as juveniles or young of the year. They spawn in either nearshore or offshore, and typically have wide salinity tolerances. They are often referred to as "estuarine dependent" because they reside in estuaries during critical early life history stages, and recruitment is thought to depend on estuarine residence. Examples are shrimps and menhaden, both extremely important commercially.

FRESHWATER RESIDENT—Applied to organisms which spawn and live in salinities of less than 0.5 ppt, and which may penetrate variously into estuaries; examples are largemouth bass, bluegill, and some catfishes.

GEOSTROPHIC CURRENT—Ocean current that is the product of a balance between gravitational forces and the Coriolis effect. Geostrophic currents move water horizontally below the depth to which wind effects can penetrate.

JUVENILE—In fish, a young fish which has attained minimum adult fin ray counts, and before sexual maturation.

LARVA—In fish, young fish between the time of hatching and attainment of minimum adult fin ray counts.

MARINE RESIDENT—Applied to organisms which are typically part of marine communities beyond the estuary, and which typically spawn in marine salinities.

PASSIVE—Refers to organisms which have no control of horizontal or vertical position in the water column; transport exclusively by water movements.

SEMI-ANADROMOUS—Applied to fish which typically move from saline water to spawn at the brackish water/freshwater interface; an example is white perch.

SWIMMING—Self-propelled locomotion through water.

SYNOPTIC—Refers to weather elements of an extensive area at a particular time.

TIDAL CURRENT—Alternating, horizontal movement of water associated with the rise and fall of the tide, caused by astronomical forces. Offshore tidal currents tend to exhibit rotary patterns, while in areas near coasts the currents follow rectilinear paths and reverse periodically (ebb and flow currents). Tidal currents often reach velocities of 2.5 m/s near shores.

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General References

Able, K.W., R.E. Matheson, W.W. Wallace, M.P. Fahay, and G. Shepherd. 1990. Patterns of summer flounder *Paralichthys dentatus* early life history in the mid-Atlantic Bight and New Jersey Estuaries. *Fishery Bulletin* 88:1-12.

Banks, M.A., G.J. Holt, and J.M. Wakeman. 1991. Age-linked changes in salinity tolerance of larval spotted seatrout (*Cynoscion nebulosus*, Cuvier). *Journal of Fish Biology* 39:505-514.

Bearman, G. 1989. Waves, tides, and shallow-water processes. The Open University/Pergamon Press, Oxford, England, 187 p.

Benfield, M.C., and D.V. Aldrich. 1992. Attraction of postlarval *Penaeus aztecus* Ives and *P. setiferus* (L.) (Crustacea: Decapoda: Penaeidae) to estuarine water in a laminar-flow choice chamber. *Journal of Experimental Marine Biology and Ecology* 156:39-52.

Bielsa, L.M., W.H. Murdoch, and R. Labisky. 1983. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates. (south Florida)—pink shrimp. U.S. Fish and Wildlife Service FWS/OBS-82(11.17). U.S. Army Corps of Engineers, TR EL-82-4, 21 p.

Boehlert, G.W., and B.C. Mundy. 1988. Roles of behavioral and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. *American Fisheries Society Symposium* 3:51-67.

Bowden, K.F. 1983. Physical oceanography of coastal waters. Ellis Howood Limited Publishers, Chichester, England, 302 p.

Bozeman, E.L., and M.J. Van Den Avyle. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (South Atlantic)—alewife and blueback herring. U.S. Fish and Wildlife Service. Serv. Biol. Rep. 82(11.111). U.S. Army Corps of Engineers, TR EL-82-4, 17 p.

Burke, J.S., J.M. Miller, and D.E. Hoss. 1991. Immigration and settlement pattern of *Paralichthys dentatus* and *P. lethostigma* in an estuarine nursery ground, North Carolina, USA. *Netherlands Journal of Sea Research* 27(3/4):395-405.

Collins, M.R., and B.W. Sender. 1989. Larval striped mullet (*Mugil cephalus*) and white mullet (*Mugil curema*) off the southeastern United States. *Bulletin of Marine Science* 45(3):580-589.

Comyns, B.H., J. Lyczkowski-Schultz, D.L. Neiland, and C.A. Wilson. 1991. Reproduction of red drum, *Sciaenops ocellatus*, in the northcentral Gulf of Mexico: seasonality and spawner biomass. In Hoyt, R.D. (ed.), Larval fish recruitment and research in the Americas. NOAA Technical Rep. NMFS 95. pp. 17-26.

Cowan, J.H. Jr., R.S. Birdsong, E.D. Houde, J.S. Priest, W.S. Sharp, and G.B. Mateja. 1992. Enclosure experiments on survival and growth of black drum eggs and larvae in lower Chesapeake Bay. *Estuaries* 15(3):392-402.

Dadswell, M.J., R.J. Klauda, C.M. Moffitt, R.L. Saunders, R.A. Rulifson, and J.E. Cooper (eds.). 1987. Common strategies of anadromous and catadromous fishes. *American Fisheries Society Symposium* 1. American Fisheries Society, Bethesda, MD.

Davis, R.A. 1991. Oceanography: an introduction to the marine environment. W.C. Brown, Dubuque, IA, 434 p.

Day, J.W. Jr., C.S.S. Hall, W.M. Kemp, and A. Yanez-Arancibia. 1989. Estuarine Ecology. John Wiley and Sons, New York, 558 p.

Ditty, J.G., and R.F. Shaw. 1992. Larval development, distribution and ecology of cobia *Rachycentron canadum* (family: Rachycentridae) in the northern Gulf

- of Mexico. *Fishery Bulletin* 90:668-677.
- Epifanio, C.E. 1988. Transport of invertebrate larvae between estuaries and the continental shelf. *American Fisheries Society Symposium* 3:104-114.
- Epifanio, C.E., A.K. Masse, and R.W. Garvine. 1989. Transport of blue crab larvae by surface currents off Delaware Bay, USA. *Marine Ecology Progress Series* 54:35-41.
- Federov, K.N., and A.I. Ginsburg. 1992. The near-surface layer of the ocean. VSP, Utrecht, The Netherlands, 259 p.
- Flores-Coto, C., and S.M. Warlen. 1993. Spawning time, growth, and recruitment of larval spot *Leiostomus xanthurus* into a North Carolina estuary. *Fishery Bulletin* 91:8-22.
- Forward, R.B., L.M. McKelvey, W.F. Hettler, and D.E. Hoss. 1993. Swimbladder inflation of the Atlantic menhaden *Brevoortia tyrannus*. *Fishery Bulletin* 91:254-259.
- Govoni, J.J., and L.J. Pietrafesa. 1994. Eulerian views of layered water currents, vertical distribution of some larval fishes, and inferred advective transport over the continental shelf off North Carolina, USA, in winter. *Fisheries Oceanography* 3(2):120-132.
- Gracia, A. 1991. Spawning stock-recruitment relationships of white shrimp in the southwestern Gulf of Mexico. *Transactions of the American Fisheries Society* 120(5):519-527.
- Grimes, B.H., M.T. Huish, J.H. Kirby, and D. Moran. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Mid-Atlantic)—summer and winter flounder. U.S. Fish and Wildlife Service. *Serv. Biol. Rep.* 82(11.112). U.S. Army Corps of Engineers, TR EL-82-4, 18 p.
- Gross, M.G. 1987. *Oceanography: a view of the earth*. Fourth edition. Prentice Hall Inc., Englewood Cliffs, NJ, 406 p.
- Grosslein, M.D., and T.H. Azarovitz. 1982. Fish distribution. *Marine Ecosystems Analysis Program, New York Bight Atlas Monograph* 15. New York Sea Grant Institute; Albany, NY, 182 p.
- Harding, S.M., and M.E. Chittenden Jr. 1987. Reproduction, movements and population dynamics of the southern kingfish, *Menticirrhus americanus*, in the northwestern Gulf of Mexico. NOAA Technical Rep. NMFS, 21 p.
- Hassler, T.J. 1988. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates. (Pacific Southwest)—striped bass. U.S. Fish and Wildlife Service. *Biol. Rep.* 82(11.82). U.S. Army Corps of Engineers, TR EL-82-4, 29 p.
- Heaps, N.S. 1972. Estimation of density currents in the Liverpool Bay area of the Irish Sea. *Geophysical Journal of the Royal Astronomical Society* 30:415-432.
- Hill, J., D.L. Fowler, and M.J. Van Den Avyle. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Mid-Atlantic)—Blue crab. U.S. Fish Wildl. Serv. *Biol. Rep.* 82(11.100). U.S. Army Corps of Engineers, TR EL-82-4, 18 p.
- Johnson, D.R., and B.S. Hester. 1989. Larval transport and its association with recruitment of blue crabs to Chesapeake Bay. *Estuarine, Coastal and Shelf Science* 28:459-472.
- Kwain, W. 1987. Biology of pink salmon in the North American Great Lakes. *American Fisheries Society Symposium* 1:57-65.
- Larson, S.C., M.J. Van Den Avyle, and E.L. Bozeman Jr. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (South Atlantic)—brown shrimp. U.S. Fish Wildl. Serv. *Biol. Rep.* 82(11.90). U.S. Army Corps of Engineers, TR EL-82-4, 14 p.
- Lee, T.N., V. Kourafalou, J.D. Wang, and W.J. Ho. 1985. Shelf circulation from Cape Canaveral to Cape Fear during winter. In L.P. Atkinson, D.W. Menzel, and K.A. Bush (eds.), *Oceanography of the southeastern U.S. continental shelf*. American Geophysical Union. Washington, DC. pp. 33-62.
- Lyczkowski-Schultz, J., and J.P. Steen. 1991. Diel vertical distribution of red drum *Sciaenops ocellatus* larvae in the northcentral Gulf of Mexico. *Fishery Bulletin* 89:631-641.
- Manooch, C.S., and D. Raver. 1984. Fishes of the southeastern United States. North Carolina State Museum of Natural History, Raleigh, NC, 362 p.
- McCleave, J.D., and G.S. Wippelhauser. 1987. Behavioral aspects of selective tidal stream transport in juvenile American eels. *American Fisheries Society Symposium* 1:138-150.
- McDowall, R.M. 1988. *Diadromy in fishes*. University Press, Cambridge, England, 308 p.

- McHugh, J.L. 1967. Estuarine nekton. In Lauff G. H. (ed.), Estuaries. American Association for the Advancement of Science, Publication 83, Washington, DC. pp. 581-620.
- McKeown, B.A. 1984. Fish migration. Timber Press, OR, 224 p.
- Mercer, L.P. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Mid-Atlantic)—weakfish. U.S. Fish Wildl. Serv. Biol. Rep. 82(11.109). U.S. Army Corps of Engineers, TR EL-82-4, 17 p.
- Miller, J.M., J.P. Reed, and L.J. Pietrafesa. 1984. Patterns, mechanisms and approaches to the study of migrations of estuarine-dependent fish larvae and juveniles. In: McCleave, J.D., G.P. Arnold, J.J. Dodson, and W.H. Neill (eds.), Mechanisms of migration in fishes. Plenum Press, NY, pp. 209-225.
- Mulholland, R. 1984. Habitat suitability index models: pink shrimp. U.S. Fish Wildl. Serv. FWS/OBS-82(10.76). 17 p.
- Muncy, R.J. 1984. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (South Atlantic)—white shrimp. U.S. Fish Wildl. Serv. FWS/OBS-82(11.27). U.S. Army Corps of Engineers, TR EL-82-4, 19 p.
- Murphy, M.D., and R.G. Taylor. 1990. Reproduction, growth, and mortality of red drum *Sciaenops ocellatus* in Florida waters. Fishery Bulletin 88:531-542.
- Myers, G.S. 1949. Usage of anadromous, catadromous, and allied terms for migratory fishes. Copeia 89-87.
- Nelson, D.M., E.A. Irlandi, L.R. Settle, M.E. Monaco, and L.C. Costen-Clements. 1991. Distribution and abundance of fishes and invertebrates in southeast estuaries. ELMR Rep. No. 9. NOAA/NOS Strategic Environmental Assessments Division, Rockville, MD, 177 p.
- Nelson, W.R., M.C. Ingram, and W.E. Schaaf. 1977. Larval transport and year-class strength of Atlantic menhaden, *Brevoortia tyrannus*. U.S. National Marine Fisheries Service Bulletin 75:23-41.
- Norcross, B.L., and H.M. Austin. 1988. Middle Atlantic Bight meridional wind component effect on bottom waters and spawning distribution of Atlantic croaker. Continental Shelf Research 8(1):69-88.
- Norcross, B.L., and D.A. Bodolus. 1991. Hypothetical northern spawning limit and larval transport of Spot. In Hoyt, R.D. (ed.), Larval fish recruitment and research in the Americas. NOAA Technical Rep. NMFS 95, pp. 77-88.
- Norcross, B.L., and R.F. Shaw. 1984. Oceanic and estuarine transport of fish eggs and larvae: a review. Transactions of the American Fisheries Society 113: 153-165.
- NMFS (National Marine Fisheries Service). 1989. Regional Commercial Fisheries Statistics for 1988. Fisheries Statistics Division, Silver Spring, MD.
- Pattillo, M.E., T.E. Czapla, D.M. Nelson, and M.E. Monaco. In prep. Distribution and abundance of fishes and invertebrates in Gulf of Mexico estuaries, Vol. II: Species life history summaries. ELMR Rep. No. 11. NOAA/NOS Strategic Environmental Assessments Division, Silver Spring, MD.
- Peebles, E.B., and S.G. Tolley. 1988. Distribution, growth, and mortality of larval spotted seatrout, *Cynoscion nebulosus*: a comparison between two adjacent estuarine areas of southwest Florida. Bulletin of Marine Science 42(3):397-410.
- Phillips, J.M., M.T. Huish, J.H. Kerby, and D.P. Moran. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Mid-Atlantic)—spot. U.S. Fish Wildl. Serv. Biol. Rep. 82(11.98). U.S. Army Corps of Engineers, TR EL-82-4, 13 p.
- Pietrafesa, L.J., and G.S. Janowitz. 1988. Physical oceanographic processes affecting larval transport around and through North Carolina inlets. American Fisheries Society Symposium 3:34-50.
- Pritchard, D.W. 1952. Salinity distribution and circulation in the Chesapeake Bay estuarine system. Journal of Marine Research 11:106-123.
- Pritchard, D.W. 1955. Estuarine circulation patterns. In: American Society of Civil Engineers proceedings 81:7-17.
- Raynie, R.C., and R.F. Shaw. 1994. Ichthyoplankton abundance along a recruitment corridor from offshore spawning to estuarine nursery ground. Estuarine, Coastal and Shelf Science 39:421-450.
- Rogers, B., R.F. Shaw, W.H. Herke, and R.H. Blanchet. 1993. Recruitment of Postlarval and Juvenile Brown Shrimp (*Penaeus aztecus* Ives) from Offshore to Estuarine Waters of the Northwestern Gulf of Mexico.

Estuarine, Coastal and Shelf Science 36:377-394.

Rogers, S.G., and M.J. Van Den Avyle. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (mid-Atlantic)—atlantic menhaden. U.S. Fish Wildl. Serv. Biol. Rep. 82(11.108). U.S. Army Corps of Engineers, TR EL-82-4, 23 p.

Seabergh, W.C. 1988. Observations on inlet flow patterns derived from numerical and physical modelling studies. American Fisheries Society Symposium 3:13-25.

Shaffer, R.V., and E.L. Nakamura. 1989. Synopsis of biological data on the cobia *Rachycentron canadum* (Pisces: Rachycentridae). NOAA Technical Rep. NMFS 82.

Sinclair, M. 1987. Marine populations: an essay on population regulation and speciation. Univ. Washington Press, Seattle, WA, 252 p.

Smith, D.E., and M. Knappenberger. 1989. Blue crab recruitment dynamics in Chesapeake Bay: a review of current knowledge. Virginia Sea Grant Publication VSG-89-01.

Smith, D.E., R.J. Orth, E. Olmi, J. van Montfrans, and R.N. Lipcius. 1989. Blue crab recruitment workshop, Feb. 5-7 1989, summary of activities. Virginia Sea Grant Publication.

Smith, J.W., and C.A. Wenner. 1985. Biology of the southern kingfish in the South Atlantic Bight. Transactions of the American Fisheries Society 114:356-366.

Thurman, H.V. 1985. Introduction to oceanography. Merrill Publishing, Columbus, OH, 503 p.

Turner, R.E. 1977. Intertidal vegetation and commercial yields of penaeid shrimp. Transactions of the American Fisheries Society 106:411-416.

U.S. Fish and Wildlife Service. 1978. Development of fishes of the Mid-Atlantic Bight. Biological Services Program, Fish and Wildlife Service, U.S. Dept. of the Interior. FWS/OBS-78/12, Vols. 1-6.

U.S. Fish and Wildlife Service. 1983. Species Profiles: life histories and environmental requirements of coastal fishes and invertebrates (Red Drum). U.S. Fish and Wildl. Serv. Biol. Rep. 82(11). U.S. Army Corps of Engineers, TR EL-82-4.

U.S. Fish and Wildlife Service. 1983. Species Profiles: life histories and environmental requirements of

coastal fishes and invertebrates (Striped Mullet). U.S. Fish and Wildl. Serv. Biol. Rep. 82(11). U.S. Army Corps of Engineers, TR EL-82-4.

Wash, W.A., C. Swanson, and C.S. Lee. 1991. Combined effects of temperature and salinity on embryonic development and hatching of striped mullet, *Mugil cephalus*. Aquaculture 97:281-289.

Wang, D. 1988. Transport model for exchange between coastal inlet and open ocean. American Fisheries Society Symposium 3:9-15.

Weinstein, M.P. (ed.). 1988. Larval fish and shellfish transport through inlets. American Fisheries Society Symposium 3. American Fisheries Society, Bethesda, MD, 165 p.

Wenner, E.L., and H.R. Beatty. 1993. Utilization of shallow estuarine habitats in South Carolina, U.S.A., by postlarval and juvenile stages of *Penaeus* spp. (Decapoda: Penaeidae). Journal of Crustacean Biology 13(2):280-295.

Wiseman, W.J., W.W. Schroeder, and S.P. Dinnel. 1988. Shelf-estuarine water exchange between the Gulf of Mexico and Mobile Bay, Alabama. American Fisheries Society Symposium 3:1-8.

Yoder, J.A. 1983. Statistical analysis of the distribution of fish eggs and larvae on the southeastern U.S. continental shelf with comments on oceanographic processes that may affect larval survival. Estuarine, Coastal and Shelf Science 17:637-650.

Zale, A.V., and S.G. Merrifield. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (South Florida)—ladyfish and tarpon. U.S. Fish Wildl. Serv. Biol. Rep. 82(11.104). U.S. Army Corps of Engineers, TR EL-82-4, 17 p.

Chapter 2

Analysis of Relative Abundance Estimates of Estuarine-catadromous Larvae and their Utilization of Coastal Inlets

Tony A. Lowery and Mark E. Monaco
Biogeographic Characterization Branch
Strategic Environmental Assessments Division
Office of Ocean Resources Conservation and Assessment
National Ocean Service
Silver Spring, MD 20910

and

Arthur J. Bulger
Clark Hall
Department of Environmental Sciences
University of Virginia
Charlottesville, Virginia 22903

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Analysis of Relative Abundance Estimates of Estuarine-catadromous Larvae and their Utilization of Coastal Inlets

Introduction

This report is from NOAA's Estuarine Living Marine Resources (ELMR) Program, which organizes and synthesizes data and information on the distribution, relative abundance, and life history characteristics of important fishes and macro-invertebrates in the Nation's estuaries. This report focuses on a group of fishes and macro-invertebrates that spend most of their adult stage and spawn in the marine environment, but migrate to and reside in estuarine environments during their early life history stages. The report has three primary objectives: 1) to define the term "estuarine catadromy" in order to advance our understanding of this important life history strategy and provide a "language" for investigators to use; 2) to characterize and organize data on East Coast estuarine-catadromous species into a single document; and 3) to conduct analyses that determine the importance of estuaries to estuarine-catadromous species along the East Coast and provide a screening index to assess potential anthropogenic impacts on these species.

Chapter 1 of this report characterized estuarine catadromy and presented information of general importance to estuarine-catadromous species, such as oceanographic processes which transport larvae shoreward where they are entrained into the estuaries. As Govoni and Pietrafesa (1994) keenly observed, "larvae that are advected toward the coast and into estuaries may survive; those that are advected elsewhere may perish." As documented in Chapter 1, these estuarine-catadromous species employ different spawning strategies, and their larvae employ different behavioral and physiological adaptations to improve larval entrainment into estuaries. Given that these strategies vary, it occurred to the authors that different species could be utilizing different sets of East Coast estuaries based on the physical and hydrodynamic characteristics of those estuaries. This is supported by differences in larval abundance estimates for the east coast estuaries (Nelson et al. 1991, Stone et al. 1993). To test the hypothesis that species respond to different combinations of physical and hydrodynamic characteristics, the larval abundance estimates of 12 estuarine-catadromous species in 29 East Coast estuaries were modelled against the estuaries' physical and hydrodynamic characteristics. The authors used these 12 species, instead of all 19 species discussed in Chapter 1, because data were not available for the other seven species. Models predicting larval abundance based on the estuaries' physical and hydrodynamic

characteristics were successfully constructed for the 12 species investigated here. This, in combination with the previously observed differences (Nelson et al. 1991, Stone et al. 1993), suggests that some estuaries are of greater utility to specific estuarine-catadromous species than others, and that these differences are due to the physical and hydrodynamic characteristics of those estuaries.

Having supported this hypothesis, the authors were interested in estimating the contribution of individual inlets to the larval abundances in these estuaries. For estuaries with one inlet (e.g., Chesapeake Bay) this is no problem, but for estuaries with multiple inlets (e.g., Barnegat Bay), some inferences were employed to assess the contribution of the individual inlets. The details of how these contributions were developed are presented in the second part of this chapter. The resulting inlet-by-inlet assessments of utilization of 12 estuarine-catadromous larvae are presented for the East Coast from Biscayne Bay, FL to Buzzards Bay, MA. This identifies inlets of greatest importance to maintaining the stocks of these estuarine-catadromous species along the East Coast. As indicated by the models mentioned previously, these utilization patterns are partially due to the physical and hydrodynamic characteristics of the estuaries and their inlets. Therefore, modifications (e.g., geomorphological changes affecting plume characteristics, tidal exchanges, and current speeds) to these inlets could impact their use by estuarine-catadromous species, and could diminish the East Coast's ability to support these stocks. This information provides a screening tool to assess potential impacts of inlet modification on these species.

In summary, this Chapter focuses on the use of larval abundance estimates in East Coast estuaries to assess the importance of specific estuaries and their associated ocean inlets to these estuarine-catadromous species. Therefore, this Chapter addresses the third objective listed above; to conduct analyses which determine the importance of estuaries to estuarine-catadromous species along the East Coast, and provide a screening index to assess potential anthropogenic impacts on these species.

Methods

The first set of analyses investigates larval abundance relationships to nine estuarine/inlet variables for 29 U.S. East Coast estuaries. The objectives of

these analyses were to: 1) determine if estuarine/inlet variables could be used to model larval abundances; 2) offer interpretation of results; and 3) identify investigative leads for further analysis. The second set of analyses investigates 12 estuarine-catadromous species' utilization of 29 U.S. East Coast estuaries and their 56 associated inlets. This was done to develop a screening index to identify inlets of importance to these inlet-sensitive species.

Estuaries from Buzzards Bay, MA to Biscayne Bay, FL (Figure 1) were included in the analysis due to their overall (geomorphologic and hydrodynamic) similarity (Lowery et al. 1994). The estuarine physical/hydrological variables used in this analysis (Table 1, Appendix 1) were compiled/developed by NOAA's Physical Environments Characterization Branch. Detailed methods describing each parameter are provided in NOAA (1985) and Lowery et al. (1994a).

