Cross-shelf and seasonal variation in larval fish assemblages on the southeast United States continental shelf off the coast of Georgia

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Abstract—Seasonal and cross-shelf patterns were investigated in larval fish assemblages on the continental shelf off the coast of Georgia. The influence of environmental factors on larval distributions also was examined, and larval transport processes on the shelf were considered. Ichthyoplankton and environmental data were collected approximately every other month from spring 2000 to winter 2002. Ten stations were repeatedly sampled along a 110-km cross-shelf transect, including four stations in the vicinity of Gray's Reef National Marine Sanctuary. Correspondence analysis (CA) on untransformed community data identified two seasonal (warm weather [spring, summer, and fall] and winter) and three cross-shelf larval assemblages (inner-, mid-, and outer-shelf). Five environmental factors (temperature, salinity, density, depth of the water column, and stratification) were related to larval cross-shelf distribution. Specifically, increased water column stratification was associated with the outer-shelf assemblage in spring, summer, and fall. The inner shelf assemblage was associated with generally lower temperatures and lower salinities in the spring and summer and higher salinities in the winter. The three cross-shelf regions indicated by the three assemblages coincided with the location of three primary water masses on the shelf. However, taxa occurring together within an assemblage were transported to different parts of the shelf; thus, transport across the continental shelf off the coast of Georgia cannot be explained solely by two-dimensional physical factors.

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The study of larval fish assemblages provides information on community structure, spawning, and larval transport. Larval fish assemblages are groups of larvae with similar temporal and spatial distributions (Cowen et al., 1993). Larval distribution patterns are initially determined by spawning time and location; larvae of species with similar spawning patterns are initially in the same larval assemblage (Rakocinski et al., 1996). Physical forcing and larval behavior then modify the structure of larval assemblages and ultimately determine the outcome of larval transport (Cowen et al., 1993; Smith et al., 1999; Hare et al., 2001).

Marine protected areas (MPAs) are portions of the marine environment designated to "provide lasting protection for part or all of the natural and cultural resources therein" (Federal Register, 2000). A number of specific conservation objectives are encompassed by this definition, such as protecting small areas with historical significance or aesthetic quality, or protecting much larger areas to enhance fisheries through increases in spawning stock biomass and the supply of recruits to surrounding areas (Crowder et al., 2000). However, whether an MPA provides recruits to other areas is difficult to quantify and involves determining the fate of larvae and juveniles spawned in a protected area (Stephenson, 1999; Warner et al., 2000).

MPAs are under consideration as a fisheries management tool on the southeast United States continental shelf (Plan Development Team, 1990), and larval assemblage studies would provide useful information regarding spawning and larval transport. Although substantial larval fish research has been conducted on the southeast U.S. continental shelf, no studies have examined the dynamics of larval fish assemblages in this area. For example, during the RV *Dolphin* cruises, the Marine Resources Monitoring, Assessment, and Prediction (MARMAP) cruises, and the Southeast Area Monitoring and Assessment Program (SEAMAP) cruises, ichthyoplankton surveys were conducted on the southeast United States continental shelf. From these surveys, spawning time was defined for a large group of species (Fahay, 1975), and the temporal and spatial distribution of larvae were described for a few select species (Kendall and Walford, 1979; Collins and Stender, 1987; 1989; Smith et al., 1994) and for multiple taxa, but mostly at the family level (Powles and Stender, 1976). Similarly, other programs (e.g., the South Atlantic Bight Recruitment Experiment) examined spawning and larval transport of "estuarine-dependent" species such as Atlantic menhaden (e.g., Judy and Lewis, 1983; Hoss et al., 1997; Hare et al., 1999; Checkley et al., 1999), but results for the entire suite of species sampled were not reported. For studies where the broader community of larval fish on the southeast U.S. shelf was addressed, the structure and dynamics of larval assemblages were not defined (Powell and Robbins, 1994, 1998; Govoni and Spach, 1999; Powell et al., 2000).

The purpose of this study was to examine larval fish assemblages on the continental shelf off the coast of Georgia, USA. This region of the continental shelf was targeted because of 1) the nature of the broad shallow shelf, 2) the location of Gray's Reef National Marine Sanctuary 20 km from shore, and 3) the location of several proposed deepwater MPAs (70–200 m water depth) in the region. Temporal and spatial patterns in larval distributions were described to explain spawning and larval transport processes on the continental shelf off the coast of Georgia, and the implications for MPAs in the region were addressed.

Materials and methods

Study site

The southeast United States continental shelf extends from West Palm Beach, Florida, to Cape Hatteras, North Carolina. Moving north from West Palm Beach (15 km), the shelf widens to Georgia (200 km) and then narrows to Cape Hatteras (35 km). Physical forcing by the Gulf Stream, which is part of the North Atlantic Western Boundary Current system, varies along the shelf. As the Gulf Stream flows northward along the shelf edge, it meanders, and cyclonic frontal eddies form in meander troughs (Lee et al., 1991). Meanders and frontal eddies grow in dimension from just north of the Straits of Florida (27°N latitude) to St. Augustine, Florida (30°N latitude), and then decrease from St. Augustine to just south of Charleston, South Carolina (32°N latitude). Meanders and frontal eddies grow in dimension again downstream of the Charleston Bump (32–33°N latitude), and then decrease again from Cape Fear, North Carolina (33°N latitude), to Cape Hatteras, North Carolina (36°N latitude).