Twelve estuarine-catadromous species were selected for these analyses. The species used are listed in Table 2. These species' larval relative abundance data were extracted from NOAA's Estuarine Living Marine Resources Program's southeast and mid-Atlantic data sets (Figure 2)(Nelson et al. 1991, Stone et al. 1993). The reader is referred to Nelson et al. (1991) and Stone et al. (1993) for detailed methodologies on the development of species' relative abundance rankings. For the purposes of these analyses, the monthly and salinity zone data were collapsed per species' larval life stage in order to extract the highest monthly abundance during any month in any salinity zone in an estuary. Further, the following relative abundance categories were consolidated to improve inter-estuarine comparability of the data: "not present" and "rare" were combined; "abundant" and "highly abundant" were combined (Table 3). Thus, the relative abundance rankings used in this analysis were "not present" or "rare" (1), "common" (2), and "abundant" or "highly abundant" (3). The authors had relative abundance data for 12 of the 19 species discussed in Chapter 1. Therefore, these analyses were not applicable to the seven species for which no data was readily available.

Due to the categorical nature of the larval abundance estimates, ordered stepwise logistic regression was selected to model larval abundance rankings (Table 3) versus the nine physical/hydrodynamic estuarine/inlet variables (Table 1). Since this is not the stepwise multiple regression with which most biostatisticians are familiar, the following background is offered. The ordered stepwise logistic regression is very similar to stepwise multiple regression; the main differences are that normality is not required and categorical data can be used in the logistic regression. However, major

differences occur in the interpretation of the modelling results between logistic and multiple regression. The main metrics used to evaluate multiple regression models are R^2 (percentage of variance accounted for by the model), and significance level (based on a normal distribution) of the model.

The main metrics used to evaluate logistic regressions are concordance (correct predictions estimator), and the significance level (based on a chi square distribution) of the model. Obviously, the higher the concordance, and the lower the model's probabilities, the better the model. The reader is referred to Hosmer and Lemeshow (1989), Freeman (1987), and SAS (1989) for more detailed discussions of the computational differences between logistic and multiple regression.

The nine estuarine/inlet variables (Table 1) for 29 estuaries (Buzzards Bay to Biscayne Bay) were logistically regressed against the larval abundance rankings (Table 3) for each of the twelve species investigated here. SAS Institute's (1988) ordered stepwise logistic regression procedure was used to carry out the stepwise logistic regressions (Appendix 2).

Summaries of these regressions are presented in Table 4, and are discussed in the following sections in terms of the 3 estuarine-catadromous life history strategies identified in Chapter 1. The SAS programs and outputs for these regressions are presented in Appendices 2-14.

Figure 1. U.S. East Coast estuaries included in analysis.

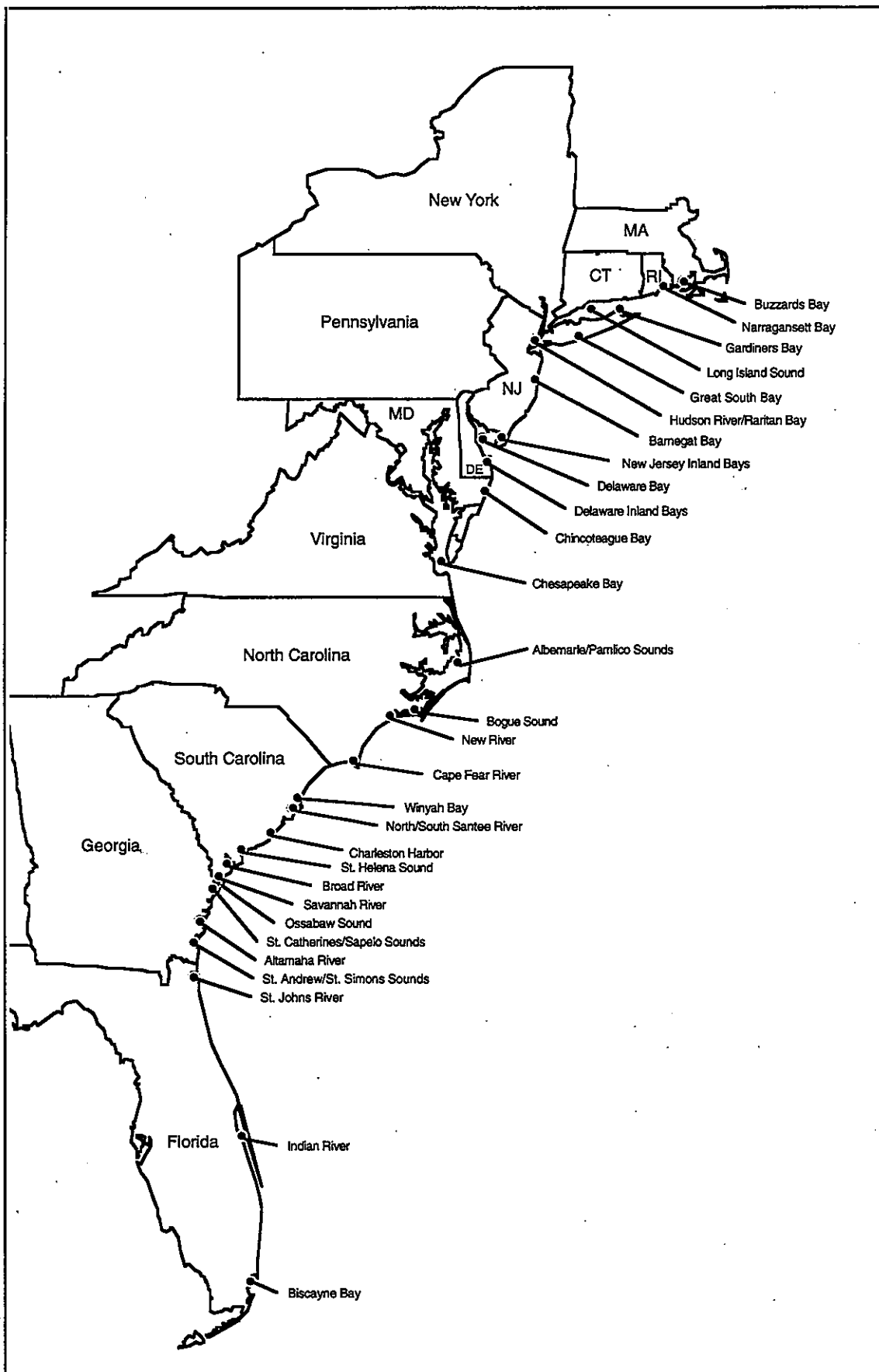


Table 1. Variables selected for variable analysis.

Variable	Abbreviation	Source	Methods
tidal prism volume	tprsm	NEI	NOAA 1985
freshwater fraction	fwfrc	NEI	NOAA 1985
dissolved concentration potential	dcpt	NEI	NOAA 1985
tidal prism flushing	tpflush	NEI	estuary volume/tidal prism
inlet width ^a	iwidth	NEI	Lowery et al. 1994
inlet average depth ^b	iavdep	NEI	Lowery et al. 1994a
inlet cross sectional area ^c	icrsec	NEI	Lowery et al. 1994a
inlet flood current speed ^d	ifcurr	NEI	Lowery et al. 1994a
inlet ebb current speed ^d	iecurr	NEI	Lowery et al. 1994a

^a Sum of inlet widths for estuaries with multiple inlets.
^b Average of inlet depths for estuaries with multiple inlets.
^c Inlet cross sectional area is inlet width multiplied by inlet average depth.
^d Prorated based on inlet cross-sectional area for estuaries with multiple inlets.

Results

The ordered stepwise logistic regressions successfully modelled all of the 12 species investigated here. These species' larval abundance categories vs. the estuary/inlet variables associations yielded an average concordance of 82.6%. These models are exploratory and indicate that additional independent variables are needed to explain the relationships driving the models. Therefore, we do not attempt to interpret the underlying relationships, as that would be premature at this time. However, we believe these types of models, with refinement, could be used in the future to improve the theoretical inlet utilizations. Descriptions of these models follow.

Offshore cold water spawners

Atlantic croaker larval abundance categories vs. the estuary/inlet variables stepwise logistic regression (Table 4, Appendix 3) found freshwater fraction and tidal prism flushing to be the variables most closely associated with the larval abundances in the estuaries from Buzzards Bay to Biscayne Bay. This is a very strong model with a model probability of 0.001 and concordance of 96.7%.

The summer flounder larval abundance vs. the estuary/inlet variables stepwise logistic regression (Table 4, Appendix 4) found freshwater fraction to be the variable most closely associated with the larval abundances in the estuaries from Buzzards Bay to Biscayne Bay. This model is fairly weak, with a probability of 0.1793 and concordance of 87.7%.

The spot larval abundance vs. the estuary/inlet variables stepwise logistic regression (Table 4, Appendix

5) found freshwater fraction, tidal prism flushing, and inlet flood current speed to be the variables most closely associated with the larval abundances in the estuaries from Buzzards Bay to Biscayne Bay. This is a fairly strong model, with a probability of 0.084 and concordance of 94.3%.

The mullet larval abundance vs. the estuary/inlet variables stepwise logistic regression (Table 4, Appendix 6) found freshwater fraction to be the variable most closely associated with the larval abundances in the estuaries from Buzzards Bay to Biscayne Bay. This is a marginally adequate model, with a probability of 0.0242 and concordance of 72.6%.

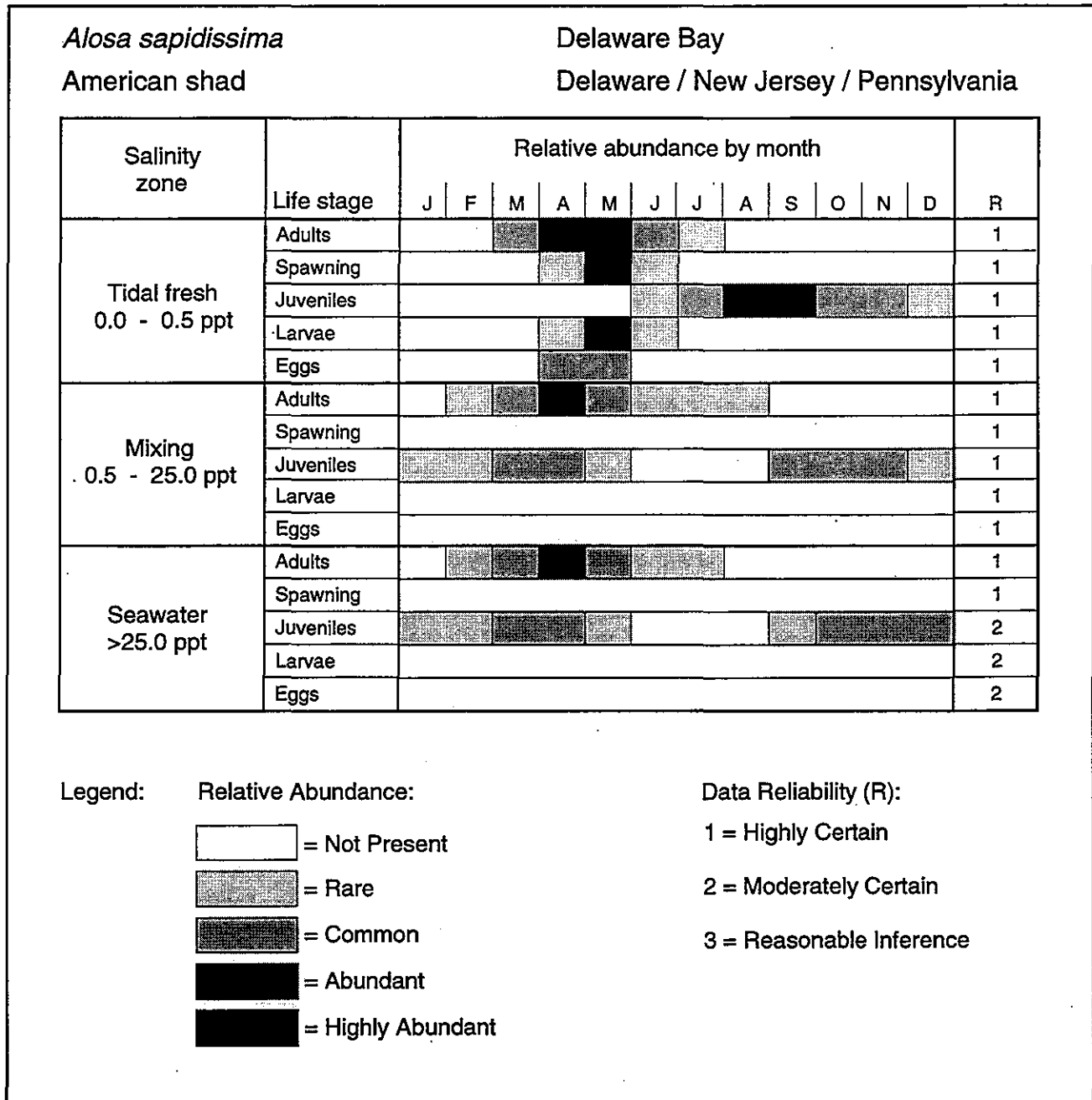
The Atlantic menhaden larval abundance vs. the estuary/inlet variables stepwise logistic regression (Table 4, Appendix 7) found freshwater fraction, inlet cross sectional area, and tidal prism to be the variables most closely associated with the larval abundances in the estuaries from Buzzards Bay to Biscayne Bay. This is a very strong model, with a probability of 0.0127 and concordance of 90.2%.

The pinfish larval abundance vs. the estuary/inlet variables stepwise logistic regression (Table 4, Appendix 8) found inlet cross sectional area to be the variable most closely associated with the larval abundances in the estuaries from Buzzards Bay to Biscayne Bay. This is a marginally adequate model with a model probability of 0.0261 and concordance of 66.8%.

Nearshore/offshore boundary spring and fall spawners

The brown shrimp larval abundance vs. the estuary/inlet variables stepwise logistic regression (Table 4,

Figure 2. Example of ELMR data sheet from mid-Atlantic data set.



Appendix 9) found inlet width to be the variable most closely associated with the larval abundances in the estuaries from Buzzards Bay to Biscayne Bay. This is a weak model, with a probability of 0.1773 and concordance of 79.6%.

Nearshore near-inlet warm water spawners

The black drum larval abundance vs. the estuary/inlet variables stepwise logistic regression (Table 4, Appendix 10) found inlet cross sectional area and tidal prism flushing to be the variables most closely associated

with the larval abundances in the estuaries from Buzzards Bay to Biscayne Bay. This is an adequate model, with a probability of 0.1011 and concordance of 90.0%.

The blue crab larval abundance vs. the estuary/inlet variables stepwise logistic regression (Table 4, Appendix 11) found inlet cross sectional area and tidal prism flushing to be the variables most closely associated with the larval abundances in the estuaries from Buzzards Bay to Biscayne Bay. This is an adequate model, with a probability of 0.1011 and concordance of 90.4%.

The red drum larval abundance vs. the estuary/inlet variables stepwise logistic regression (Table 4, Appen-

Table 2. ELMR species selected for analysis.

Common name	Genus species	Family	Abbreviation
Atlantic menhaden	<i>Brevoortia tyrannus</i>	Clupeidae	MENHADEN
black drum	<i>Pogonias cromis</i>	Sciaenidae	BLKDRUM
blue crab	<i>Callinectes sapidus</i>	Portunidae	BLUECRAB
brown shrimp	<i>Penaeus aztecus</i>	Penaeidae	BRSHRIMP
Atlantic croaker	<i>Micropogonias undulatus</i>	Sciaenidae	CROAKER
mullet	<i>Mugil cephalus & curema</i>	Mugilidae	MULLET
pinfish	<i>Lagodon rhomboides</i>	Sparidae	PINFISH
red drum	<i>Sciaenops ocellatus</i>	Sciaenidae	REDDRUM
spot	<i>Leiostomus xanthurus</i>	Sciaenidae	SPOT
spotted seatrout	<i>Cynoscion nebulosus</i>	Sciaenidae	SEATROUT
summer flounder	<i>Paralichthys dentatus</i>	Bothidae	SUMFLOUN
weakfish	<i>Cynoscion regalis</i>	Sciaenidae	WEAKFISH

Table 3. Larval abundances by estuary (1 = not present and rare, 2 = common, 3 = abundant and highly abundant)

ESTUARY	BRSHRIMP	BLUECRAB	PINFISH	SEATROUT	SPOT	CROAKER	REDDRUM	BLKDRUM	WEAKFISH	SUMFLOUN	MENHADEN	MULLET
Buzzards Bay	1	2	1	1	1	1	1	1	2	1	3	1
Narragansett Bay	1	2	1	1	1	1	1	1	2	1	3	1
Gardiners Bay	1	2	1	1	1	1	1	1	3	1	3	1
Long Island Sound	1	1	1	1	1	1	1	1	1	1	3	1
Great South Bay	1	3	1	1	1	1	1	1	2	1	3	1
Hudson River/Raritan Bay	1	2	1	1	1	1	1	1	2	1	3	1
Barneget Bay	1	3	1	1	1	1	1	1	1	1	2	1
New Jersey Inland Bays	1	3	1	1	1	1	1	1	1	1	2	1
Delaware Bay	1	3	1	1	3	1	1	1	3	1	2	2
Delaware Inland Bays	1	3	1	1	2	1	1	1	2	3	1	1
Chinoteague Bay	1	3	1	1	1	1	1	1	1	1	1	1
Chesapeake Bay	1	3	1	2	1	1	1	2	3	2	3	1
Albemarle/Pamlico Sound	1	1	1	1	1	1	1	1	1	2	3	3
Bogue Sound	3	3	3	1	3	3	2	1	2	2	3	3
New River	3	3	3	1	3	3	1	1	1	2	3	3
Cape Fear River	3	3	2	3	3	3	2	1	3	2	3	3
Winyah Bay	3	3	3	2	3	3	2	1	2	2	3	1
Charleston Harbor	2	3	3	1	3	3	1	1	3	2	3	3
North and South Santee Rivers	3	3	2	2	3	3	2	2	3	2	3	3
St. Helena Sound	3	3	3	2	3	3	2	2	2	2	3	3
Broad River	3	3	3	2	3	3	2	2	2	2	3	3
Savannah Sound	1	3	2	3	3	3	2	2	3	2	3	2
Ossabaw Sound	1	3	2	3	3	3	2	2	3	2	3	2
St. Catherines/Sapelo Sound	1	3	2	3	3	3	2	2	3	2	3	2
Altamaha River	1	3	2	3	3	3	2	2	3	2	3	2
St. Andrew/Simon Sound	1	3	2	3	3	3	2	2	3	2	3	2
St. Johns River	3	3	3	2	2	3	3	3	3	2	2	3
Indian River	2	3	3	3	1	1	3	3	1	1	2	3
Biscayne Bay	1	3	3	2	2	1	1	1	1	1	1	2

Table 4. Summary of ordered stepwise logistic regression results (see Appendices 2-14 for SAS programming and complete outputs).

DEPENDENT VARIABLE	INDEPENDENT VARIABLES ADDED TO MODEL	MODEL CONCORDANCE	MODEL PROBABILITY
Atlantic menhaden larval abundance	freshwater fraction, inlet cross-sectional area, tidal prism	90.2%	0.0127
blue crab larval abundance	inlet cross-sectional area, tidal prism flushing	90.4%	0.1011
weakfish larval abundance	freshwater fraction, inlet flood current speed	77.2%	0.075
Atlantic croaker larval abundance	freshwater fraction, tidal prism flushing	96.7%	0.001
black drum larval abundance	inlet cross-sectional area, tidal prism flushing	90.0%	0.1011
brown shrimp larval abundance	inlet width	79.6%	0.1773
mullet larval abundance	freshwater fraction	72.6%	0.0242
pinfish larval abundance	inlet cross-sectional area	66.8%	0.0261
red drum larval abundance	freshwater fraction inlet ebb current speed	77.4%	0.0951
spotted seatrout larval abundance	freshwater fraction	68.3%	0.015
spot larval abundance	freshwater fraction tidal prism flushing inlet flood current speed	94.3%	0.084
summer flounder larval abundance	freshwater fraction	87.7%	0.1793

dix 12) found freshwater fraction and inlet ebb current speed to be the variables most closely associated with the larval abundances in the estuaries from Buzzards Bay to Biscayne Bay. This is an adequate model, with a probability of 0.0951 and concordance of 77.4%.

The spotted seatrout larval abundance vs. the estuary/inlet variables stepwise logistic regression (Table 4, Appendix 13) found freshwater fraction to be the variable most closely associated with the larval abundances in the estuaries from Buzzards Bay to Biscayne Bay. This is an adequate model, with a probability of 0.015 and concordance of 68.3%.

The weakfish larval abundance vs. the estuary/inlet variables stepwise logistic regression (Table 4, Appendix 14) found freshwater fraction and inlet flood current speed to be the variables most closely associated with the larval abundances in the estuaries from Buzzards Bay to Biscayne Bay. This is an adequate model, with a probability of 0.075 and concordance of 77.2%.

Estuary and inlet utilizations

Estuarine-catadromous species do not utilize U.S. East Coast estuaries equally (Table 3). Therefore, this section presents an investigation of their utilization patterns to determine which estuaries and associated inlets are important to estuarine-catadromous species along the U.S. East Coast. The estuary/larval abundance rankings are used to generate the number of estuarine-catadromous species utilizing each estuary (i.e., estuarine perspective (Table 6)), and the number of estuaries utilized by each estuarine-catadromous species (i.e., species perspective (Table 7)). An estuarine perspective section follows which summarizes the estuaries are utilized by the selected estuarine-catadromous species (i.e., collectively). The species perspective section summarizes the estuaries that are most important to individual estuarine-catadromous species based on a screening "index of importance".

The Life History Tables in Chapter 1 indicate tidal currents are likely to be important for the majority of larval transport into estuaries. It is further assumed that individual inlet flood current volumes indicate an inlet's contribution to marine/estuarine exchanges per estuary (Table 5). The estuaries' inlet variables (Table 5) used to carry out these calculations were compiled/developed by NOAA's Physical Environments Assessment Branch. The estuarine larval abundances (Table 3) are multiplied by these percent inlet exchange contributions to produce theoretical inlet utilization estimates per species. These inlet utilization estimates provide surrogate indications of an inlet's contribution to the estuary's larval abundance.

$$\text{inlet flood volume} = \text{flood current speed} * \text{inlet cross sectional area} * \text{flood tide duration}$$

$$\text{percent inlet exchange} = \text{individual inlet flood volume} / \text{sum of inlet flood volumes for estuary}$$

$$\text{theoretical inlet utilization} = \text{percent inlet exchange} * \text{estuary's larval abundance}$$

The following inlet utilization ranges were placed into these categories: inlet utilizations ≤ 1 were assigned to the "low to no utilization" category; inlet utilizations $1 < x \leq 2$ were assigned to the "moderate utilization" category; and inlet utilizations > 2 were assigned to the "high utilization" category (Figures 3-14).

There is a clear difference between the species utilization patterns below Cape Hatteras and those above (Tables 3 and 6). The average number of species utilizing the estuaries from Buzzards Bay to Albemarle/Pamlico Sound in larval abundances of common and greater was 3 (i.e., 25% of the 12 species). The southern estuaries averaged 10 (i.e., 85%). Clearly, the estuaries from Bogue Sound to Biscayne Bay are more heavily utilized by this group of estuarine-catadromous species than those north of Bogue Sound. This is most likely due to water temperature differences associated with the divergence of the Gulf Stream, which parallels the coast from Biscayne Bay to Cape Hatteras, where it moves offshore. For example, the long-term annual water temperature at Diamond Shoal Light (off Cape Hatteras) is 20.7 C, and drops to 14.7 C at Chesapeake Light (off the mouth of Chesapeake Bay) (NOAA 1973). Blue crab, weakfish, and Atlantic menhaden are not restricted by these regional differences. However, the other nine species show restricted use of the northern estuaries. Hence, overall the southern estuaries are apparently more important to these species.

Estuarine perspectives

Buzzards Bay is utilized by blue crab, weakfish, and Atlantic menhaden in larval abundances \geq common (Table 3). These larvae enter through two inlets with the mouth of Buzzards Bay accounting for 85% of the flood tidal flux (Quicks Hole Inlet accounts for the remaining 15%) (Table 5).

Narragansett Bay is utilized by blue crab, weakfish, and Atlantic menhaden in larval abundances \geq common (Table 3). These larvae enter through 2 inlets, with the Narrows Point-Brenton Point Inlet accounting for 70% of the flood tidal flux (Sachuest Point-Breakwater Point Inlet accounts for the remaining 30%) (Table 5).

Gardiners Bay is utilized by blue crab, weakfish, and Atlantic menhaden in larval abundances \geq common (Table 3). These larvae enter through two inlets, with the north mouth of Gardiners Bay Inlet accounting for 77% of the flood tidal flux (south mouth of Gardiners Bay accounts for the remaining 23%)(Table 5).

Long Island Sound is utilized by Atlantic menhaden in larval abundances \geq common (Table 3). These larvae enter through two inlets, with Orient Point-Race Point Inlet accounting for 97% of the flood tidal flux (East Point-Napatree Point Inlet accounts for the remaining

3%)(Table 5).

Great South Bay is utilized by blue crab, weakfish, and Atlantic menhaden in larval abundances \geq common (Table 3). These larvae enter through three inlets: Fire Island Inlet accounts for 47% of the flood tidal flux; Jones Inlet accounts for 30%, and East Rockaway Inlet for 23% (Table 5).

Hudson River/Raritan Bay is utilized by blue crab, weakfish, and Atlantic menhaden in larval abundances \geq common (Table 3). These larvae enter through one

Table 5. Estuary inlet information.

Estuary name	number of inlets	inlet(s) name	inlet width m	average depth m	maximum depth m	cross section m ²	flood current ms ⁻¹	flood influx m ³	percent estuarine influx
Buzzards Bay	2	mouth of Buzzards Bay	10424	14.9	21.3	155051.5	0.31	1.08E+09	85.3%
		Quicks Hole	1289	6.6	14.5	8449.1	0.98	1.86E+08	14.7%
Narragansett Bay	2	Narrows Point-Brenton Point	7041	19.4	33.1	136595.4	0.21	6.45E+08	70.1%
		Sachuest Point-Breakwater Point	3859	15.1	16.3	58270.9	0.21	2.75E+08	29.9%
Gardiners Bay	2	north mouth of Gardiners Bay	9354	12.9	18.0	120605.5	0.62	1.68E+09	76.9%
		south mouth of Gardiners Bay	10250	14.6	21.3	149967.8	0.15	5.06E+08	23.1%
Long Island Sound	2	Orient Point-Race Point	18974	29.0	73.8	549983.7	1.70	2.10E+10	96.8%
		East Point-Napatree Point	3383	9.2	61.9	31246.1	0.98	6.89E+08	3.2%
Great South Bay	3	East Rockaway Inlet	741	3.4	5.5	2483.3	1.13	6.31E+07	23.5%
		Jones Inlet	640	3.5	10.4	2240.3	1.60	8.07E+07	30.0%
		Fire Island Inlet	878	5.1	8.7	4476.9	1.24	1.25E+08	46.5%
Hudson River	1	Hudson River entrance	9135	8.4	14.1	76289.9	0.82	1.41E+09	100.0%
Barnegat Bay	2	Barnegat Inlet (jetty)	347	2.9	3.5	1007.7	1.13	2.56E+07	8.5%
		Little Egg Inlet	3264	3.6	6.4	11840.4	1.03	2.74E+08	91.5%
New Jersey Inland Bays	7	Brigantine Inlet	366	3.9	7.0	1438.1	0.98	3.16E+07	6.5%
		Absecon Inlet (jetty)	662	5.5	9.8	3632.1	2.10	1.72E+08	35.1%
		Great Egg Inlet	1463	5.7	11.5	8383.6	1.03	1.94E+08	39.7%
		Corsons Inlet	777	0.6	7.3	497.4	0.05	5.76E+05	0.1%
		Townsend Inlet	274	3.2	4.3	877.8	0.87	1.73E+07	3.5%
		Hereford Inlet	892	2.3	4.9	2050.5	0.82	3.80E+07	7.8%
		Cape May Inlet (jetty)	251	6.9	10.1	1731.9	0.93	3.62E+07	7.4%
Delaware Bay	1	mouth of Delaware Bay	18197	12.6	30.8	228508.0	0.72	3.70E+09	100.0%
Delaware Inland Bays	1	Indian River Inlet (jetty)	152	4.5	5.0	685.8	0.93	1.44E+07	100.0%
Chincoteague Bay	2	mouth of Sinapuxent Bay	247	3.0	4.7	741.0	0.87	1.46E+07	4.7%
		Chincoteague Inlet	4695	3.4	8.9	16099.2	0.82	2.98E+08	95.3%
Chesapeake Bay	1	mouth of Chesapeake Bay	17730	7.8	15.7	137806.3	0.41	1.27E+09	100.0%
Albamarle/Pamlico Sounds	4	Oregon Inlet	1582	2.9	4.0	4587.5	1.10	1.14E+08	41.5%
		Hatteras Inlet	880	1.5	2.8	1319.5	1.10	3.27E+07	11.9%
		Ocracoke Inlet	2057	2.7	14.0	5643.9	0.88	1.12E+08	40.8%
		Drum Inlet	604	1.3	3.3	754.4	0.93	1.58E+07	5.8%
Bogue Sound	3	Barden Inlet	777	1.7	3.0	1303.0	0.98	2.87E+07	16.7%
		Beauford Inlet	1054	7.7	14.2	8098.1	0.62	1.13E+08	65.7%
		Bogue Inlet	1554	1.7	3.1	2642.6	0.51	3.03E+07	17.6%
New River	1	New River Inlet	1006	1.9	3.5	1901.0	0.51	2.18E+07	100.0%
Cape Fear River	1	mouth of Cape Fear River	2114	1.6	3.8	3286.3	1.10	8.13E+07	100.0%
Winyah Bay	1	mouth of Winyah Bay	1975	3.4	10.0	6742.5	0.98	1.49E+08	100.0%
N/S Santee River	2	mouth of North Santee River	572	3.4	5.3	1968.4	0.77	3.41E+07	65.3%
		mouth of South Santee River	562	1.9	2.8	1045.6	0.77	1.81E+07	34.7%
Charleston Harbor	1	Charleston Harbor (jetty)	914	7.8	13.8	7135.0	0.93	1.49E+08	100.0%
St. Helena Sound	2	mouth of St. Helena Sound	12349	4.7	11.0	57588.7	0.77	9.98E+08	89.7%
		Fripp Inlet	1381	5.9	8.3	8206.6	0.62	1.14E+08	10.3%
Broad River	1	mouth of Port Royal Sound	4206	10.5	17.1	44163.0	0.93	9.24E+08	100.0%
Savannah River	1	mouth of Savannah River	9400	5.9	13.1	55870.0	0.93	1.17E+09	100.0%
Ossabaw Sound	1	mouth of Ossabaw Sound	5395	4.8	7.5	25817.0	0.82	4.76E+08	100.0%
St. Catherines/Sapelo Sounds	3	mouth of Doboy Sound	2016	6.4	13.9	12844.2	0.82	2.37E+08	20.5%
		mouth of Sapelo Sound	4065	5.8	13.6	23414.5	0.88	4.64E+08	40.2%
		mouth of St. Catherine Sound	2652	8.2	14.9	21663.2	0.93	4.53E+08	39.3%
Altamaha River	1	mouth of Altamaha River	3667	2.3	6.0	8493.9	0.57	1.09E+08	100.0%
St. Andrew/St. Simons Sounds	2	mouth of St. Andrew Sound	4398	6.6	16.9	28822.7	1.10	7.13E+08	53.5%
		mouth of St. Simon Sound	1911	9.0	12.4	17242.1	1.60	6.21E+08	46.5%
St. Johns River	1	mouth of St. John's River (jetty)	471	13.9	19.8	6530.9	0.97	1.43E+08	100.0%
Indian River	2	Fort Pierce Inlet (jetty)	206	6.0	8.7	1236.0	1.34	3.73E+07	69.7%
		Sebastian Inlet (jetty)	180	1.9	4.0	342.0	2.11	1.62E+07	30.3%
Biscayne Bay	4	Miami Beach - Key Biscayne	4171	0.8	12.3	3178.7	0.62	4.41E+07	29.3%
		Soldier Key - Key Biscayne	8230	2.1	5.4	17558.7	0.10	4.06E+07	26.9%
		Sand Key - Soldier Key	8120	1.5	4.4	12127.2	0.10	2.81E+07	18.6%
		Broad/Angelfish Creek	2414	1.1	5.1	2722.4	0.62	3.80E+07	25.2%

Table 6. Number of species utilized by estuaries in larval abundances \geq common (Table 3).

Estuary	# species utilizing estuary in abundances \geq common
Buzzards Bay	3
Narragansett Bay	4
Gardiners Bay	3
Long Island Sound	1
Great South Bay	3
Hudson River/Raritan Bay	3
Barnegat Bay	2
New Jersey Inland Bays	2
Delaware Bay	5
Delaware Inland Bays	4
Chinoteague Bay	1
Chesapeake Bay	5
Albemarle/Pamlico Sounds	3
Bogue Sound	10
New River	8
Cape Fear River	11
Winyah Bay	10
Charleston Harbor	12
North and South Santee Rivers	9
St. Helena Sound	12
Broad River	12
Savannah Sound	11
Ossabaw Sound	11
St. Catherine's/Sapelo Sounds	11
Altamaha River	11
St. Andrew/St. Simon Sounds	11
St. Johns River	12
Indian River	8
Biscayne Bay	5

inlet (Table 5).

Barnegat Bay is utilized by blue crab and menhaden in larval abundances \geq common (Table 3). These larvae enter through two inlets, with Little Egg Inlet accounting for 91% of the flood tidal flux (Barnegat Inlet accounts for 9%) (Table 5).

New Jersey Inland Bays are utilized by blue crab and menhaden in larval abundances \geq common (Table 3). These larvae enter through seven inlets: Great Egg Inlet accounts for 40%; Absecon Inlet accounts for 35%; Hereford Inlet for 8%; Cape May Inlet for 7%; Brigatine Inlet for 6%; Townsend Inlet 4%; and Corsons Inlet <1% (Table 5).

Delaware Bay is utilized by blue crab, spot, weakfish, menhaden, and mullets in larval abundances \geq common (Table 3). These larvae enter through one inlet (Table 5).

Delaware Inland Bays are utilized by blue crab, spot, weakfish, and summer flounder in larval abundances \geq common (Table 3). These larvae enter through one inlet at Indian River Inlet (Table 5).

Chincoteague Bay is utilized by blue crab in larval abundances \geq common (Table 3). These larvae enter through two inlets, with Chincoteague Inlet accounting for 95% of the flood tidal flux (the mouth of Sinapuxent Bay accounts for the remaining 5%) (Table 5).

Chesapeake Bay is utilized by blue crab, seatrout, black drum, weakfish, summer flounder, and menhaden in larval abundances \geq common (Table 3). These larvae enter through one inlet (Table 5).

Albemarle/Pamlico Sounds are utilized by summer flounder, menhaden, and mullet in larval abundances \geq common (Table 3). These larvae enter through four inlets: Oregon Inlet accounts for 41% of the flood tidal flux; Ocracoke Inlet for 41%; Hatteras Inlet 12%; Drum Inlet 6% (Table 5).

Bogue Sound is utilized by brown shrimp, blue crab, pinfish, spot, croaker, red drum, weakfish, summer flounder, menhaden, and mullet in larval abundances \geq common (Table 3). These larvae enter through three inlets: Beaufort Inlet accounts for 66% of the flood tidal flux; Bogue Inlet for 18%; Barden Inlet 16% (Table 5).

New River is utilized by brown shrimp, blue crab, pinfish, spot, croaker, summer flounder, menhaden, and mullet in larval abundances \geq common (Table 3). These larvae enter through one inlet (Table 5).

Cape Fear River is utilized by brown shrimp, blue crab, pinfish, spot, croaker, red drum, seatrout, weakfish, summer flounder, menhaden, and mullet in larval abundances \geq common (Table 3). These larvae enter through one inlet (Table 5).

Winyah Bay is utilized by brown shrimp, blue crab, pinfish, spot, croaker, red drum, seatrout, weakfish, summer flounder, and menhaden in larval abundances \geq common (Table 3). These larvae enter through one inlet (Table 5).

Charleston Harbor is utilized by brown shrimp, blue crab, pinfish, spot, croaker, weakfish, summer flounder, menhaden, and mullet in larval abundances \geq common (Table 3). These larvae enter through one inlet (Table 5).

North and South Santee Rivers are utilized by brown shrimp, blue crab, pinfish, spot, croaker, black drum,

red drum, seatrout, weakfish, summer flounder, menhaden, and mullet in larval abundances \geq common (Table 3). These larvae enter through two inlets, with the mouth of the North Santee River accounting for 65% of the flood tidal flux (the mouth of the South Santee accounts for the remaining 35%) (Table 5).

St. Helena Sound is utilized by brown shrimp, blue crab, pinfish, spot, croaker, black drum, red drum, seatrout, weakfish, summer flounder, menhaden, and mullet in larval abundances \geq common (Table 3). These larvae enter through two inlets, with the mouth of St. Helena Sound accounting for 90% of the flood tidal flux (Fripp Inlet accounts for the remaining 10%) (Table 5).

Broad River is utilized by brown shrimp, blue crab, pinfish, spot, croaker, black drum, red drum, seatrout, weakfish, summer flounder, menhaden, and mullet in larval abundances \geq common (Table 3). These larvae enter through one inlet (Table 5).

Savannah River is utilized by blue crab, pinfish, spot, croaker, black drum, red drum, seatrout, weakfish, summer flounder, menhaden, and mullet in larval abundances \geq common (Table 3). These larvae enter through one inlet (Table 5).

Ossabaw Sound is utilized by blue crab, pinfish, spot, croaker, black drum, red drum, seatrout, weakfish, summer flounder, menhaden, and mullet in larval abundances \geq common (Table 3). These larvae enter through one inlet (Table 5).

St. Catherines/Sapelo Sounds are utilized by blue crab, pinfish, spot, croaker, black drum, red drum, seatrout, weakfish, summer flounder, menhaden, and mullet in larval abundances \geq common (Table 3). These larvae enter through three inlets: the mouth of Sapelo Sound

accounts for 40% of the flood tidal flux; the mouth of St. Catherine Sound for 40%; and the mouth of Doboy Sound the remaining 20% (Table 5).

Altamaha River is utilized by blue crab, pinfish, spot, croaker, black drum, red drum, seatrout, weakfish, summer flounder, menhaden, and mullet in larval abundances \geq common (Table 3). These larvae enter through one inlet (Table 5).

St. Andrew/St. Simons Sounds are utilized by blue crab, pinfish, spot, croaker, black drum, red drum, seatrout, weakfish, summer flounder, menhaden, and mullet in larval abundances \geq common (Table 3). These larvae enter through two inlets, with the mouth of St. Andrew Sound accounting for 53% of the flood tidal flux (the mouth of St. Simon Sound accounts for the remaining 47%) (Table 5).

St. Johns River is utilized by brown shrimp, blue crab, pinfish, spot, croaker, black drum, red drum, seatrout, weakfish, summer flounder, menhaden, and mullet in larval abundances \geq common (Table 3). These larvae enter through one inlet (Table 5).

Indian River is utilized by brown shrimp, blue crab, pinfish, black drum, red drum, seatrout, menhaden, and mullet in larval abundances \geq common (Table 3). These larvae enter through two inlets, with Fort Pierce Inlet accounting for 70% of the flood tidal flux (Sebastian Inlet accounts for the remaining 30%) (Table 5).

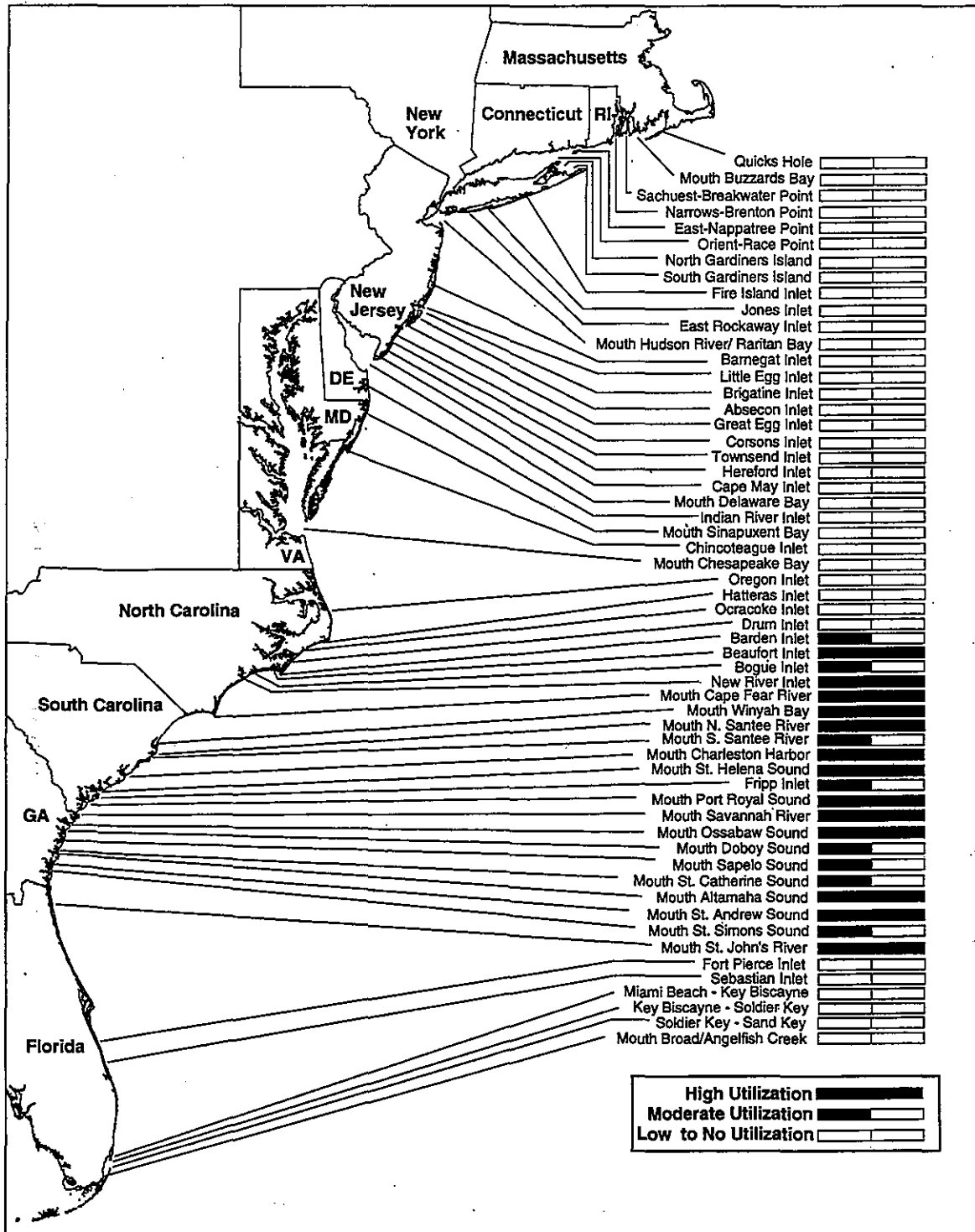
Biscayne Bay is utilized by blue crab, pinfish, seatrout, spot, and mullet in larval abundances \geq common (Table 3). These larvae enter through four inlets: Miami Beach-Key Biscayne Inlet accounts for 29% of the flood tidal flux; Soldier Key-Key Biscayne for 27%; Broad/Angelfish Creek Inlet 25%; and Sand Key-Soldier Key Inlet 19% (Table 5).

Table 7. Number of estuaries utilized by species in larval abundances \geq common (Table 3).

Common name	Genus species	# estuaries utilized \geq common
Atlantic croaker	<i>Micropogonias undulatus</i>	14
Atlantic menhaden	<i>Brevoortia tyrannus</i>	26
black drum	<i>Pogonias cromis</i>	11
blue crab	<i>Callinectes sapidus</i>	27
brown shrimp	<i>Penaeus aztecus</i>	10
mullet	<i>Mugil cephalus & curema</i>	16
pinfish	<i>Lagodon rhomboides</i>	16
red drum	<i>Sciaenops ocellatus</i>	13
spot	<i>Leiostomus xanthurus</i>	17
spotted seatrout	<i>Cynoscion nebulosus</i>	14
summer flounder	<i>Paralichthys dentatus</i>	17
weakfish	<i>Cynoscion regalis</i>	21

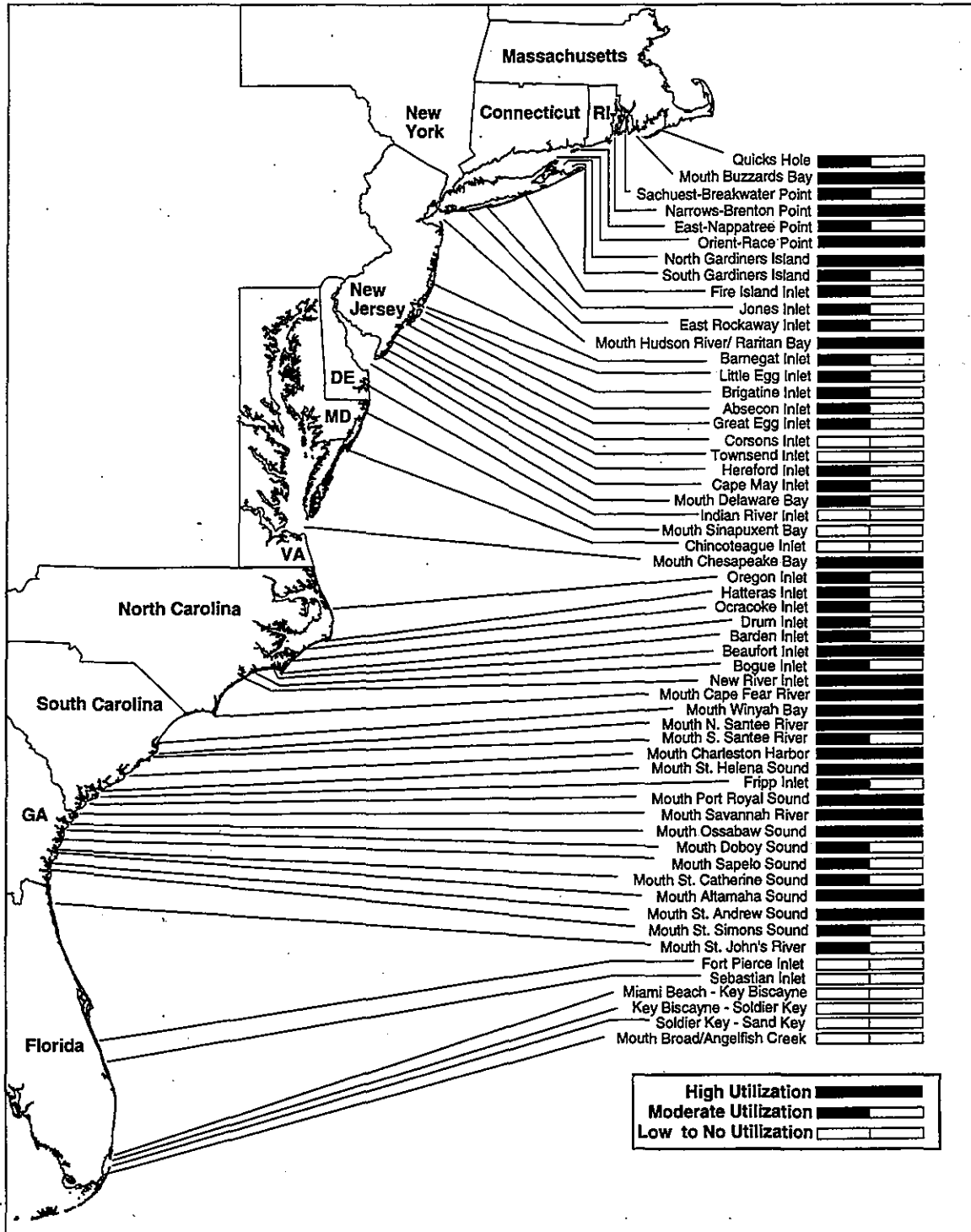
Species perspectives

Figure 3. Relative screening index to assess importance of individual inlets to Atlantic croaker