Table 1

Year, month, and season of ichthyoplankton sampling and number of stations sampled in the Georgia Bight region of the southeast United States continental shelf.

Year	Month	Season	Number of stations
2000	April	spring	4
2000	August	summer	8
2000	October	fall	7
2001	January	winter	8
2001	March	winter	8
2001	May	spring	7
2001	June	summer	7
2001	August	summer	10
2001	October	fall	8
2002	February	winter	10

In addition to along-shelf variation in geophysical structure and Gulf Stream forcing, the southeast United States continental shelf can be divided into three cross-shelf zones based on physical circulation dynamics (Boicourt et al., 1998). Circulation on the inner-shelf (0–20 m water depth) is influenced by tidal currents, river inflow, and wind (Atkinson and Menzel, 1985; Pietrafesa et al., 1985a). Wind-driven flow predominates on the mid-shelf (20–40 m water depth) and there is only minor Gulf Stream and tidal influence (Atkinson and Menzel, 1985). Flow on the outer-shelf (40–75 m water depth) is dominated by the passage of Gulf Stream frontal eddies and upwelling at the shelf break (Pietrafesa et al., 1985b).

Inner and mid-shelf physical processes are relatively more important off the coast of Georgia compared to other segments of the southeast United States continental shelf (Boicourt et al., 1998). The continental shelf off the coast of Georgia is the area of diminishing meanders and eddies from St. Augustine, Florida, to Charleston, South Carolina. Tidal range and freshwater inflow is greatest in the Georgia portion of the southeast shelf (Atkinson and Menzel, 1985). Further, because the shelf is widest off the coast of Georgia (approximately 200 km), the Gulf Stream is less influential on mid- and inner-shelf dynamics compared to the rest of the southeast United States continental shelf (Lee et al., 1991).

Collection of larval fish and CTD data

Ichthyoplankton sampling was conducted approximately every other month from April 2000 through February 2002 (Table 1). A maximum of ten stations, approximately 18.5 km apart, were sampled during each cruise. Stations were missed on some cruises owing to weather and equipment failure. The transect was 110 km long and spanned 10 to 50 m water depth (Fig. 1). Four sta-

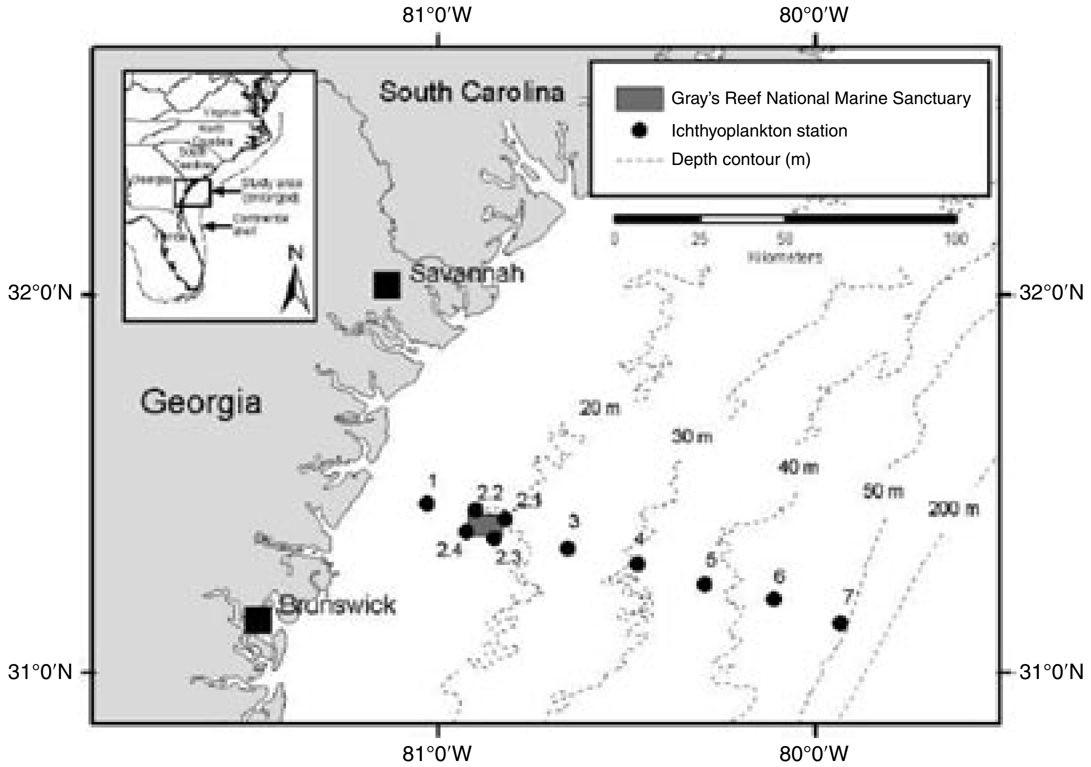


Figure 1

Map of the study area and the cross-shelf transect used for sampling larval abundance and environmental data bimonthly from April 2000 to February 2002 (see Table 1). Four stations (stations 2.1–2.4) were located around Gray's Reef National Marine Sanctuary.