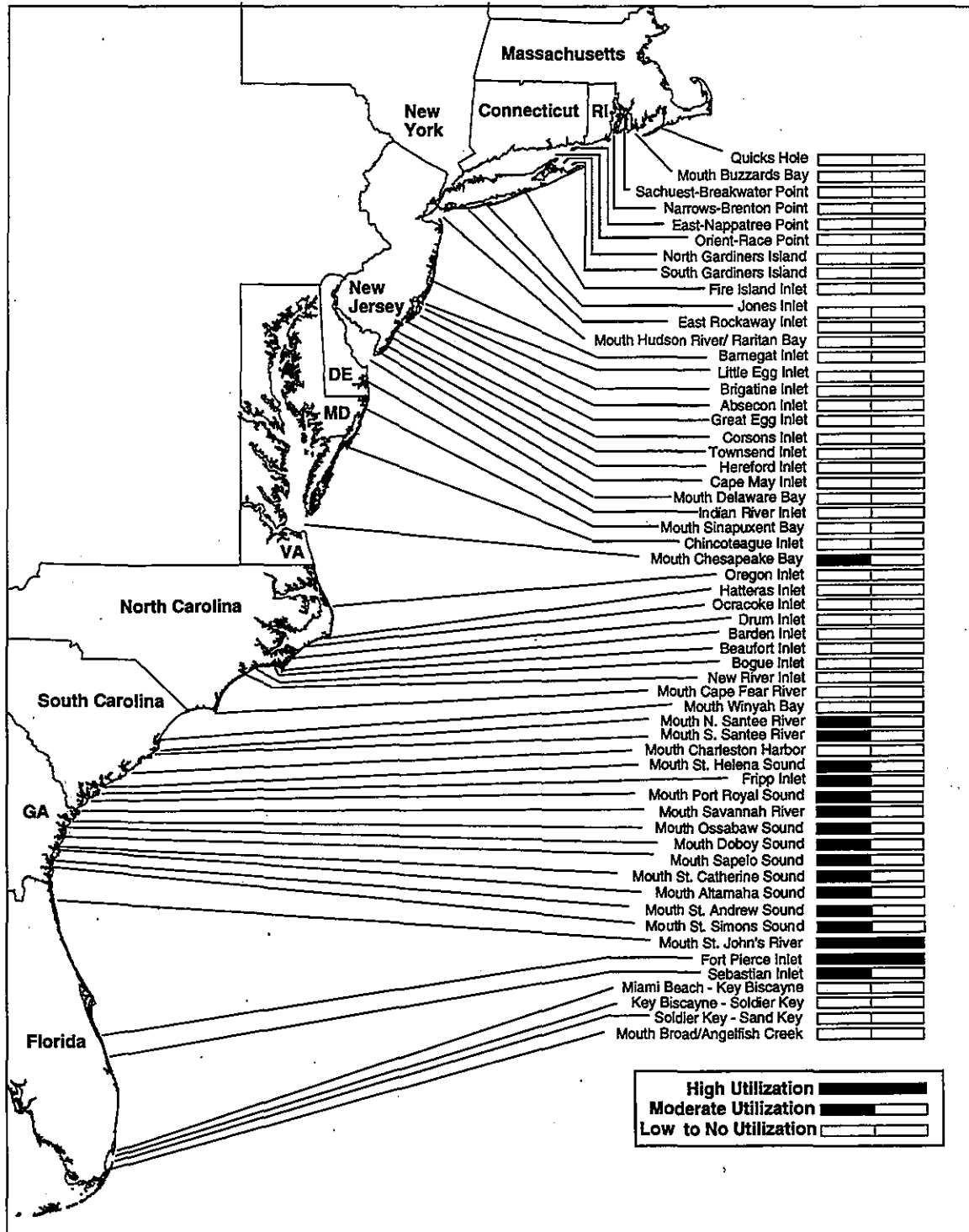
Atlantic croaker utilize 48.3% of the estuaries in larval abundances \geq common (Table 3). Bogue Sound, New River, Cape Fear River, Winyah Bay, North and South Santee Rivers, Charleston Harbor, St. Helena Sound, Broad River, Savannah Sound, Ossabaw Sound, St. Catherines Sound, Altamaha River, St. Andrew/St. Simons Sounds, and St. Johns River were utilized at abundances \geq common. Based on their \geq moderate inlet utilizations, 21 inlets from Barden Inlet to the mouth of St. John's River (Figure 3) appear to be important to Atlantic croaker.

Figure 4. Relative screening index to assess importance of individual inlets to Atlantic menhaden



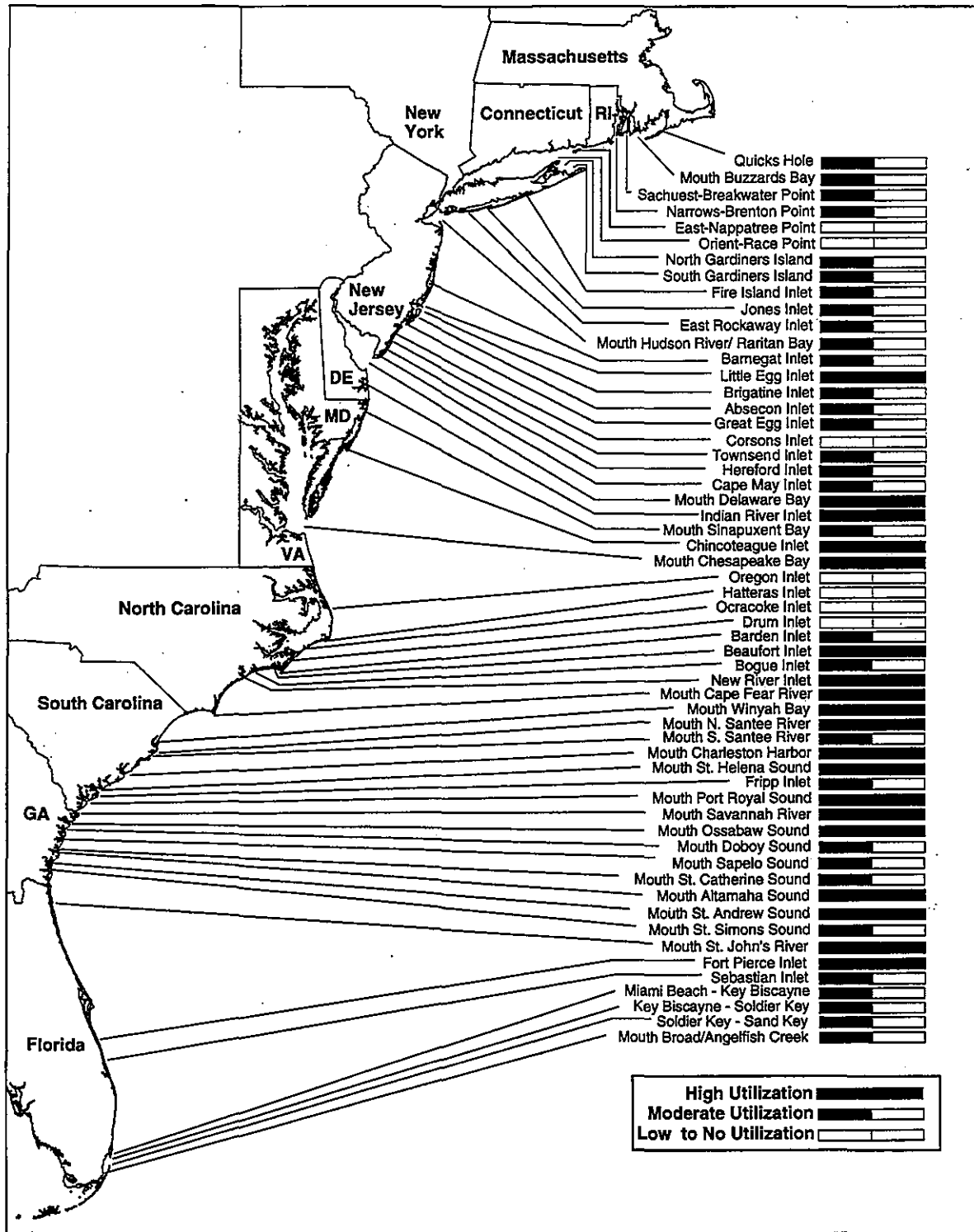
Atlantic menhaden utilize 89.7% of the estuaries in larval abundances \geq common (Table 3). Biscayne Bay, Chincoteague Bay, and Delaware Inland Bays were utilized the least (i.e., abundances below common). Based on their \geq moderate inlet utilizations, 46 inlets from Quicks Hole to the mouth of St. John's River (Figure 4) appear to be important to Atlantic menhaden.

Figure 5. Relative screening index to assess importance of individual inlets to black drum



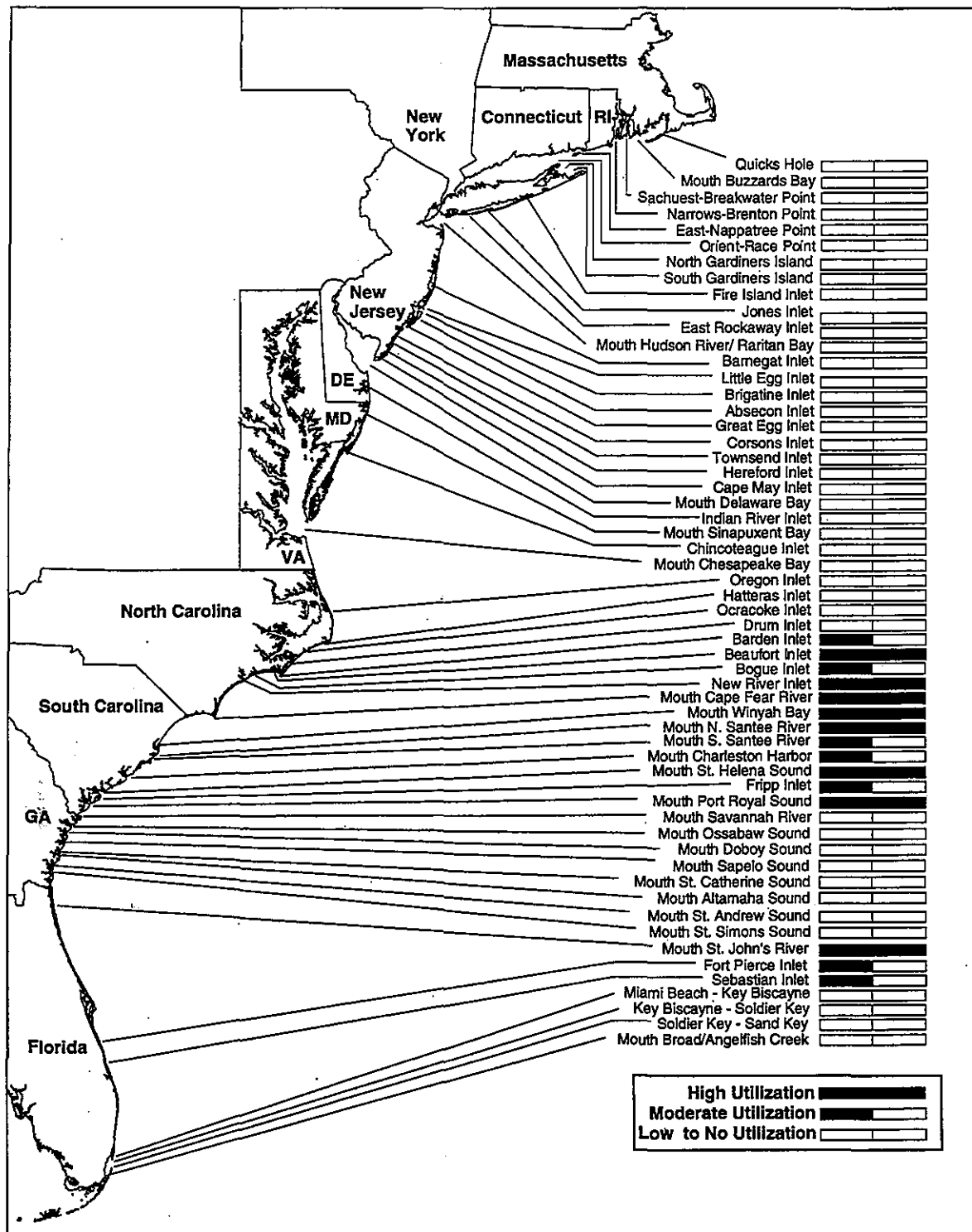
Black drum utilize 37.9% of the estuaries in larval abundances \geq common (Table 3). Chesapeake Bay, North and South Santee Rivers, St. Helena Sound, Broad River, Savannah Sound, Ossabaw Sound, St. Catherines Sound, Altamaha River, St. Andrew/St. Simons Sounds, St. Johns River, and Indian River being utilized in abundances greater than rare. Based on their \geq moderate inlet utilizations, 17 inlets from the mouth of Chesapeake Bay to Sebastian Inlet (Figure 5) appear to be important to black drum.

Figure 6. Relative screening index to assess importance of individual inlets to blue crab



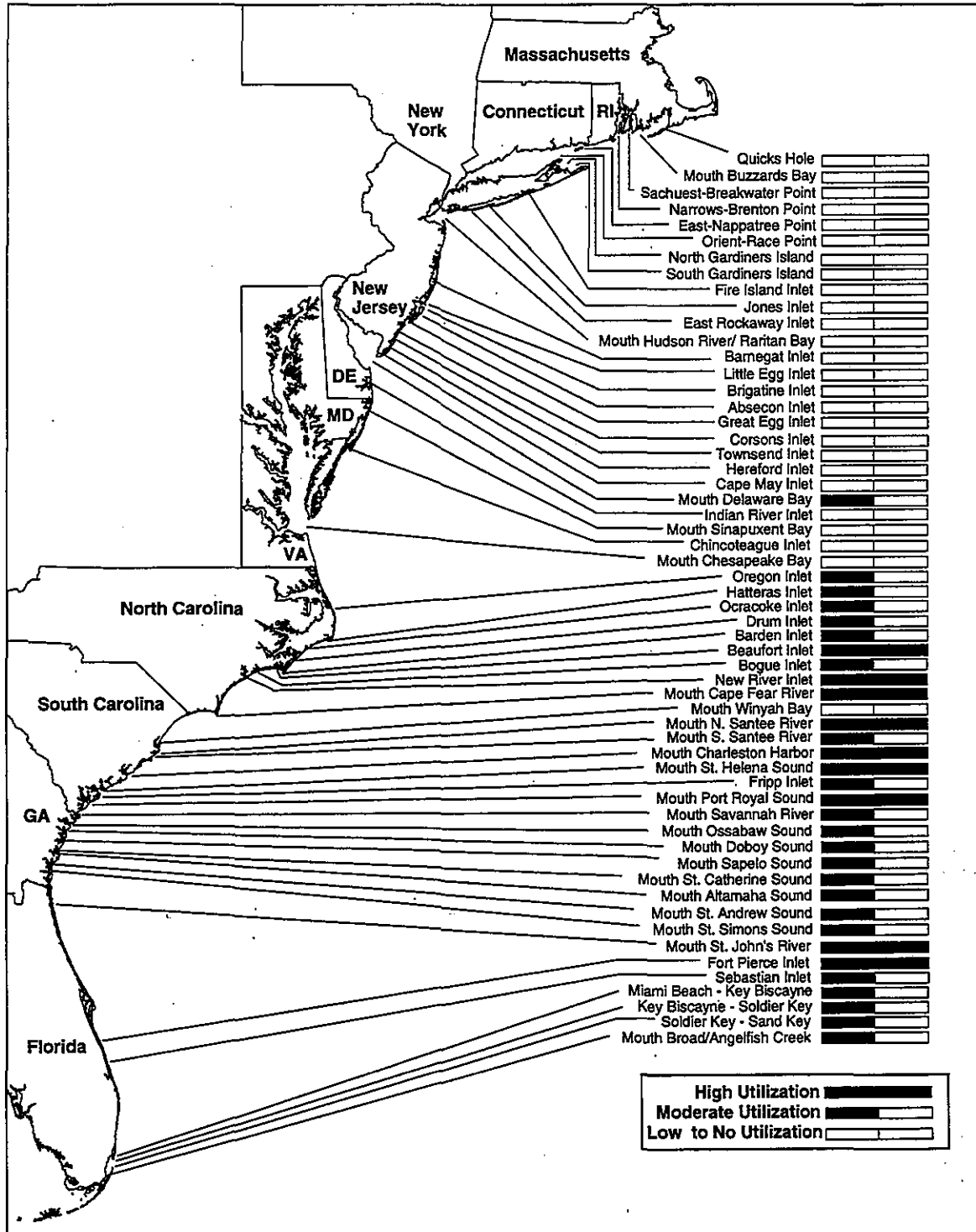
Blue crab utilize 93.1% of the estuaries in larval abundances \geq common (Table 3). Albemarle/Pamlico Sound and Long Island Sound were utilized the least (i.e., abundances below common). Based on their \geq moderate inlet utilizations, 50 inlets from Quicks Hole to the mouth of Broad/Angelfish Creek (Figure 6) appear to be important to blue crab.

Figure 7. Relative screening index to assess importance of individual inlets to brown shrimp



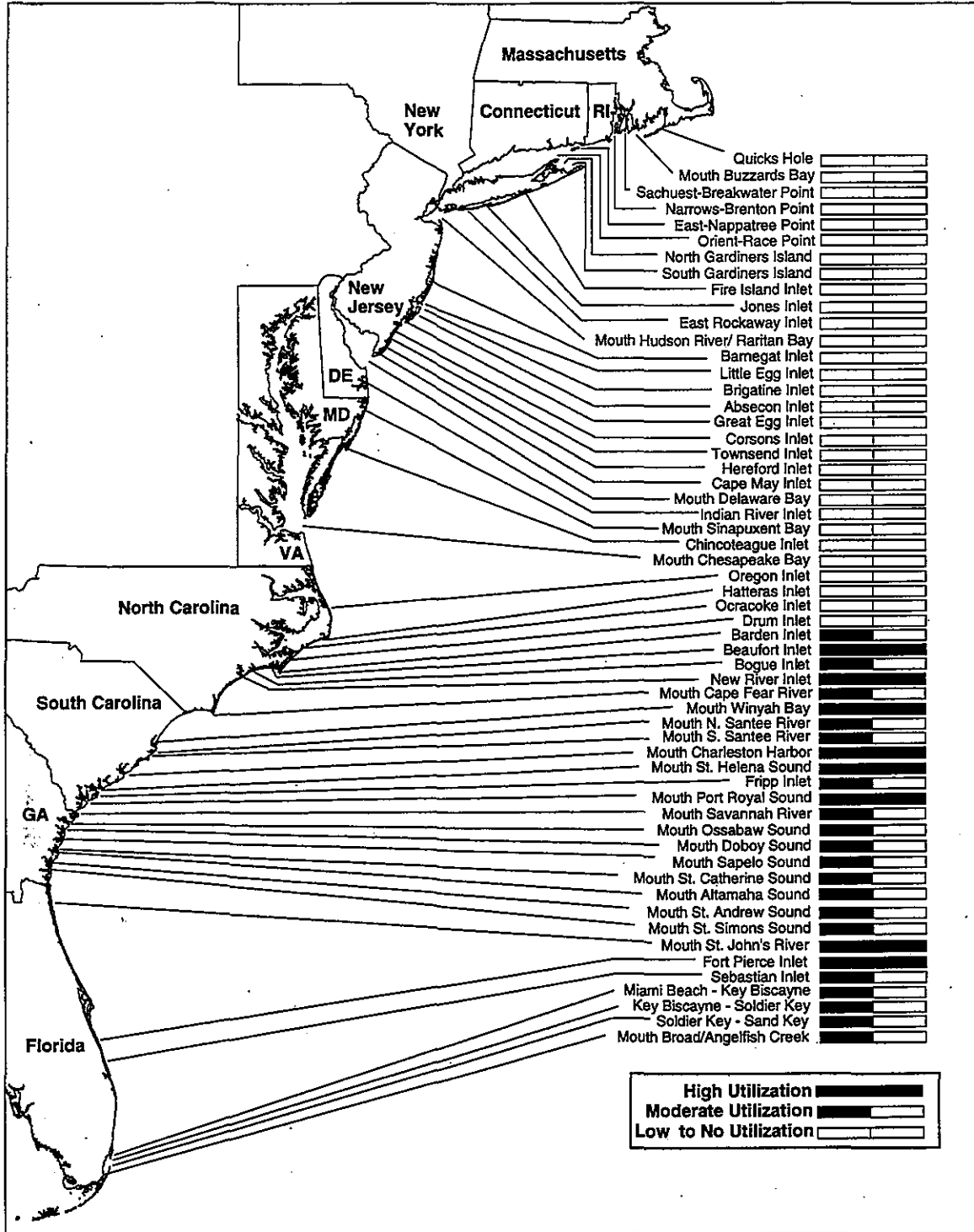
Brown shrimp utilize 34.5% of the estuaries in larval abundances \geq common (Table 3). Bogue Sound, New River, Cape Fear River, Winyah Bay, North and South Santee Rivers, Charleston Harbor, St. Helena Sound, Broad River, St. Johns River, and Indian River were utilized the most (i.e., abundances \geq common). Based on their inlet \geq moderate utilizations, 15 inlets from Barden Inlet to Sebastian Inlet (Figure 7) appear to be important to brown shrimp.

Figure 8. Relative screening index to assess importance of individual inlets to mullet



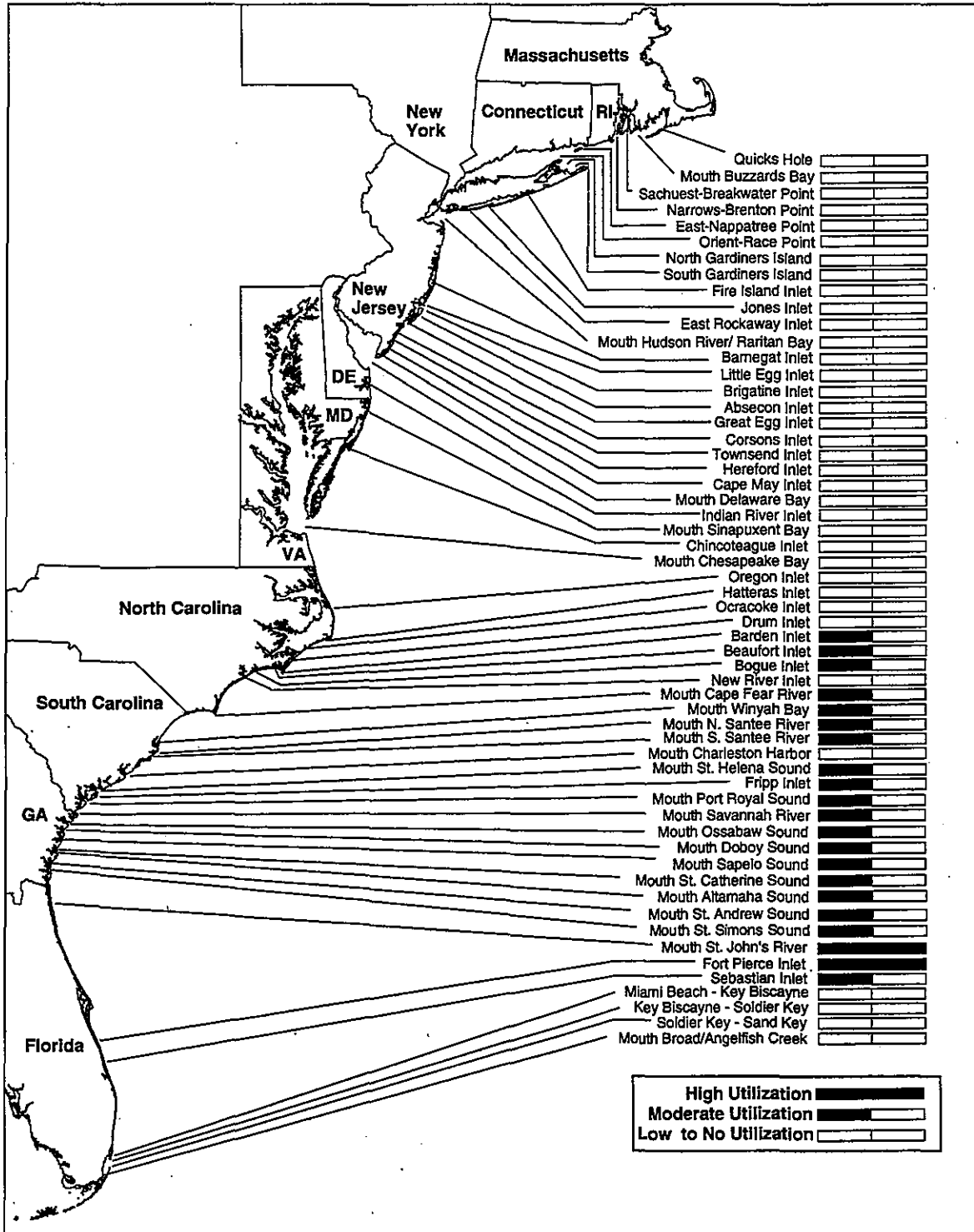
Mullet utilize 55.2% of the estuaries in larval abundances \geq common (Table 3). Delaware Bay, Albemarle/Pamlico-Sound, Bogue Sound, New River, Cape Fear River, North and South Santee Rivers, Charleston Harbor, St. Helena Sound, Broad River, Savannah Sound, Ossabaw Sound, St. Catherines Sound, Altamaha River, St. Andrew/St. Simons Sounds, and St. Johns River were utilized the most (i.e., abundances \geq common). Based on their \geq moderate inlet utilizations, 31 inlets from the mouth of Delaware Bay to the mouth of Broad/Angelfish Creek (Figure 8) appear to be important to mullet.

Figure 9. Relative screening index to assess importance of individual inlets to pinfish



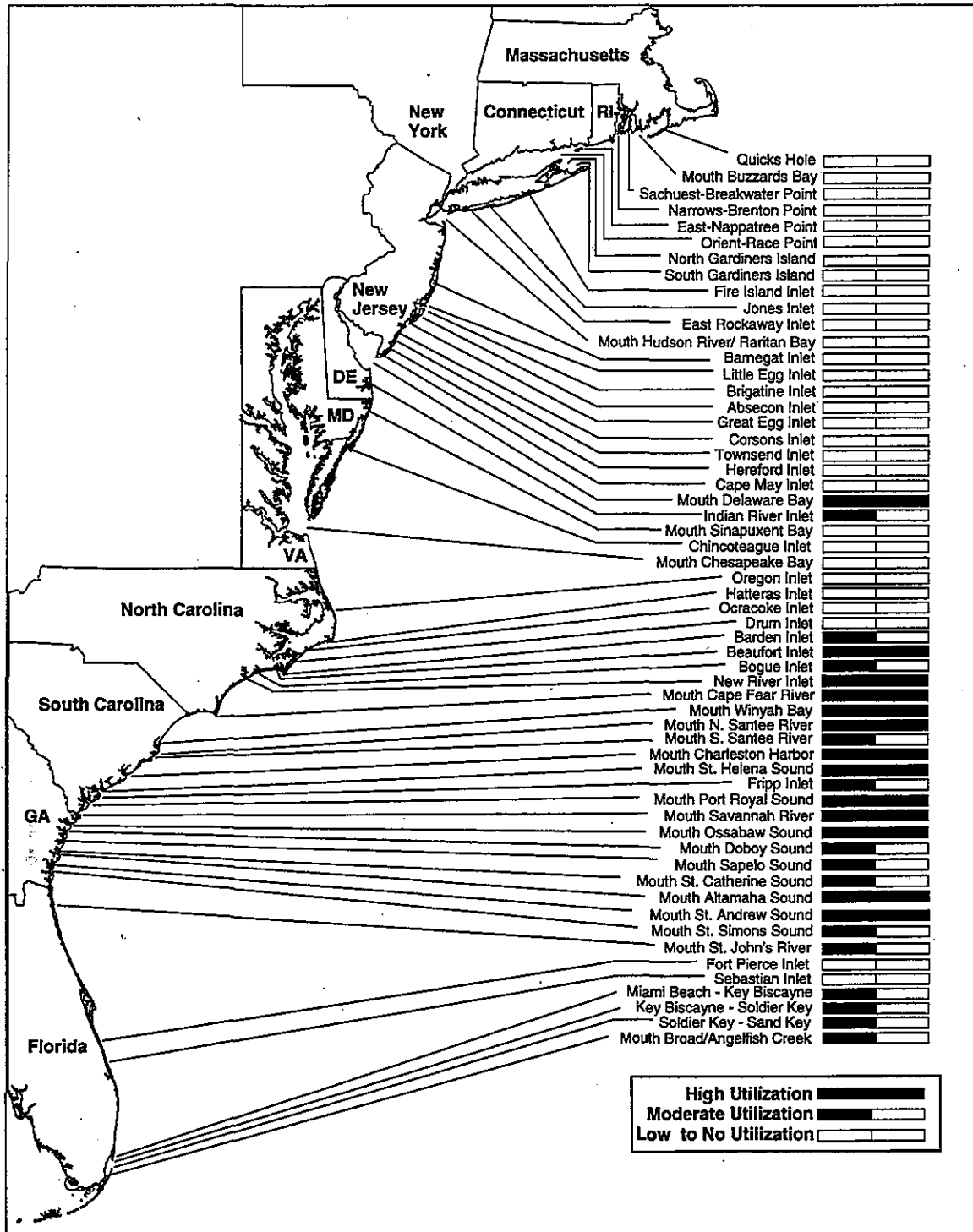
Pinfish utilize 55.2% of the estuaries in larval abundances \geq common (Table 3). Bogue Sound, New River, Cape Fear River, Winyah Bay, North and South Santee Rivers, Charleston Harbor, St. Helena Sound, Broad River, Savannah Sound, Ossabaw Sound, St. Catherines Sound, Altamaha River, St. Andrew/St. Simons Sounds, St. Johns River, Indian River, and Biscayne Bay were utilized the most (i.e., abundances \geq common). Based on their \geq moderate inlet utilizations, 27 inlets from Barden Inlet to the mouth of Broad/Angelfish Creek (Figure 9) appear to be important to pinfish.

Figure 10. Relative screening index to assess importance of individual inlets to red drum



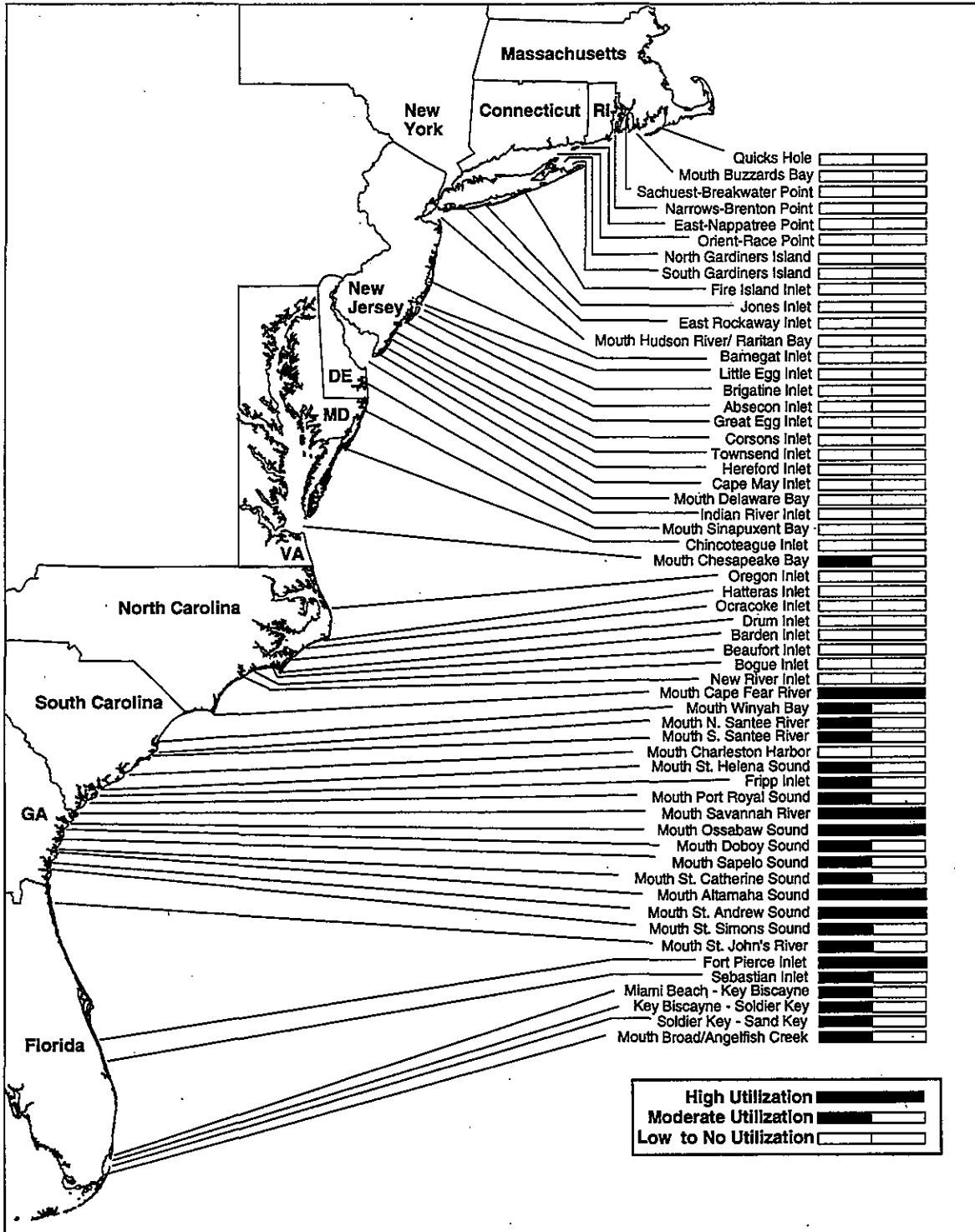
Red drum utilize 44.8% of the estuaries in larval abundances \geq common (Table 3). Bogue Sound, Cape Fear River, Winyah Bay, North and South Santee Rivers, St. Helena Sound, Broad River, Savannah Sound, Ossabaw Sound, St. Catherines Sound, Altamaha River, St. Andrew/St. Simons Sounds, St. Johns River, and Indian River were utilized the most (i.e., abundances \geq common). Based on their \geq moderate inlet utilizations, 21 inlets from Barden Inlet to Sebastian Inlet (Figure 10) appear to be important to red drum.

Figure 11. Relative screening index to assess importance of individual inlets to spot



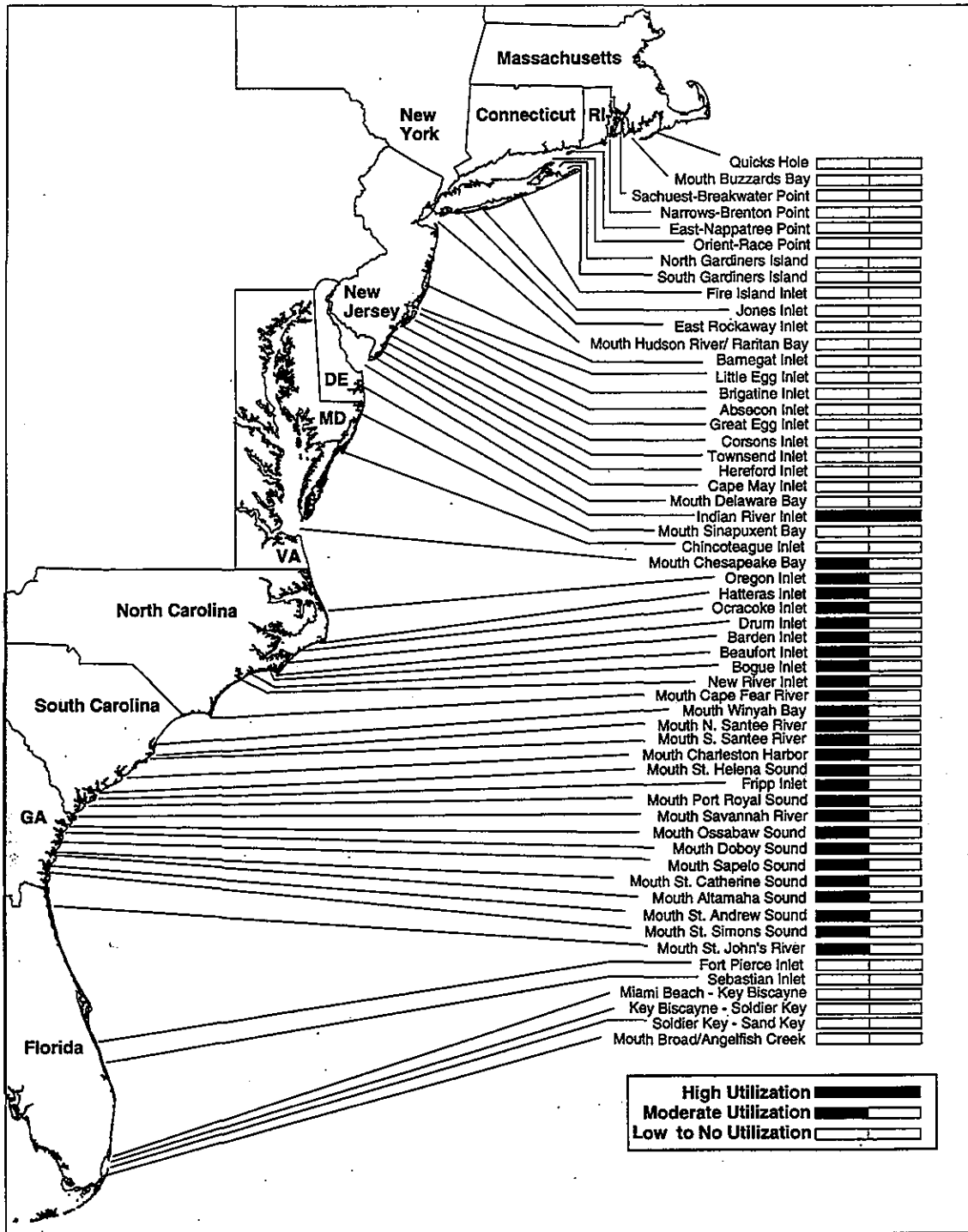
Spot utilize 58.6% of the estuaries in larval abundances \geq common (Table 3). Delaware Bay, Delaware Inland Bays, Bogue Sound, New River, Cape Fear River, Winyah Bay, North and South Santee Rivers, Charleston Harbor, St. Helena Sound, Broad River, Savannah Sound, Ossabaw Sound, St. Catherine Sound, Altamaha River, St. Andrew/St. Simons Sounds, St. Johns River, and Biscayne Bay were utilized the most (i.e., abundances \geq common). Based on their \geq moderate inlet utilizations, 27 inlets from the mouth of Delaware Bay to the mouth of Broad/Angelfish Creek (Figure 11) appear to be important to spot.

Figure 12. Relative screening index to assess importance of individual inlets to spotted seatrout



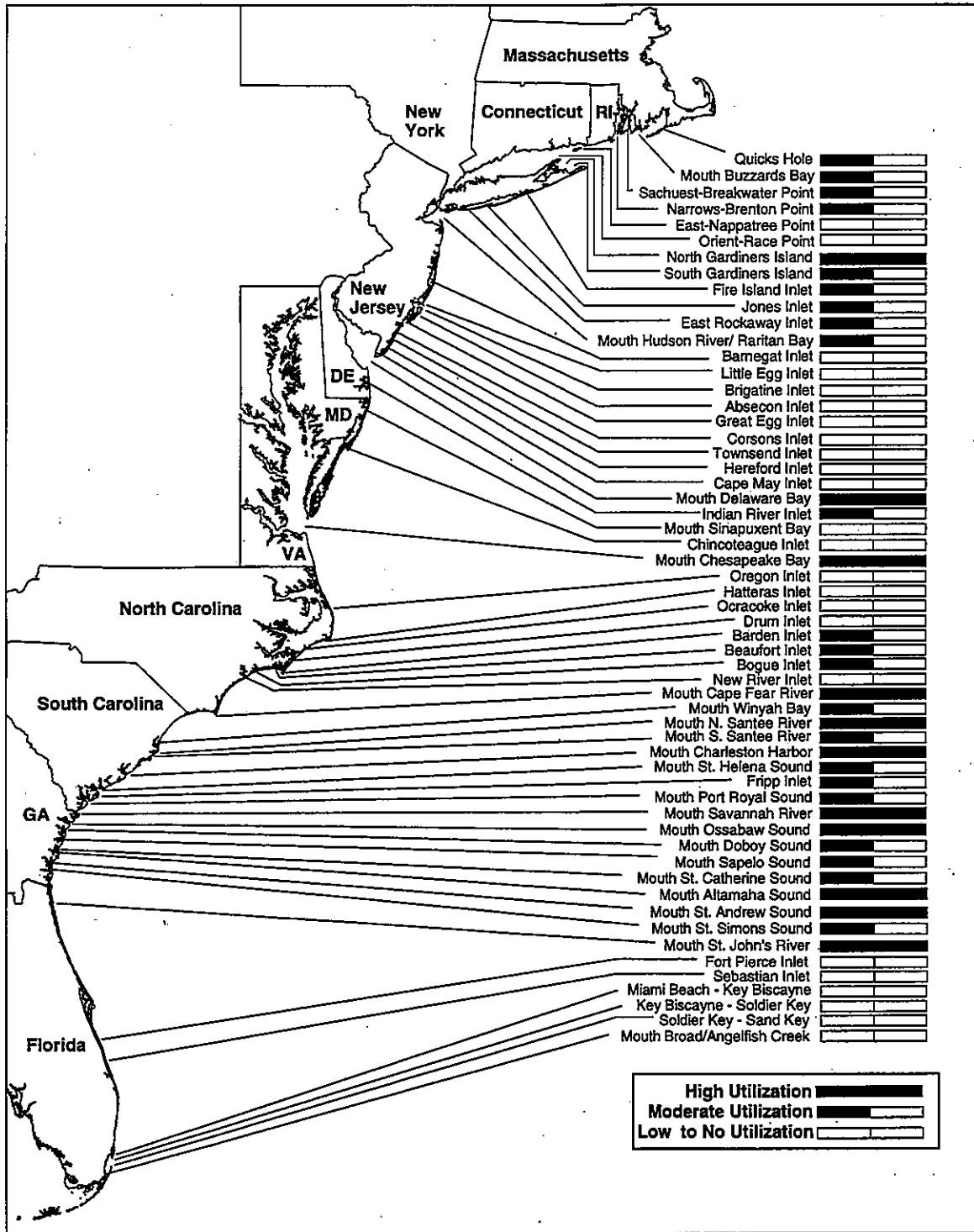
Spotted seatrout utilize 48.3% of the estuaries in larval abundances \geq common (Table 3). Chesapeake Bay, Cape Fear River, Winyah Bay, North and South Santee Rivers, St. Helena Sound, Broad River, Savannah Sound; Ossabaw Sound, St. Catherines Sound, Altamaha River, St. Andrew/St. Simons Sounds, St. Johns River, Indian River, and Biscayne Bay were utilized the most (i.e., abundances \geq common). Based on their \geq moderate inlet utilizations, 22 inlets from the mouth of Chesapeake Bay to the mouth of Broad/Angelfish Creek (Figure 12) appear to be important to spotted seatrout.

Figure 13. Relative screening index to assess importance of individual inlets to summer flounder



Summer flounder utilize 58.6% of the estuaries in larval abundances \geq common (Table 3). Delaware Inland Bays, Chesapeake Bay, Albemarle/Pamlico Sound, Bogue Sound, New River, Cape Fear River, Winyah Bay, North and South Santee Rivers, Charleston Harbor, St. Helena Sound, Broad River, Savannah Sound, Ossabaw Sound, St. Catherine's Sound, Altamaha River, St. Andrew/St. Simons Sounds, and St. Johns River were utilized the most (i.e., abundances \geq common). Based on their \geq moderate inlet utilizations, 27 inlets from Indian River Inlet to the mouth of St. John's River (Figure 13) appear to be important to summer flounder.

Figure 14. Relative screening index to assess importance of individual inlets to weakfish



Weakfish utilize 72.4% of the estuaries in larval abundances \geq common (Table 3). Long Island Sound, Barnegat Bay, New Jersey Inland Bays, Chincoteague Bay, New River, Indian River, and Biscayne Bay were utilized the least (i.e., abundances \leq common). Based on their \geq moderate inlet utilizations, 33 inlets from Quick Hole to the mouth of St. John's River (Figure 14) appear to be important to weakfish.

Discussion

The ordered stepwise logistic regressions (Table 4) reveal that estuarine/inlet variables can be used to model estuarine-catadromous larval abundance rankings for the 12 species investigated here. Estuarine hydrodynamic characteristics and inlet geomorphology appear to explain much of the variance in larval abundance of these estuarine-catadromous larvae. With further refinements, the relationships driving these models may be understood and used to improve the theoretical inlet utilizations. Other inter-annual, regional and sub-regional factors affecting variance include offshore-to-nearshore oceanography, predation, larval survivorship, spawning stocks, and year class strengths, with additional related variables (Bailey and Houde 1989, Govoni and Pietrafesa 1994, Pietrafesa and Janowitz 1988, Sinclair 1987, Houde 1989, Miller et al. 1984, Norcross and Shaw 1984, Yoder 1983).

The regressions often identified variables (e.g., freshwater fraction, tidal prism flushing) that would impact tidal plume characteristics at the inlets. Since some estuarine-catadromous species apparently respond to inlet plumes (Benfield and Aldrich 1992, Boehlert and Mundy 1988, Epifanio et al. 1989, McCleave and Wippelhauser 1987, Pietrafesa and Janowitz 1988, Rogers et al. 1993), the development of plume characterizations and their inclusion in a similar set of analyses may improve these models' explanatory power.

In addition to improving the independent variables, the dependent variables (i.e., larval relative abundance estimates) may be improved. These relative abundance estimates are surrogates for density estimates. Obviously, if density estimates were ever developed for these species and estuaries, they should be used to re-run these analyses to see if any significant improvement occurs. Unfortunately, the present lack of coordination of fisheries sampling programs in the U.S. and the resulting disparate nature of the data prohibits the development of usable density estimates for more than a handful of estuaries at a time. Therefore, the larval relative abundance rankings developed by the ELMR program are the best available data to conduct these types of analyses. There is no effort under way to coordinate sampling programs to produce comparable inter-estuarine density estimates. The relative abundance estimates are the only data capable of supporting these types of analyses; thus, improvement to the dependent variables of these regression models is unlikely in the near future.

The investigation of the estuarine perspectives and

species perspectives of larval utilizations of U.S. East Coast estuaries and inlets is of paramount importance in identifying estuaries and inlets which support these estuarine-catadromous species. This information provides the cornerstone for understanding estuarine-to-marine coupling with respect to estuarine-catadromous species. These inlets have, and continue to be modified for navigational and stabilization purposes, without knowing how these modifications impact the estuarine-catadromous stocks which depend on these inlets. The results of this report reveal that for the majority of these species, the southeastern estuaries from Bogue Sound, NC to Biscayne Bay, FL are more heavily utilized (i.e., used by more species) than the estuaries from Albemarle/Pamlico Sounds, NC to Buzzards Bay, MA. Like the patterns of inlet utilization, the regional harvest indicates that these species are more highly associated with the southeastern region. Interestingly, these estuarine-catadromous species accounted for 81% of the South Atlantic region's shellfish landings; 63% of the South Atlantic Region's finfish landings; 54% of the Chesapeake region's shellfish landings; and 45% of the Mid-Atlantic region's finfish landings (NMFS Regional Commercial Fisheries Statistics 1989). These estuary and inlet utilization patterns' linkage to regional harvest underscores the importance of maintaining estuarine-catadromous species access to these estuarine habitats via the inlets.

Therefore, inlet modifications should be viewed as having the potential to diminish estuarine-catadromous access to the critically important estuarine habitats that support stocks, and subsequently the commercial and recreational fisheries that rely on them. As a result, the relative screening indexes presented in this report should be consulted in order to assess the potential impact of inlet modifications to these species from Cape Cod, MA to Biscayne Bay, FL.

Improvement of these inlet utilization estimates may be possible by conducting extensive field samplings of the inlets using comparable methods or pursuing the modelling effort initiated here. Because this type of sampling program is unlikely to be initiated, however, the use of inlet flood tidal flux volume to estimate the proportion of an inlet's contribution to larval recruitment into estuaries with multiple inlets is the most plausible means of assessing an inlet's contribution to recruitment. Short of extensive field surveys and advances in the models, the use of the volumetrically-based proportionality presented in this report is the best possible estimator, and will likely remain so for the near future.

Conclusions

This report was undertaken to develop a better understanding of 12 estuarine-catadromous species' larval utilization of estuaries along the U.S. East Coast from Buzzard Bay, MA to Biscayne Bay, FL. These species' larval abundance rankings were modelled (i.e., ordered stepwise logistic regression) using estuarine/inlet variables with a great deal of success (i.e., 82.6% average concordance). The models suggest that additional estuarine/inlet independent variables, such as tidal plume characterizations, may improve the models and identify additional relationships. This investigation of larval utilization of estuaries and inlets indicates a regional difference in the utilization of south-

eastern estuaries vs. mid-Atlantic estuaries, and provides a screening tool to identify estuaries and inlets of importance to estuarine-catadromous stocks of the U.S. East Coast. Additional refinements and analysis may be initiated, if additional estuarine and inlet variables (e.g., tidal plume characteristics) become available. With further improvement and an understanding of the relationships driving the models, improvements in the theoretical inlet utilization estimates are likely.

References

- Bailey, K.M., and E.D. Houde. 1989. Predation on eggs and larvae of marine fishes and the recruitment problem. *Advances in Marine Biology* 25:1-83.
- Benfield, M.C., and D.V. Aldrich. 1992. Attraction of postlarval *Penaeus aztecus* Ives and *P. setiferus* (L.) (Crustacea: Decapoda: Penaeidae) to estuarine water in a laminar-flow choice chamber. *Journal of Experimental Marine Biology and Ecology* 156:39-52.
- Boehlert, G.W., and B.C. Mundy. 1988. Roles of behavioral and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. *American Fisheries Society Symposium* 3:51-67.
- Bulger, A.J., T.A. Lowery, and M.E. Monaco. 1995. Characterizing the estuarine-catadromous life history strategy. In: Bulger, A.J., T.A. Lowery, and M.E. Monaco. *Estuarine-catadromy: a life history strategy coupling marine and estuarine environments via coastal inlets*, Chapter 1. ELMR Rep. No.14. NOAA/NOS Strategic Environmental Assessments Division, Silver Spring, MD, pp. 1-44.
- Epifanio, C.E., A.K. Masse, and R.W. Garvine. 1989. Transport of blue crab larvae by surface currents off Delaware Bay, USA. *Marine Ecology Progress Series* 54:35-41.
- Freeman, D.H. 1987. *Applied categorical data analysis*. Marcel Dekker, Inc., New York, NY, 318 p.
- Gabriel, W.L. 1992. Persistence of demersal fish assemblages between Cape Hatteras and Nova Scotia, Northwest Atlantic. *Journal of Northwestern Atlantic Fisheries Science* 14:29-46.
- Govoni, J.J., and L.J. Pietrafesa. 1994. Eulerian views of layered water currents, vertical distribution of some larval fishes, and inferred advective transport over the continental shelf off North Carolina, USA, in winter. *Fisheries Oceanography* 3(2):120-132.
- Hosmer, D.W., and S. Lemeshow. 1989. *Applied logistic regression*. John Wiley and Sons, New York, NY, 307 p.
- Houde, E.D. 1989. Subtleties and episodes in the early life of fishes. *Journal of Fish Biology* 35(suppl. A):29-38.
- Hume, T.M., and C.E. Herdendorf. 1993. On the use of empirical stability relationships for characterising estuaries. *Journal of Coastal Research* 9(2):413-422.
- Lowery, T.A., M.E. Monaco, S.P. Orlando, and M. Harris. 1994. *Assemblages of U.S. East Coast Inlets Based on Physical and Hydrodynamic Characteristics*. ELMR Tech Rep. No.1. NOAA/NOS Strategic Environmental Assessments Division, Silver Spring, MD, 15 p.
- Lowery, T.A., M.E. Monaco, M. Harris, C.J. Klein, and S.P. Orlando. 1994a. *Assemblages of U.S. East Coast Inlets Based on Physical and Hydrodynamic Characteristics*. ELMR Tech Rep. No. 2. NOAA/NOS Strategic Environmental Assessments Division, Silver Spring, MD, 12 p.
- McCleave, J.D., and G.S. Wippelhauser. 1987. Behavioral aspects of selective tidal stream transport in juvenile American eels. *American Fisheries Society Symposium* 1:138-150.

- Miller, J.M., J.P. Reed, and L.J. Pietrafesa. 1984. Patterns, mechanisms and approaches to the study of estuarine dependent fish larvae and juveniles. *In: Mechanisms of migration in fishes.* McCleave J.D., G.P. Arnold, J.J. Dodson, and W.H. Neill (eds.), New York, NY, Plenum Press, pp. 209-255.
- Monaco, M.E., T.A. Lowery, and R.L. Emmett. 1992. Assemblages of U.S. west coast estuaries based on the distribution of fishes. *Journal of Biogeography* 19: 251-267.
- Monaco, M.E., and T.A. Lowery. 1994. Biogeographic estuary assemblages: the coupling of physical and biological characteristics. ELMR Rep. No. 8. NOAA/NOS Strategic Environmental Assessments Division. Silver Spring, MD, in prep.
- NMFS (National Marine Fisheries Service). 1989. Regional Commercial Fisheries Statistics for 1988. Fisheries Statistics Division, Silver Spring, MD.
- National Oceanic and Atmospheric Administration (NOAA). 1973. Surface Water Temperature and Density: Atlantic Coast, North and South America. National Ocean Survey, Rockville, MD. 109p.
- National Oceanic and Atmospheric Administration (NOAA). 1985. National Estuarine Inventory data atlas, Vol. 1: physical and hydrologic characteristics. NOAA/NOS Strategic Assessment Branch, Rockville, MD, 177 p.
- Nelson, D.M., E.A. Irlandi, L.R. Settle, M.E. Monaco, and L.C. Coston-Clements. 1991. Distribution and abundance of fishes and invertebrates in Southeast estuaries. NOAA/NOS Strategic Assessment Branch, Rockville, MD, 177 p.
- Nelson, D.M., M.E. Monaco, C.D. Williams, T.E. Czapla, M.E. Patillo, L. Coston-Clements, L.R. Settle, and E.A. Irlandi. 1992. Distribution and abundance of fishes and invertebrate in Gulf of Mexico estuaries, Vol. 1: Data Summaries. NOAA/NOS Strategic Environmental Assessments Division, Rockville, MD, 273 p.
- Norcross, B.L., and R.F. Shaw. 1984. Oceanic and estuarine transport of fish eggs and larvae: a review. *Transactions of the American Fisheries Society* 113: 153-165.
- Overholtz, W.J., and A.V. Tyler. 1985. Long-term responses of demersal fish assemblages of Georges Bank. *Fishery Bulletin* 83(4):507-520.
- Pietrafesa, L.J., and G.S. Janowitz. 1988. Physical oceanographic processes affecting larval transport around and through North Carolina inlets. *American Fisheries Society Symposium* 3:34-50.
- Rogers, B., R.F. Shaw, W.H. Herke, and R.H. Blanchet. 1993. Recruitment of postlarval and juvenile brown shrimp (*Penaeus aztecus* Ives) from offshore to estuarine waters of the northwestern Gulf of Mexico. *Estuarine, Coastal and Shelf Science* 36:377-394.
- SAS. 1989. SAS/STAT users guide, version 6, Fourth edition, Vol. 2. SAS Institute Inc., Cary, NC, pp. 1071-1126.
- Sinclair, M. 1987. Marine populations: an essay on population regulation and speciation. University of Washington Press, Seattle, WA, 252 pp.
- Stone, S.L., T.A. Lowery, J.D. Field, S.H. Jury, D.M. Nelson, M.E. Monaco, C.D. Williams, and L. Andreasen. 1993. Distribution and abundance of fishes and invertebrates in Mid-Atlantic estuaries. NOAA/NOS Strategic Environmental Assessments Division, Silver Spring, MD, 280 p.
- Vincent, C.L., and W.D. Corson. 1980. The geometry of selected U.S. tidal inlets. U.S. Army Corps of Engineers, Coastal Engineering Research Center, Fort Belvoir, VA, and Waterways Experiment Station, Vicksburg, MS, 163 p.
- Yoder, J.A. 1983. Statistical analysis of the distribution of fish eggs and larvae on the southeastern U.S. continental shelf with comments on oceanographic processes that may affect larval survival. *Estuarine, Coastal and Shelf Science* 17:637-650.

Appendix 1. Estuarine variables.

Estuaries	tprsm	fwfrc	dcptl	tpflush	iwidth	iavdep	icrsec	ifcurr	iecurr
	m3	%	mg/l	tidal/cycles	m	m	m2	cms	cms
Buzzards Bay	6.80E+08	0.1230	1.041	8.95802688	11713	14.4	169192.1	0.34	0.30
Narragansett Bay	4.93E+08	0.1636	0.519	7.995653297	10900	18.1	197444.5	0.21	0.28
Gardiners Bay	3.26E+08	0.1222	1.773	9.65341081	19605	13.9	271643.0	0.36	0.50
Long Island Sound	3.74E+09	0.1595	0.054	16.539622	22357	27.9	624314.6	1.66	1.57
Great South Bay	7.48E+07	0.3423	4.967	14.128224	1829	4.2	7700.0	1.28	1.24
Hudson River/Raritan Bay	7.36E+07	0.5087	0.194	66.33879729	9135	8.4	76732.8	0.82	0.88
Barnegat Bay	8.55E+07	0.3030	1.338	4.425465219	347	4.0	1389.9	1.13	1.29
New Jersey Inland Bays	7.97E+07	0.2185	3.171	3.477553776	7949	4.9	38951.6	1.35	1.54
Delaware Bay	2.89E+09	0.2602	0.134	4.387759511	18197	12.6	229276.7	0.72	0.67
Delaware Inland Bays	1.80E+07	0.2099	6.273	5.841944	152	4.5	685.8	0.93	1.10
Chinoteague Bay	4.67E+07	0.1212	3.078	13.6570368	4942	3.4	16852.8	0.83	0.88
Chesapeake Bay	8.69E+08	0.5968	0.071	69.65566457	17730	7.8	137806.3	0.41	0.62
Albemarle/Pamlico Sound	8.21E+08	0.6234	0.138	33.87793103	5122	2.6	13199.6	0.99	0.92
Bogue Sound	1.35E+08	0.1867	1.459	2.734182828	3386	5.4	18245.1	0.67	0.85
New River	1.72E+07	0.5903	7.496	8.505429754	1006	2.0	2007.4	0.51	1.13
Cape Fear River	1.00E+08	0.5964	0.600	3.433610847	2114	1.6	3286.3	1.10	1.50
Winyah Bay	8.61E+07	0.7663	0.382	3.031776	1975	5.0	9821.8	0.98	1.00
North and South Santee Rivers	2.51E+07	0.7679	2.889	2.360496614	1134	2.9	3281.8	0.77	0.89
Charleston Harbor	1.35E+08	0.6852	0.432	3.953823396	914	7.8	7135.0	0.93	0.93
St. Helena Sound	3.94E+08	0.4200	0.928	2.20339642	13730	4.7	65144.3	0.75	0.78
Broad River	5.41E+08	0.4268	4.818	3.501293504	4206	10.5	44163.0	0.93	0.93
Savannah Sound	1.75E+08	0.5351	0.425	2.260897706	9400	5.9	55870.0	0.93	1.60
Ossabaw Sound	1.76E+08	0.5749	1.947	2.117591188	5395	4.8	25817.0	0.82	1.18
St. Catherines/Sapelo Sound	4.16E+08	0.5814	7.382	2.057122482	8733	6.8	59352.0	0.89	0.99
Altamaha River	6.68E+07	0.5299	0.361	1.810914712	3667	2.3	8493.9	0.57	0.62
St. Andrew/Simon Sound	3.88E+08	0.5831	2.369	2.090269524	6309	7.5	47177.0	1.29	1.13
St. Johns River	5.32E+07	0.6336	0.825	45.85848511	471	13.9	6530.9	0.97	1.19
Indian River	6.46E+07	0.1400	1.016	22.56927663	386	4.7	1832.6	1.51	1.85
Biscayne Bay	3.00E+08	0.1262	0.401	5.450490204	22935	2.3	52807.7	0.26	0.27

Appendix 2. Example of SAS ordered stepwise logistic regression program.

```
LIBNAME ELMO v604 'a:\123LOGI&';OPTIONS PAGESIZE=54 LINESIZE=80;
proc logistic data=elmo.menhaden order=formatted;
model menhaden=TPRSM FWFRC DCPTL TPFLUSH IWIDTH IAVDEP ICRSEC IFCURR IECURR
/ SELECTION=STEPWISE SLENTRY=.15 SLSTAY=.15 MAXITER=50 DETAILS;
RUN;
```

Appendix 3. Ordered stepwise logistic regression of ATLANTIC CROAKER larval abundance (i.e., dependent variable) vs. inlet/estuary variables (i.e., independent variables) for 29 estuaries (Buzzards Bay to Biscayne Bay).

Data Set: ELMO.ALLAR1
 Response Variable: CROAKER
 Response Levels: 2
 Number of Observations: 29
 Link Function: Logit

Response Profile

Ordered Value	CROAKER	Count
1	1	15
2	3	14

Stepwise Selection Procedure

Step 0. Intercept entered:

Analysis of Maximum Likelihood Estimates

Variable	DF	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square	Standardized Estimate	Odds Ratio
INTERCPT	1	0.0690	0.3716	0.0345	0.8527		

Residual Chi-Square = 22.0248 with 9 DF (p=0.0088)

Analysis of Variables Not in the Model

Variable	Score Chi-Square	Pr > Chi-Square
TPRSM	2.8049	0.0940
FWFRC	13.5607	0.0002
DCPTL	0.7421	0.3890
TPFLUSH	3.7753	0.0520
IWIDTH	5.0341	0.0249
IAVDEP	2.1601	0.1416
ICRSEC	4.2811	0.0385
IFCURR	0.0075	0.9311
IECURR	0.7153	0.3977

Appendix 3.-continued

Step 1. Variable FWFRC entered:

Testing Global Null Hypothesis: BETA=0

Criterion	Intercept Only	Intercept and Covariates	Chi-Square for Covariates
AIC	42.168	28.347	.
SC	43.535	31.081	.
-2 LOG L Score	40.168	24.347	15.821 with 1 DF (p=0.0001)
			13.561 with 1 DF (p=0.0002)

Analysis of Maximum Likelihood Estimates

Variable	DF	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square	Standardized Estimate	Odds Ratio
INTERCPT	1	3.8425	1.3868	7.6770	0.0056	.	.
FWFRC	1	-8.9493	2.9306	9.3251	0.0023	-1.081634	0.000

Association of Predicted Probabilities and Observed Responses

Concordant = 86.7%	Somers' D = 0.738
Discordant = 12.9%	Gamma = 0.742
Tied = 0.5%	Tau-a = 0.382
(210 pairs)	c = 0.869

Residual Chi-Square = 14.2442 with 8 DF (p=0.0756)

Analysis of Variables Not in the Model

Variable	Score Chi-Square	Pr > Chi-Square
TPRSM	1.2748	0.2589
DCPTL	1.1168	0.2906
TPFLUSH	10.7805	0.0010
IWIDTH	1.7819	0.1819
IAVDEP	0.1644	0.6851
ICRSEC	1.2257	0.2683
IFCURR	0.0218	0.8827
IECURR	0.2442	0.6212

Appendix 3.-continued

Step 2. Variable TPFLUSH entered:

Testing Global Null Hypothesis: BETA=0

Criterion	Intercept Only	Intercept and Covariates	Chi-Square for Covariates
AIC	42.168	18.815	.
SC	43.535	22.917	.
-2 LOG L	40.168	12.815	27.353 with 2 DF (p=0.0001)
Score	.	.	19.812 with 2 DF (p=0.0001)

Analysis of Maximum Likelihood Estimates

Variable	DF	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square	Standardized Estimate	Odds Ratio
INTERCPT	1	4.7756	1.9887	5.7668	0.0163	.	.
FWFRC	1	-16.1966	6.2131	6.7957	0.0091	-1.957570	0.000
TPFLUSH	1	0.1328	0.0655	4.1099	0.0426	1.340417	1.142

Association of Predicted Probabilities and Observed Responses

Concordant = 96.7%	Somers' D = 0.933
Discordant = 3.3%	Gamma = 0.933
Tied = 0.0%	Tau-a = 0.483
(210 pairs)	c = 0.967

Residual Chi-Square = 6.1386 with 7 DF (p=0.5237)

Analysis of Variables Not in the Model

Variable	Score Chi-Square	Pr > Chi-Square
TPRSM	0.9175	0.3381
DCPTL	0.0002	0.9888
IWIDTH	0.4138	0.5200
IADVEP	1.0485	0.3058
ICRSEC	0.2916	0.5892
IFCURR	1.1494	0.2837
IECURR	0.0582	0.8093

NOTE: No (additional) variables met the 0.15 significance level for entry into the model.

Summary of Stepwise Procedure

Step	Variable Entered	Variable Removed	Number In	Score Chi-Square	Wald Chi-Square	Pr > Chi-Square
1	FWFRC		1	13.5607	.	0.0002
2	TPFLUSH		2	10.7805	.	0.0010

Appendix 4. Ordered stepwise logistic regression of SUMMMER FLOUNDER larval abundance (i.e., dependent variable) vs. inlet/estuary variables (i.e., independent variables) for 29 estuaries (Buzzards Bay to Biscayne Bay).

Data Set: ELMO.ALLAR1
 Response Variable: SUMFLOUN
 Response Levels: 3
 Number of Observations: 29
 Link Function: Logit

Response Profile

Ordered Value	SUMFLOUN	Count
1	1	12
2	2	16
3	3	1

Stepwise Selection Procedure

Step 0. Intercepts entered:

Analysis of Maximum Likelihood Estimates

Variable	DF	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square	Standardized Estimate	Odds Ratio
INTERCP1	1	-0.3483	0.3770	0.8534	0.3556		
INTERCP2	1	3.3322	1.0177	10.7207	0.0011		

Residual Chi-Square = 16.6529 with 9 DF (p=0.0544)

Analysis of Variables Not in the Model

Variable	Score Chi-Square	Pr > Chi-Square
TPRSM	2.4778	0.1155
FWFRC	13.3663	0.0003
DCPTL	1.8464	0.1742
TPFLUSH	0.2969	0.5858
IWIDTH	5.4833	0.0192
IADVDP	3.9026	0.0482
ICRSEC	5.3949	0.0202
IFCURR	0.0148	0.9032
IECURR	0.3411	0.5592

Appendix 4.-continued

Step 1. Variable FWFRC entered:

Score Test for the Proportional Odds Assumption

Chi-Square = 20.6440 with 1 DF (p=0.0001)

Testing Global Null Hypothesis: BETA=0

Criterion	Intercept	Intercept	Chi-Square for Covariates
	Only	and Covariates	
AIC	50.943	37.442	
SC	53.677	41.544	
-2 LOG L	46.943	31.442	15.501 with 1 DF (p=0.0001)
Score			13.366 with 1 DF (p=0.0003)

Analysis of Maximum Likelihood Estimates

Variable	DF	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square	Standardized Estimate	Odds Ratio
INTERCP1	1	3.0367	1.1198	7.3548	0.0067		
INTERCP2	1	8.0672	1.9822	16.5640	0.0001		
FWFRC	1	-8.4574	2.6603	10.1066	0.0015	-1.022191	0.000

Association of Predicted Probabilities and Observed Responses

Concordant = 87.7%	Somers' D = 0.755
Discordant = 12.3%	Gamma = 0.755
Tied = 0.0%	Tau-a = 0.409
(220 pairs)	c = 0.877

Residual Chi-Square = 4.6529 with 8 DF (p=0.7939)

Analysis of Variables Not in the Model

Variable	Score Chi-Square	Pr > Chi-Square
TPRSM	0.4812	0.4879
DCPTL	1.6982	0.1925
TPFLUSH	2.0892	0.1483
IWIDTH	1.0194	0.3127
IAVDEP	0.8095	0.3683
ICRSEC	1.1338	0.2870
IFCURR	0.2996	0.5841
IECURR	0.0010	0.9749

Appendix 4.-continued

Step 2. Variable TPFLUSH entered:

Score Test for the Proportional Odds Assumption

Chi-Square = 24.2672 with 2 DF (p=0.0001)

Testing Global Null Hypothesis: BETA=0

Criterion	Intercept Only	Intercept and Covariates	Chi-Square for Covariates
AIC	50.943	37.551	.
SC	53.677	43.020	.
-2 LOG L	46.943	29.551	17.392 with 2 DF (p=0.0002)
Score	.	.	14.541 with 2 DF (p=0.0007)

Analysis of Maximum Likelihood Estimates

Variable	DF	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square	Standardized Estimate	Odds Ratio
INTERCP1	1	2.9452	1.1476	6.5868	0.0103	.	.
INTERCP2	1	8.4629	2.2008	14.7866	0.0001	.	.
FWFRC	1	-9.5419	3.0208	9.9776	0.0016	-1.153262	0.000
TPFLUSH	1	0.0340	0.0253	1.8025	0.1794	0.343147	1.035

Association of Predicted Probabilities and Observed Responses

Concordant = 88.6%	Somers' D = 0.773
Discordant = 11.4%	Gamma = 0.773
Tied = 0.0%	Tau-a = 0.419
(220 pairs)	c = 0.886

Appendix 4.-continued

Step 3. Variable TPFLUSH is removed:

Score Test for the Proportional Odds Assumption

Chi-Square = 20.6440 with 1 DF (p=0.0001)

Testing Global Null Hypothesis: BETA=0

Criterion	Intercept Only	Intercept and Covariates	Chi-Square for Covariates
AIC	50.943	37.442	.
SC	53.677	41.544	.
-2 LOG L	46.943	31.442	15.501 with 1 DF (p=0.0001)
Score	.	.	13.366 with 1 DF (p=0.0003)

Analysis of Maximum Likelihood Estimates

Variable	DF	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square	Standardized Estimate	Odds Ratio
INTERCP1	1	3.0367	1.1198	7.3548	0.0067	.	.
INTERCP2	1	8.0672	1.9822	16.5640	0.0001	.	.
FWFRC	1	-8.4574	2.6603	10.1066	0.0015	-1.022191	0.000

Association of Predicted Probabilities and Observed Responses

Concordant = 87.7%	Somers' D = 0.755
Discordant = 12.3%	Gamma = 0.755
Tied = 0.0%	Tau-a = 0.409
(220 pairs)	c = 0.877

Summary of Stepwise Procedure

Step	Variable Entered	Variable Removed	Number In	Score Chi-Square	Wald Chi-Square	Pr > Chi-Square
1	FWFRC		1	13.3663	.	0.0003
2	TPFLUSH		2	2.0892	.	0.1483
3		TPFLUSH	1	.	1.8025	0.1794

Appendix 5. Ordered stepwise logistic regression of SPOT larval abundance (i.e., dependent variable) vs. inlet/estuary variables (i.e., independent variables) for 29 estuaries (Buzzards Bay to Biscayne Bay).

Data Set: ELMO.ALLAR1
 Response Variable: SPOT
 Response Levels: 3
 Number of Observations: 29
 Link Function: Logit

Response Profile

Ordered Value	SPOT	Count
1	1	12
2	2	3
3	3	14

Stepwise Selection Procedure

Step 0. Intercepts entered:

Analysis of Maximum Likelihood Estimates

Variable	DF	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square	Standardized Estimate	Odds Ratio
INTERCP1	1	-0.3483	0.3770	0.8534	0.3556	.	.
INTERCP2	1	0.0690	0.3716	0.0345	0.8527	.	.

Residual Chi-Square = 22.6318 with 9 DF (p=0.0071)

Analysis of Variables Not in the Model

Variable	Score Chi-Square	Pr > Chi-Square
TPRSM	0.4062	0.5239
FWFRC	8.9411	0.0028
DCPTL	0.8580	0.3543
TPFLUSH	7.6750	0.0056
IWIDTH	1.7726	0.1831
IAVDEP	2.8602	0.0908
ICRSEC	3.0252	0.0820
IFCURR	0.1619	0.6874
IECURR	0.0363	0.8489

Appendix 5.-continued

Step 1. Variable FWFC entered:

Score Test for the Proportional Odds Assumption

Chi-Square = 0.4379 with 1 DF (p=0.5081)

Testing Global Null Hypothesis: BETA=0

Criterion	Intercept Only	Intercept and Covariates	Chi-Square for Covariates
AIC	59.180	51.700	.
SC	61.915	55.802	.
-2 LOG L	55.180	45.700	9.480 with 1 DF (p=0.0021)
Score	.	.	8.941 with 1 DF (p=0.0028)

Analysis of Maximum Likelihood Estimates

Variable	DF	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square	Standardized Estimate	Odds Ratio
INTERCP1	1	1.7825	0.8867	4.0411	0.0444	.	.
INTERCP2	1	2.3566	0.9405	6.2785	0.0122	.	.
FWFC	1	-5.6113	2.0508	7.4868	0.0062	-0.678195	0.004

Association of Predicted Probabilities and Observed Responses

Concordant = 76.4%	Somers' D = 0.533
Discordant = 23.2%	Gamma = 0.535
Tied = 0.4%	Tau-a = 0.323
(246 pairs)	c = 0.766

Residual Chi-Square = 19.5297 with 8 DF (p=0.0123)

Analysis of Variables Not in the Model

Variable	Score Chi-Square	Pr > Chi-Square
TPRSM	0.0029	0.9572
DCPTL	1.2172	0.2699
TPFLUSH	15.7542	0.0001
IWIDTH	0.0021	0.9633
IADVEP	1.5372	0.2150
ICRSEC	0.6561	0.4180
IFCURR	0.8870	0.3463
IECURR	0.3087	0.5785

Appendix 5.-continued

Step 2. Variable TPFLUSH entered:

Score Test for the Proportional Odds Assumption

Chi-Square = 4.4702 with 2 DF (p=0.1070)

Testing Global Null Hypothesis: BETA=0

Criterion	Intercept Only	Intercept and Covariates	Chi-Square for Covariates
AIC	59.180	34.000	.
SC	61.915	39.469	.
-2 LOG L	55.180	26.000	29.180 with 2 DF (p=0.0001)
Score	.	.	19.410 with 2 DF (p=0.0001)

Analysis of Maximum Likelihood Estimates

Variable	DF	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square	Standardized Estimate	Odds Ratio
INTERCP1	1	1.7648	1.1369	2.4095	0.1206	.	.
INTERCP2	1	2.9468	1.2747	5.3439	0.0208	.	.
FWERC	1	-12.8005	4.5185	8.0255	0.0046	-1.547105	0.000
TPFLUSH	1	0.1665	0.0633	6.9176	0.0085	1.680647	1.181

Association of Predicted Probabilities and Observed Responses

Concordant = 92.3%	Somers' D = 0.846
Discordant = 7.7%	Gamma = 0.846
Tied = 0.0%	Tau-a = 0.512
(246 pairs)	c = 0.923

Residual Chi-Square = 8.6270 with 7 DF (p=0.2806)

Analysis of Variables Not in the Model

Variable	Score Chi-Square	Pr > Chi-Square
TPRSM	0.2907	0.5897
DCPTL	0.2106	0.6463
IWIDTH	0.9520	0.3292
IAVDEP	0.2242	0.6359
ICRSEC	0.0001	0.9905
IFCURR	2.9860	0.0840
IECURR	1.8701	0.1715

Appendix 5.-continued

Step 3. Variable IFCURR entered:

Score Test for the Proportional Odds Assumption

Chi-Square = 3.9709 with 3 DF (p=0.2646)

Testing Global Null Hypothesis: BETA=0

Criterion	Intercept	Intercept	Chi-Square for Covariates
	Only	and Covariates	
AIC	59.180	32.358	.
SC	61.915	39.195	.
-2 LOG L	55.180	22.358	32.822 with 3 DF (p=0.0001)
Score	.	.	20.079 with 3 DF (p=0.0002)

Analysis of Maximum Likelihood Estimates

Variable	DF	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square	Standardized Estimate	Odds Ratio
INTERCP1	1	0.1816	1.3684	0.0176	0.8944	.	.
INTERCP2	1	1.5713	1.4493	1.1754	0.2783	.	.
FWFRC	1	-19.5910	8.3649	5.4852	0.0192	-2.367828	0.000
TPFLUSH	1	0.2155	0.0953	5.1152	0.0237	2.176314	1.241
IFCURR	1	3.7175	2.2885	2.6388	0.1043	0.739326	41.160

Association of Predicted Probabilities and Observed Responses

Concordant = 94.3%	Somers' D = 0.886
Discordant = 5.7%	Gamma = 0.886
Tied = 0.0%	Tau-a = 0.537
(246 pairs).	c = 0.943

Residual Chi-Square = 10.0078 with 6 DF (p=0.1243)

Analysis of Variables Not in the Model

Variable	Score Chi-Square	Pr > Chi-Square
TPRSM	0.1598	0.6893
DCPTL	0.8705	0.3508
IWIDTH	0.0323	0.8574
IAVDEP	0.0004	0.9835
ICRSEC	0.5691	0.4506
IECURR	1.6998	0.1923

NOTE: No (additional) variables met the 0.15 significance level for entry into the model.

Summary of Stepwise Procedure

Step	Variable		Number In	Score Chi-Square	Wald Chi-Square	Pr > Chi-Square
	Entered	Removed				
1	FWFRC		1	8.9411	.	0.0028
2	TPFLUSH		2	15.7542	.	0.0001
3	IFCURR		3	2.9860	.	0.0840

Appendix 6. Ordered stepwise logistic regression of MULLET larval abundance (i.e., dependent variable) vs. inlet/estuary variables (i.e., independent variables) for 29 estuaries (Buzzards Bay to Biscayne Bay).

Data Set: ELMO.ALLAR1
 Response Variable: SUMFLOUN
 Response Levels: 3
 Number of Observations: 29
 Link Function: Logit

Response Profile

Ordered Value	SUMFLOUN	Count
1	1	12
2	2	16
3	3	1

Stepwise Selection Procedure

Step 0. Intercepts entered:

Analysis of Maximum Likelihood Estimates

Variable	DF	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square	Standardized Estimate	Odds Ratio
INTERCP1	1	-0.3483	0.3770	0.8534	0.3556	.	.
INTERCP2	1	3.3322	1.0177	10.7207	0.0011	.	.

Residual Chi-Square = 16.6529 with 9 DF (p=0.0544)

Analysis of Variables Not in the Model

Variable	Score Chi-Square	Pr > Chi-Square
TPRSM	2.4778	0.1155
FWFRC	13.3663	0.0003
DCPTL	1.8464	0.1742
TPFLUSH	0.2969	0.5858
IWIDTH	5.4833	0.0192
IAVDEP	3.9026	0.0482
ICRSEC	5.3949	0.0202
IFCURR	0.0148	0.9032
IECURR	0.3411	0.5592

Appendix 6.-continued

Step 1. Variable FWERC entered:

Score Test for the Proportional Odds Assumption

Chi-Square = 20.6440 with 1 DF (p=0.0001)

Testing Global Null Hypothesis: BETA=0

Criterion	Intercept Only	Intercept and Covariates	Chi-Square for Covariates
AIC	50.943	37.442	.
SC	53.677	41.544	.
-2 LOG L Score	46.943	31.442	15.501 with 1 DF (p=0.0001) 13.366 with 1 DF (p=0.0003)

Analysis of Maximum Likelihood Estimates

Variable	DF	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square	Standardized Estimate	Odds Ratio
INTERCP1	1	3.0367	1.1198	7.3548	0.0067	.	.
INTERCP2	1	8.0672	1.9822	16.5640	0.0001	.	.
FWERC	1	-8.4574	2.6603	10.1066	0.0015	-1.022191	0.000

Association of Predicted Probabilities and Observed Responses

Concordant = 87.7%	Somers' D = 0.755
Discordant = 12.3%	Gamma = 0.755
Tied = 0.0%	Tau-a = 0.409
(220 pairs)	c = 0.877

Residual Chi-Square = 4.6529 with 8 DF (p=0.7939)

Analysis of Variables Not in the Model

Variable	Score Chi-Square	Pr > Chi-Square
TPRSM	0.4812	0.4879
DCPTL	1.6982	0.1925
TPFLUSH	2.0892	0.1483
IWIDTH	1.0194	0.3127
IAVDEP	0.8095	0.3683

Appendix 6.-continued

Step 2. Variable TPFLUSH entered:

Score Test for the Proportional Odds Assumption

Chi-Square = 24.2672 with 2 DF (p=0.0001)

Testing Global Null Hypothesis: BETA=0

Criterion	Intercept Only	Intercept and Covariates	Chi-Square for Covariates
AIC	50.943	37.551	.
SC	53.677	43.020	.
-2 LOG L	46.943	29.551	17.392 with 2 DF (p=0.0002)
Score			14.541 with 2 DF (p=0.0007)

Analysis of Maximum Likelihood Estimates

Variable	DF	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square	Standardized Estimate	Odds Ratio
INTERCP1	1	2.9452	1.1476	6.5868	0.0103	.	.
INTERCP2	1	8.4629	2.2008	14.7866	0.0001	.	.
FWFRC	1	-9.5419	3.0208	9.9776	0.0016	-1.153262	0.000
TPFLUSH	1	0.0340	0.0253	1.8025	0.1794	0.343147	1.035

Association of Predicted Probabilities and Observed Responses

Concordant = 88.6%	Somers' D = 0.773
Discordant = 11.4%	Gamma = 0.773
Tied = 0.0%	Tau-a = 0.419
(220 pairs)	c = 0.886

Appendix 6.-continued

Step 3. Variable TPFLUSH is removed:

Score Test for the Proportional Odds Assumption

Chi-Square = 20.6440 with 1 DF (p=0.0001)

Testing Global Null Hypothesis: BETA=0

Criterion	Intercept	Intercept	Chi-Square for Covariates
	Only	and Covariates	
AIC	50.943	37.442	
SC	53.677	41.544	
-2 LOG L	46.943	31.442	15.501 with 1 DF (p=0.0001)
Score			13.366 with 1 DF (p=0.0003)

Analysis of Maximum Likelihood Estimates

Variable	DF	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square	Standardized Estimate	Odds Ratio
INTERCP1	1	3.0367	1.1198	7.3548	0.0067		
INTERCP2	1	8.0672	1.9822	16.5640	0.0001		
FWFRC	1	-8.4574	2.6603	10.1066	0.0015	-1.022191	0.000

Association of Predicted Probabilities and Observed Responses

Concordant = 87.7%	Somers' D = 0.755
Discordant = 12.3%	Gamma = 0.755
Tied = 0.0%	Tau-a = 0.409
(220 pairs)	c = 0.877

Summary of Stepwise Procedure

Step	Variable		Number In	Score Chi-Square	Wald Chi-Square	Pr > Chi-Square
	Entered	Removed				
1	FWFRC		1	13.3663		0.0003
2	TPFLUSH		2	2.0892		0.1483
3		TPFLUSH	1		1.8025	0.1794

Appendix 7. Ordered stepwise logistic regression of MENHADEN larval abundance (i.e., dependent variable) vs. inlet\estuary variables (i.e., independent variables) for 29 estuaries (Buzzards Bay to Biscayne Bay).

Data Set: ELMO.ALLAR1
 Response Variable: MENHADEN
 Response Levels: 3
 Number of Observations: 29
 Link Function: Logit

Response Profile

Ordered Value	MENHADEN	Count
1	1	3
2	2	5
3	3	21

Stepwise Selection Procedure

Step 0. Intercepts entered:

Analysis of Maximum Likelihood Estimates

Variable	DF	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square	Standardized Estimate	Odds Ratio
INTERCP1	1	-2.1595	0.6097	12.5429	0.0004	.	.
INTERCP2	1	-0.9651	0.4155	5.3956	0.0202	.	.

Residual Chi-Square = 16.1479 with 9 DF (p=0.0639)

Analysis of Variables Not in the Model

Variable	Score Chi-Square	Pr > Chi-Square
TPRSM	0.0379	0.8457
FWERC	6.6272	0.0100
DCPTL	0.0986	0.7535
TPFLUSH	0.0008	0.9774
IWIDTH	0.0160	0.8992
IADVDP	0.6574	0.4175
ICRSEC	0.7922	0.3734
IFCURR	0.4587	0.4982
IECURR	0.3893	0.5327

Appendix 7.-continued

Step 1. Variable FWFC entered:

Score Test for the Proportional Odds Assumption

Chi-Square = 1.1368 with 1 DF (p=0.2863)

Testing Global Null Hypothesis: BETA=0

Criterion	Intercept Only	Intercept and Covariates	Chi-Square for Covariates
AIC	48.747	43.121	.
SC	51.482	47.222	.
-2 LOG L	44.747	37.121	7.627 with 1 DF (p=0.0058)
Score	.	.	6.627 with 1 DF (p=0.0100)

Analysis of Maximum Likelihood Estimates

Variable	DF	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square	Standardized Estimate	Odds Ratio
INTERCP1	1	-0.1649	0.9031	0.0333	0.8551	.	.
INTERCP2	1	1.2795	0.8961	2.0390	0.1533	.	.
FWFC	1	-6.2643	2.6044	5.7854	0.0162	-0.757127	0.002

Association of Predicted Probabilities and Observed Responses

Concordant = 76.5%	Somers' D = 0.530
Discordant = 23.5%	Gamma = 0.530
Tied = 0.0%	Tau-a = 0.239
(183 pairs)	c = 0.765

Residual Chi-Square = 9.8382 with 8 DF (p=0.2766)

Analysis of Variables Not in the Model

Variable	Score Chi-Square	Pr > Chi-Square
TPRSM	0.7430	0.3887
DCPTL	0.4604	0.4974
TPFLUSH	0.3886	0.5330
IWIDTH	1.4232	0.2329
IAVDEP	3.2036	0.0735

Appendix 7.-continued

Step 2. Variable ICRSEC entered:

Score Test for the Proportional Odds Assumption

Chi-Square = 0.8376 with 2 DF (p=0.6578)

Testing Global Null Hypothesis: BETA=0

Criterion	Intercept Only	Intercept and Covariates	Chi-Square for Covariates
AIC	48.747	39.100	.
SC	51.482	44.569	.
-2 LOG L	44.747	31.100	13.647 with 2 DF (p=0.0011)
Score	.	.	11.141 with 2 DF (p=0.0038)

Analysis of Maximum Likelihood Estimates

Variable	DF	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square	Standardized Estimate	Odds Ratio
INTERCP1	1	1.3260	1.1522	1.3246	0.2498	.	.
INTERCP2	1	3.2633	1.3518	5.8278	0.0158	.	.
FWFRC	1	-9.2191	3.1694	8.4610	0.0036	-1.114246	0.000
ICRSEC	1	-0.00001	7.162E-6	3.4433	0.0635	-0.942706	1.000

Association of Predicted Probabilities and Observed Responses

Concordant = 83.6% Somers' D = 0.694
 Discordant = 14.2% Gamma = 0.709
 Tied = 2.2% Tau-a = 0.313
 (183 pairs) c = 0.847

Residual Chi-Square = 10.7022 with 7 DF (p=0.1521)

Analysis of Variables Not in the Model

Variable	Score Chi-Square	Pr > Chi-Square
TPRSM	6.2100	0.0127
DCPTL	0.0229	0.8798
TPFLUSH	0.9948	0.3186
IWIDTH	1.0573	0.3038

Appendix 7.-continued

Step 3. Variable TPRSM entered:

Score Test for the Proportional Odds Assumption

Chi-Square = 1.6590 with 3 DF (p=0.6461)

Testing Global Null Hypothesis: BETA=0

Criterion	Intercept		Chi-Square for Covariates
	Intercept Only	Intercept and Covariates	
AIC	48.747	36.801	.
SC	51.482	43.638	.
-2 LOG L	44.747	26.801	17.946 with 3 DF (p=0.0005)
Score			14.193 with 3 DF (p=0.0027)

Analysis of Maximum Likelihood Estimates

Variable	DF	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square	Standardized Estimate	Odds Ratio
INTERCP1	1	1.9260	1.2763	2.2771	0.1313	.	.
INTERCP2	1	4.1403	1.5817	6.8515	0.0089	.	.
TPRSM	1	2.587E-9	1.552E-9	2.7807	0.0954	1.190591	1.000
FWFRC	1	-11.5437	3.8751	8.8740	0.0029	-1.395205	0.000
ICRSEC	1	-0.00003	0.000018	3.7089	0.0541	-2.456780	1.000

Association of Predicted Probabilities and Observed Responses

Concordant = 90.2%	Somers' D = 0.814
Discordant = 8.7%	Gamma = 0.823
Tied = 1.1%	Tau-a = 0.367
(183 pairs)	c = 0.907

Residual Chi-Square = 9.3768 with 6 DF (p=0.1535)

Analysis of Variables Not in the Model

Variable	Score Chi-Square	Pr > Chi-Square
DCPTL	0.0018	0.9661
TPFLUSH	1.9863	0.1587
IWIDTH	1.0978	0.2948
IAVDEP	0.9646	0.3260
IFCURR	0.5542	0.4566
IECURR	0.4128	0.5206

NOTE: No (additional) variables met the 0.15 significance level for entry into the model.

Summary of Stepwise Procedure

Step	Variable		Number In	Score Chi-Square	Wald Chi-Square	Pr > Chi-Square
	Entered	Removed				
1	FWFRC		1	6.6272	.	0.0100
2	ICRSEC		2	3.9064	.	0.0481
3	TPRSM		3	6.2100	.	0.0127

Appendix 8. Ordered stepwise logistic regression of PINFISH larval abundance (i.e., dependent variable) vs. inlet/estuary variables (i.e., independent variables) for 29 estuaries (Buzzards Bay to Biscayne Bay).

Data Set: ELMO.ALLAR1
 Response Variable: PINFISH
 Response Levels: 3
 Number of Observations: 29
 Link Function: Logit

Response Profile

Ordered Value	PINFISH	Count
1	1	13
2	2	7
3	3	9

Stepwise Selection Procedure

Step 0. Intercepts entered:

Analysis of Maximum Likelihood Estimates

Variable	DF	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square	Standardized Estimate	Odds Ratio
INTERCP1	1	-0.2076	0.3734	0.3092	0.5782	.	.
INTERCP2	1	0.7985	0.4014	3.9576	0.0467	.	.

Residual Chi-Square = 11.8076 with 9 DF (p=0.2244)

Analysis of Variables Not in the Model

Variable	Score Chi-Square	Pr > Chi-Square
TPRSM	3.2049	0.0734
FWFRC	3.9980	0.0456
DCPTL	0.0907	0.7633
TPFLUSH	1.9758	0.1598
IWIDTH	2.7002	0.1003
IADVDEP	2.5920	0.1074
ICRSEC	4.9485	0.0261
IFCURR	0.0010	0.9749
IECURR	0.4306	0.5117

Appendix 8.-continued

Step 1. Variable ICRSEC entered:

Score Test for the Proportional Odds Assumption

Chi-Square = 0.0018 with 1 DF (p=0.9659)

Testing Global Null Hypothesis: BETA=0

Criterion	Intercept Only	Intercept and Covariates	Chi-Square for Covariates
AIC	65.822	58.619	.
SC	68.556	62.721	.
-2 LOG L	61.822	52.619	9.203 with 1 DF (p=0.0024)
Score	.	.	4.949 with 1 DF (p=0.0261)

Analysis of Maximum Likelihood Estimates

Variable	DF	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square	Standardized Estimate	Odds Ratio
INTERCP1	1	-1.2102	0.5501	4.8394	0.0278	.	.
INTERCP2	1	0.0258	0.5006	0.0027	0.9589	.	.
ICRSEC	1	0.000018	8.893E-6	4.2925	0.0383	1.306985	1.000

Association of Predicted Probabilities and Observed Responses

Concordant = 66.8%	Somers' D = 0.339
Discordant = 32.8%	Gamma = 0.341
Tied = 0.4%	Tau-a = 0.227
(271 pairs)	c = 0.670

Residual Chi-Square = 12.5668 with 8 DF (p=0.1276)

Analysis of Variables Not in the Model

Variable	Score Chi-Square	Pr > Chi-Square
TPRSM	0.0000	0.9986
FWFRC	0.7446	0.3882
DCPTL	0.1898	0.6631
TPFLUSH	1.0828	0.2981
IWIDTH	1.3827	0.2396
IAVDEP	1.4905	0.2221
IFCURR	1.4952	0.2214
IECURR	0.3864	0.5342

NOTE: No (additional) variables met the 0.15 significance level for entry into the model.

Summary of Stepwise Procedure

Step	Variable Entered	Variable Removed	Number In	Score Chi-Square	Wald Chi-Square	Pr > Chi-Square
1	ICRSEC		1	4.9485	.	0.0261

Appendix 9. Ordered stepwise logistic regression of BRSHRIMP larval abundance (i.e., dependent variable) vs. inlet/estuary variables (i.e., independent variables) for 29 estuaries (Buzzards Bay to Biscayne Bay).

Data Set: ELMO.ALLAR1
 Response Variable: BRSHRIMP
 Response Levels: 3
 Number of Observations: 29
 Link Function: Logit

Response Profile

Ordered Value	BRSHRIMP	Count
1	1	19
2	2	2
3	3	8

Stepwise Selection Procedure

Step 0. Intercepts entered:

Analysis of Maximum Likelihood Estimates

Variable	DF	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square	Standardized Estimate	Odds Ratio
INTERCP1	1	0.6419	0.3907	2.6992	0.1004	.	.
INTERCP2	1	0.9651	0.4155	5.3956	0.0202	.	.

Residual Chi-Square = 9.2941 with 9 DF (p=0.4106)

Analysis of Variables Not in the Model

Variable	Score Chi-Square	Pr > Chi-Square
TPRSM	1.9657	0.1609
FWFRC	4.4966	0.0340
DCPTL	0.1665	0.6833
TPFLUSH	0.4929	0.4826
IWIDTH	5.8802	0.0153
IAVDEP	1.1420	0.2852
ICRSEC	3.2066	0.0733
IFCURR	0.1204	0.7286
IECURR	0.9168	0.3383

Appendix 9.-continued

Step 1. Variable IWIDTH entered:

Score Test for the Proportional Odds Assumption

Chi-Square = 28.1373 with 1 DF (p=0.0001)

Testing Global Null Hypothesis: BETA=0

Criterion	Intercept Only	Intercept and Covariates	Chi-Square for Covariates
AIC	51.371	45.703	.
SC	54.105	49.804	.
-2 LOG L	47.371	39.703	7.668 with 1 DF (p=0.0056)
Score	.	.	5.880 with 1 DF (p=0.0153)

Analysis of Maximum Likelihood Estimates

Variable	DF	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square	Standardized Estimate	Odds Ratio
INTERCP1	1	-0.5856	0.6328	0.8564	0.3547	.	.
INTERCP2	1	-0.1745	0.6257	0.0778	0.7803	.	.
IWIDTH	1	0.000229	0.000111	4.2289	0.0397	0.885740	1.000

Association of Predicted Probabilities and Observed Responses

Concordant = 74.8%	Somers' D = 0.495
Discordant = 25.2%	Gamma = 0.495
Tied = 0.0%	Tau-a = 0.251
(206 pairs)	c = 0.748

Residual Chi-Square = 5.2562 with 8 DF (p=0.7299)

Analysis of Variables Not in the Model

Variable	Score Chi-Square	Pr > Chi-Square
TPRSM	0.0221	0.8817
FWFRC	2.3084	0.1287
DCPTL	0.0769	0.7815
TPFLUSH	0.2446	0.6209
IAVDEP	0.0599	0.8066

Appendix 9.-continued

Step 2. Variable FWERC entered:

Score Test for the Proportional Odds Assumption

Chi-Square = 32.1304 with 2 DF (p=0.0001)

Testing Global Null Hypothesis: BETA=0

Criterion	Intercept Only	Intercept and Covariates	Chi-Square for Covariates
AIC	51.371	45.515	.
SC	54.105	50.984	.
-2 LOG L	47.371	37.515	9.856 with 2 DF (p=0.0072)
Score	.	.	7.379 with 2 DF (p=0.0250)

Analysis of Maximum Likelihood Estimates

Variable	DF	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square	Standardized Estimate	Odds Ratio
INTERCP1	1	0.8622	1.2725	0.4591	0.4981	.	.
INTERCP2	1	1.3134	1.2915	1.0343	0.3092	.	.
FWERC	1	-3.0756	2.2799	1.8198	0.1773	-0.371726	0.046
IWIDTH	1	0.000218	0.000119	3.3535	0.0671	0.843909	1.000

Association of Predicted Probabilities and Observed Responses

Concordant = 79.6%	Somers' D = 0.592
Discordant = 20.4%	Gamma = 0.592
Tied = 0.0%	Tau-a = 0.300
(206 pairs)	c = 0.796

Appendix 9.-continued

Step 3. Variable FWFRC is removed:

Score Test for the Proportional Odds Assumption

Chi-Square = 28.1373 with 1 DF (p=0.0001)

Testing Global Null Hypothesis: BETA=0

Criterion	Intercept	Intercept	Chi-Square for Covariates
	Only	and Covariates	
AIC	51.371	45.703	.
SC	54.105	49.804	.
-2 LOG L	47.371	39.703	7.668 with 1 DF (p=0.0056)
Score	.	.	5.880 with 1 DF (p=0.0153)

Analysis of Maximum Likelihood Estimates

Variable	DF	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square	Standardized Estimate	Odds Ratio
INTERCP1	1	-0.5856	0.6328	0.8564	0.3547	.	.
INTERCP2	1	-0.1745	0.6257	0.0778	0.7803	.	.
IWIDTH	1	0.000229	0.000111	4.2289	0.0397	0.885740	1.000

Association of Predicted Probabilities and Observed Responses

Concordant = 74.8%	Somers' D = 0.495
Discordant = 25.2%	Gamma = 0.495
Tied = 0.0%	Tau-a = 0.251
(206 pairs)	c = 0.748

Summary of Stepwise Procedure

Step	Variable		Number In	Score	Wald	Pr >
	Entered	Removed		Chi-Square	Chi-Square	Chi-Square
1	IWIDTH		1	5.8802	.	0.0153
2	FWFRC		2	2.3084	.	0.1287
3		FWFRC	1	.	1.8198	0.1773

Appendix 10. Ordered stepwise logistic regression of BLKDRUM larval abundance (i.e., dependent variable) vs. inlet/estuary variables (i.e., independent variables) for 29 estuaries (Buzzards Bay to Biscayne Bay).

Data Set: ELMO.ALLAR1
 Response Variable: BLKDRUM
 Response Levels: 3
 Number of Observations: 29
 Link Function: Logit

Response Profile

Ordered Value	BLKDRUM	Count
1	1	18
2	2	9
3	3	2

Stepwise Selection Procedure

Step 0. Intercepts entered:

Analysis of Maximum Likelihood Estimates

Variable	DF	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square	Standardized Estimate	Odds Ratio
INTERCP1	1	0.4925	0.3827	1.6559	0.1982	.	.
INTERCP2	1	2.6027	0.7328	12.6136	0.0004	.	.

Residual Chi-Square = 10.0008 with 9 DF (p=0.3504)

Analysis of Variables Not in the Model

Variable	Score Chi-Square	Pr > Chi-Square
TPRSM	0.8739	0.3499
FWFRC	4.1862	0.0408
DCPTL	0.0154	0.9014
TPFLUSH	0.3991	0.5276
IWIDTH	0.6903	0.4061
IAVDEP	0.2442	0.6212
ICRSEC	1.4588	0.2271
IFCURR	0.4672	0.4943
IECURR	1.4486	0.2288

Appendix 10.-continued

Step 1. Variable FWFC entered:

Score Test for the Proportional Odds Assumption

Chi-Square = 6.4745 with 1 DF (p=0.0109)

Testing Global Null Hypothesis: BETA=0

Criterion	Intercept	Intercept	Chi-Square for Covariates
	Only	and Covariates	
AIC	52.927	50.261	.
SC	55.662	54.362	.
-2 LOG L	48.927	44.261	4.667 with 1 DF (p=0.0308)
Score	.	.	4.186 with 1 DF (p=0.0408)

Analysis of Maximum Likelihood Estimates

Variable	DF	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square	Standardized Estimate	Odds Ratio
INTERCP1	1	2.3657	1.0421	5.1533	0.0232	.	.
INTERCP2	1	4.6632	1.3223	12.4363	0.0004	.	.
FWFC	1	-4.2061	2.0555	4.1874	0.0407	-0.508364	0.015

Association of Predicted Probabilities and Observed Responses

Concordant = 69.0%	Somers' D = 0.384
Discordant = 30.6%	Gamma = 0.386
Tied = 0.5%	Tau-a = 0.204
(216 pairs)	c = 0.692

Residual Chi-Square = 6.7668 with 8 DF (p=0.5620)

Analysis of Variables Not in the Model

Variable	Score Chi-Square	Pr > Chi-Square
TPRSM	0.2309	0.6309
DCPTL	0.0088	0.9252
TPFLUSH	0.1464	0.7020
IWIDTH	0.0055	0.9407
IAVDEP	0.1876	0.6649
ICRSEC	0.2415	0.6231
IFCURR	0.3251	0.5686
IECURR	0.9649	0.3260

NOTE: No (additional) variables met the 0.15 significance level for entry into the model.

Summary of Stepwise Procedure

Step	Variable Entered	Variable Removed	Number In	Score Chi-Square	Wald Chi-Square	Pr > Chi-Square
1	FWFC		1	4.1862	.	0.0408

Appendix 11. Ordered stepwise logistic regression of BLUECRAB larval abundance (i.e., dependent variable) vs. inlet/estuary variables (i.e., independent variables) for 29 estuaries (Buzzards Bay to Biscayne Bay).

Data Set: ELMO.ALLAR1
 Response Variable: BLUECRAB
 Response Levels: 3
 Number of Observations: 29
 Link Function: Logit

Response Profile

Ordered Value	BLUECRAB	Count
1	1	2
2	2	4
3	3	23

Stepwise Selection Procedure

Step 0. Intercepts entered:

Analysis of Maximum Likelihood Estimates

Variable	DF	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square	Standardized Estimate	Odds Ratio
INTERCP1	1	-2.6027	0.7328	12.6136	0.0004	.	.
INTERCP2	1	-1.3437	0.4584	8.5923	0.0034	.	.

Residual Chi-Square = 18.2120 with 9 DF (p=0.0328)

Analysis of Variables Not in the Model

Variable	Score Chi-Square	Pr > Chi-Square
TPRSM	4.7123	0.0299
FWFRC	2.2953	0.1298
DCPTL	2.9341	0.0867
TPFLUSH	2.8581	0.0909
IWIDTH	5.1624	0.0231
IADVDEP	10.7950	0.0010
ICRSEC	11.4018	0.0007
IFCURR	0.4490	0.5028
IECURR	2.1150	0.1459

Appendix 11.-continued

Step 1. Variable ICRSEC entered:

Score Test for the Proportional Odds Assumption

Chi-Square = 4.9060 with 1 DF (p=0.0268)

Testing Global Null Hypothesis: BETA=0

Criterion	Intercept	Intercept	Chi-Square for Covariates
	Only	and Covariates	
AIC	41.207	31.261	.
SC	43.942	35.363	.
-2 LOG L	37.207	25.261	11.947 with 1 DF (p=0.0005)
Score	.	.	11.402 with 1 DF (p=0.0007)

Analysis of Maximum Likelihood Estimates

Variable	DF	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square	Standardized Estimate	Odds Ratio
INTERCP1	1	-4.9203	1.4383	11.7034	0.0006	.	.
INTERCP2	1	-2.7751	0.8373	10.9839	0.0009	.	.
ICRSEC	1	0.000014	5.948E-6	5.8673	0.0154	1.021990	1.000

Association of Predicted Probabilities and Observed Responses

Concordant = 83.6%	Somers' D = 0.712
Discordant = 12.3%	Gamma = 0.743
Tied = 4.1%	Tau-a = 0.256
(146 pairs)	c = 0.856

Residual Chi-Square = 7.7050 with 8 DF (p=0.4628)

Analysis of Variables Not in the Model

Variable	Score Chi-Square	Pr > Chi-Square
TPRSM	0.7348	0.3913
FWFRC	0.0187	0.8911
DCPTL	1.1700	0.2794
TPFLUSH	2.6886	0.1011
IWIDTH	0.4898	0.4840

Appendix 11.-continued

Step 2. Variable TPFLUSH entered:

Score Test for the Proportional Odds Assumption

Chi-Square = 5.8792 with 2 DF (p=0.0529)

Testing Global Null Hypothesis: BETA=0

Criterion	Intercept Only	Intercept and Covariates	Chi-Square for Covariates
AIC	41.207	31.019	.
SC	43.942	36.488	.
-2 LOG L	37.207	23.019	14.189 with 2 DF (p=0.0008)
Score	.	.	13.343 with 2 DF (p=0.0013)

Analysis of Maximum Likelihood Estimates

Variable	DF	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square	Standardized Estimate	Odds Ratio
INTERCP1	1	-5.6557	1.6295	12.0470	0.0005	.	.
INTERCP2	1	-3.4900	1.1051	9.9731	0.0016	.	.
TPFLUSH	1	0.0364	0.0243	2.2341	0.1350	0.367181	1.037
ICRSEC	1	0.000015	6.311E-6	5.6835	0.0171	1.067282	1.000

Association of Predicted Probabilities and Observed Responses

Concordant = 90.4%	Somers' D = 0.808
Discordant = 9.6%	Gamma = 0.808
Tied = 0.0%	Tau-a = 0.291
(146 pairs)	c = 0.904

Residual Chi-Square = 6.2333 with 7 DF (p=0.5128)

Analysis of Variables Not in the Model

Variable	Score Chi-Square	Pr > Chi-Square
TPRSM	0.5742	0.4486
FWFRC	0.3961	0.5291
DCPTL	0.5119	0.4743
IWIDTH	1.3992	0.2369
IAVDEP	0.5632	0.4530
IFCURR	0.1564	0.6925
IECURR	1.1262	0.2886

NOTE: No (additional) variables met the 0.15 significance level for entry into the model.

Summary of Stepwise Procedure

Step	Variable Entered	Variable Removed	Number In	Score Chi-Square	Wald Chi-Square	Pr > Chi-Square
1	ICRSEC		1	11.4018	.	0.0007
2	TPFLUSH		2	2.6886	.	0.1011

Appendix 12. Ordered stepwise logistic regression of REDDRUM larval abundance (i.e., dependent variable) vs. inlet/estuary variables (i.e., independent variables) for 29 estuaries (Buzzards Bay to Biscayne Bay).

Data Set: ELMO.ALLAR1
 Response Variable: REDDRUM
 Response Levels: 3
 Number of Observations: 29
 Link Function: Logit

Response Profile

Ordered Value	REDDRUM	Count
1	1	16
2	2	11
3	3	2

Stepwise Selection Procedure

Step 0. Intercepts entered:

Analysis of Maximum Likelihood Estimates

Variable	DF	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square	Standardized Estimate	Odds Ratio
INTERCP1	1	0.2076	0.3734	0.3092	0.5782	.	.
INTERCP2	1	2.6027	0.7328	12.6136	0.0004	.	.

Residual Chi-Square = 13.3386 with 9 DF (p=0.1479)

Analysis of Variables Not in the Model

Variable	Score Chi-Square	Pr > Chi-Square
TPRSM	2.3615	0.1244
FWFRC	4.7819	0.0288
DCPTL	0.0201	0.8874
TPFLUSH	0.9108	0.3399
IWIDTH	4.3786	0.0364
IADVDEP	1.1994	0.2734
ICRSEC	3.5819	0.0584
IFCURR	1.7328	0.1881
IECURR	3.5503	0.0595

Appendix 12.-continued

Step 1. Variable FWERC entered:

Score Test for the Proportional Odds Assumption

Chi-Square = 3.9259 with 1 DF (p=0.0475)

Testing Global Null Hypothesis: BETA=0

Criterion	Intercept and Covariates		Chi-Square for Covariates
	Intercept Only	Intercept and Covariates	
AIC	55.054	51.852	.
SC	57.789	55.954	.
-2 LOG L Score	51.054	45.852	5.202 with 1 DF (p=0.0226) 4.782 with 1 DF (p=0.0288)

Analysis of Maximum Likelihood Estimates

Variable	DF	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square	Standardized Estimate	Odds Ratio
INTERCP1	1	2.0408	0.9577	4.5407	0.0331	.	.
INTERCP2	1	4.7035	1.2866	13.3644	0.0003	.	.
FWERC	1	-4.2240	1.9659	4.6165	0.0317	-0.510523	0.015

Association of Predicted Probabilities and Observed Responses

Concordant = 70.0%	Somers' D = 0.404
Discordant = 29.6%	Gamma = 0.406
Tied = 0.4%	Tau-a = 0.229
(230 pairs)	c = 0.702

Residual Chi-Square = 9.2647 with 8 DF (p=0.3205)

Analysis of Variables Not in the Model

Variable	Score Chi-Square	Pr > Chi-Square
TPRSM	1.3167	0.2512
DCPTL	0.0286	0.8656
TPFLUSH	1.3543	0.2445
IWIDTH	2.0037	0.1569
IAVDEP	0.0689	0.7929
ICRSEC	1.6858	0.1942
IFCURR	1.4630	0.2264
IECURR	2.7857	0.0951

Appendix 12.-continued

Step 2. Variable IECURR entered:

Score Test for the Proportional Odds Assumption

Chi-Square = 5.3562 with 2 DF (p=0.0687)

Testing Global Null Hypothesis: BETA=0

Criterion	Intercept	Intercept	Chi-Square for Covariates
	Only	and Covariates	
AIC	55.054	50.626	.
SC	57.789	56.096	.
-2 LOG L	51.054	42.626	8.428 with 2 DF (p=0.0148)
Score			7.227 with 2 DF (p=0.0270)

Analysis of Maximum Likelihood Estimates

Variable	DF	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square	Standardized Estimate	Odds Ratio
INTERCP1	1	4.2384	1.8920	5.0181	0.0251	.	.
INTERCP2	1	7.0696	2.1761	10.5547	0.0012	.	.
FWFRC	1	-4.1285	2.1331	3.7457	0.0529	-0.498979	0.016
IECURR	1	-2.2003	1.2404	3.1467	0.0761	-0.487332	0.111

Association of Predicted Probabilities and Observed Responses

Concordant = 77.4%	Somers' D = 0.548
Discordant = 22.6%	Gamma = 0.548
Tied = 0.0%	Tau-a = 0.310
(230 pairs)	c = 0.774

Residual Chi-Square = 6.7316 with 7 DF (p=0.4574)

Analysis of Variables Not in the Model

Variable	Score Chi-Square	Pr > Chi-Square
TPRSM	1.3700	0.2418
DCPTL	0.1386	0.7097
TPFLUSH	0.7419	0.3890
IWIDTH	1.1391	0.2858
IAVDEP	0.0690	0.7928
ICRSEC	1.5173	0.2180
IFCURR	0.0696	0.7919

NOTE: No (additional) variables met the 0.15 significance level for entry into the model.

Summary of Stepwise Procedure

Step	Variable		Number In	Score Chi-Square	Wald Chi-Square	Pr > Chi-Square
	Entered	Removed				
1	FWFRC		1	4.7819	.	0.0288
2	IECURR		2	2.7857	.	0.0951

Appendix 13. Ordered stepwise logistic regression of SEATROUT larval abundance (i.e., dependent variable) vs. inlet/estuary variables (i.e., independent variables) for 29 estuaries (Buzzards Bay to Biscayne Bay).

Data Set: ELMO.ALLAR1
 Response Variable: SEATROUT
 Response Levels: 3
 Number of Observations: 29
 Link Function: Logit

Response Profile

Ordered Value	SEATROUT	Count
1	1	15
2	2	7
3	3	7

Stepwise Selection Procedure

Step 0. Intercepts entered:

Analysis of Maximum Likelihood Estimates

Variable	DF	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square	Standardized Estimate	Odds Ratio
INTERCP1	1	0.0690	0.3716	0.0345	0.8527	.	.
INTERCP2	1	1.1451	0.4339	6.9636	0.0083	.	.

Residual Chi-Square = 14.0226 with 9 DF (p=0.1215)

Analysis of Variables Not in the Model

Variable	Score Chi-Square	Pr > Chi-Square
TPRSM	1.6194	0.2032
FWFRC	5.9214	0.0150
DCPTL	0.0985	0.7536
TPFLUSH	0.4619	0.4968
IWIDTH	0.3924	0.5310
IAVDEP	2.6089	0.1063
ICRSEC	2.4988	0.1139
IFCURR	0.3997	0.5272
IECURR	1.7977	0.1800

Appendix 13.-continued

Step 1. Variable FWFRC entered:

Score Test for the Proportional Odds Assumption

Chi-Square = 1.0139 with 1 DF (p=0.3140)

Testing Global Null Hypothesis: BETA=0

Criterion	Intercept	Intercept	Chi-Square for Covariates
	Only	and Covariates	
AIC	63.576	59.638	
SC	66.311	63.740	
-2 LOG L	59.576	53.638	5.938 with 1 DF (p=0.0148)
Score			5.921 with 1 DF (p=0.0150)

Analysis of Maximum Likelihood Estimates

Variable	DF	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square	Standardized Estimate	Odds Ratio
INTERCP1	1	1.8454	0.9046	4.1617	0.0413		
INTERCP2	1	3.1153	1.0227	9.2794	0.0023		
FWFRC	1	-4.1775	1.8746	4.9660	0.0259	-0.504907	0.015

Association of Predicted Probabilities and Observed Responses

Concordant = 68.3%	Somers' D = 0.371
Discordant = 31.3%	Gamma = 0.372
Tied = 0.4%	Tau-a = 0.236
(259 pairs)	c = 0.685

Residual Chi-Square = 11.5493 with 8 DF (p=0.1725)

The LOGISTIC Procedure

Analysis of Variables Not in the Model

Variable	Score Chi-Square	Pr > Chi-Square
TPRSM	0.6567	0.4177
DCPTL	0.0716	0.7890
TPFLUSH	1.5181	0.2179
IWIDTH	0.4295	0.5122
IAVDEP	1.3701	0.2418
ICRSEC	0.7568	0.3843
IFCURR	0.1897	0.6632
IECURR	1.1700	0.2794

NOTE: No (additional) variables met the 0.15 significance level for entry into the model.

Summary of Stepwise Procedure

Step	Variable Entered	Variable Removed	Number In	Score Chi-Square	Wald Chi-Square	Pr > Chi-Square
1	FWFRC		1	5.9214		0.0150

Appendix 14. Ordered stepwise logistic regression of WEAKFISH larval abundance (i.e., dependent variable) vs. inlet/estuary variables (i.e., independent variables) for 29 estuaries (Buzzards Bay to Biscayne Bay).

Data Set: ELMO.ALLAR1
 Response Variable: WEAKFISH
 Response Levels: 3
 Number of Observations: 29
 Link Function: Logit

Response Profile

Ordered Value	WEAKFISH	Count
1	1	8
2	2	9
3	3	12

Stepwise Selection Procedure

Step 0. Intercepts entered:

Analysis of Maximum Likelihood Estimates

Variable	DF	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square	Standardized Estimate	Odds Ratio
INTERCP1	1	-0.9651	0.4155	5.3956	0.0202	.	.
INTERCP2	1	0.3483	0.3770	0.8534	0.3556	.	.

Residual Chi-Square = 13.1277 with 9 DF (p=0.1569)

Analysis of Variables Not in the Model

Variable	Score Chi-Square	Pr > Chi-Square
TFRSM	0.1069	0.7437
FWERC	7.3715	0.0066
DCPTL	0.3339	0.5634
TPFLUSH	0.0162	0.8987
IWIDTH	0.0000	0.9977
IADVEP	0.0429	0.8359
ICRSEC	0.1129	0.7369
IFCURR	1.3475	0.2457
IECURR	0.6605	0.4164

Appendix 14.-continued

Step 1. Variable FWERC entered:

Score Test for the Proportional Odds Assumption

Chi-Square = 0.4263 with 1 DF (p=0.5138)

Testing Global Null Hypothesis: BETA=0

Criterion	Intercept	Intercept	Chi-Square for Covariates
	Only	and Covariates	
AIC	66.844	60.612	.
SC	69.579	64.714	.
-2 LOG L	62.844	54.612	8.232 with 1 DF (p=0.0041)
Score	.	.	7.372 with 1 DF (p=0.0066)

Analysis of Maximum Likelihood Estimates

Variable	DF	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square	Standardized Estimate	Odds Ratio
INTERCP1	1	0.8302	0.7790	1.1358	0.2865	.	.
INTERCP2	1	2.5050	0.9236	7.3558	0.0067	.	.
FWERC	1	-5.1094	1.9028	7.2105	0.0072	-0.617541	0.006

Association of Predicted Probabilities and Observed Responses

Concordant = 73.6%	Somers' D = 0.478
Discordant = 25.7%	Gamma = 0.482
Tied = 0.7%	Tau-a = 0.325
(276 pairs)	c = 0.739

Residual Chi-Square = 7.5574 with 8 DF (p=0.4779)

Appendix 14.-continued

Step 2. Variable IFCURR entered:

Score Test for the Proportional Odds Assumption

Chi-Square = 0.7035 with 2 DF (p=0.7034)

Testing Global Null Hypothesis: BETA=0

Criterion	Intercept and Covariates		Chi-Square for Covariates
	Intercept Only	Intercept and Covariates	
AIC	66.844	59.195	.
SC	69.579	64.664	.
-2 LOG L Score	62.844	51.195	11.650 with 2 DF (p=0.0030) 9.278 with 2 DF (p=0.0097)

Analysis of Maximum Likelihood Estimates

Variable	DF	Parameter Estimate	Standard Error	Wald Chi-Square	Pr > Chi-Square	Standardized Estimate	Odds Ratio
INTERCP1	1	-0.6504	1.1378	0.3268	0.5675	.	.
INTERCP2	1	1.1810	1.1677	1.0230	0.3118	.	.
FWFRC	1	-5.9816	2.0676	8.3693	0.0038	-0.722955	0.003
IFCURR	1	2.0294	1.1790	2.9627	0.0852	0.403614	7.610

Association of Predicted Probabilities and Observed Responses

Concordant = 77.2%	Somers' D = 0.543
Discordant = 22.8%	Gamma = 0.543
Tied = 0.0%	Tau-a = 0.369
(276 pairs)	c = 0.772

Residual Chi-Square = 4.0257 with 7 DF (p=0.7768)

Analysis of Variables Not in the Model

Variable	Score Chi-Square	Pr > Chi-Square
TPRSM	0.5169	0.4722
DCPTL	0.0046	0.9459
TPFLUSH	0.7431	0.3887
IWIDTH	0.3427	0.5583
IAVDEP	1.9451	0.1631
ICRSEC	1.0841	0.2978
IECURR	0.0102	0.9194

NOTE: No (additional) variables met the 0.15 significance level for entry into the model.

Summary of Stepwise Procedure

Step	Variable		Number In	Score Chi-Square	Wald Chi-Square	Pr > Chi-Square
	Entered	Removed				
1	FWFRC		1	7.3715	.	0.0066
2	IFCURR		2	3.1703	.	0.0750