tions were placed immediately adjacent to the four sides of Gray's Reef National Marine Sanctuary. At each station, temperature, salinity, density, and water depth were measured from the water's surface to one meter above the bottom with a Seabird conductivity-temperature-depth (CTD probe (SBE19, Seabird Electronics, Inc., Bellevue, WA). Ichthyoplankton was collected at each station with a five-minute single oblique net tow to within one meter of the bottom. For all but one cruise (August 2000), a 61-cm paired bongo frame fitted with 333-μm or 505-μm mesh nets was used. During the remaining cruise, a 1-m ichthyoplankton sled with 333-μm mesh net was used because of the smaller size of the research vessel. A flow meter (General Oceanica) was used to measure the volume of water filtered.

A gear comparison study, conducted during October 2000, showed that ichthyoplankton samples collected with the two gear types (61-cm bongo versus 1-m^2 ichthyoplankton sled) were similar. An analysis of variance (ANOVA) on the mean larval concentration revealed no significant differences between the two gear types (one-way ANOVA: F=0.489; df=1; P>0.5). Also, an analysis of similarities (ANOSIM, Clarke and Warwick, 2001) determined that the community structure varied more within than between gear types (ANOSIM: R=−0.11; S=77.57). Similarly, preliminary analysis of the effect of gear selectivity due to mesh size indicated that the larval communities collected by 333-μm mesh and by 505-μm mesh nets were similar. Thus, data from all cruises were combined in the subsequent analyses (see Marancik, 2003, for more details).

Preparation of ichthyoplankton data

All ichthyoplankton samples were sorted and larval fish were identified to the lowest possible taxonomic level by using previously published descriptions (e.g., Fahay, 1983; Johnson and Keener, 1984; Richards, 2001) and descriptions developed as part of this study. Identification to species was not easy given the diversity of species along the southeast United States continental shelf (see Kendall and Matarese, 1994), yet every effort was made to identify larvae to species-level (46.3% to species, 27.4% to genus, 6.7% unidentified). Larval concentrations were calculated as number of larvae/100 m^3.

Two data sets were used for statistical analyses, differing in the inclusion of rare taxa. Rare taxa pose a problem in community analyses. Some rare taxa occur because of transport anomalies (Cowen et al., 1993), and their inclusion in data analyses can confound the definition of larval assemblages. However, rare taxa can also be indicative of consistent, but low larval abun-

Table 2

Taxa collected during two years of sampling (April 2000–February 2002) constituting one or ten percent of any one sample from the continental shelf off the coast of Georgia and included in the analyses. The taxonomic codes used in the figures of this article are also shown. Taxa included in the one percent and ten percent data sets are marked by an "X." Also indicated are the seasonal assemblage (warm weather [WA] and winter [WI]) and larval assemblage (I=inner-shelf, M=mid-shelf, O=outer-shelf) in which larvae were collected (based on correspondence analyses).

Family	Species	Taxonomic code	Included in 1% data set	Included in 10% data set	Season	Assemblage
Muraenidae	*Gymnothorax* sp.		X		WA/WI	I/O
Ophichthidae	*Ophichthus* sp.		X		WA/WI	M/O
	Myrophis punctatus	Mpun	X	X	WI	M
Clupeidae	*Brevoortia tyrannus*	Btyr	X	X	WI	M
	Etrumeus teres		X		WI	O
	Opisthonema oglinum	Oogl	X	X	WA	I/O
Engraulidae	*Anchoa hepsetus*	Ahep	X	X	WA	I/M
	Engraulis eurystole		X		WA	O
Gonostomatidae	*Cyclothone* spp.		X		WA	O
Phosichthyidae	*Vinciguerria nimbaria*		X		WA	O
Paralepidae	*Lestidium atlanticum*		X		WI	O
Myctophidae	*Diaphus* spp.		X		WA/WI	M/O
	Lepidophanes spp.		X		WA	O
	Ceratoscopelus maderensis		X		WA/WI	M/O
	Ceratoscopelus warmingii		X		WI	M
	Electrona risso		X		WI	O
	Hygophum hygemii		X		WI	O
	Hygophum reinhardtii		X		WA	O
	Lampadena urophaos		X		WA	M
	Myctophum affini		X		WA	O
	Myctophum selenops		X		WA	O
Bregmacerotidae	*Bregmaceros atlanticus*		X		WA	O
	Bregmaceros cantori		X		WA/WI	I/O
	Bregmaceros houdei		X		WA/WI	M
Gadidae	*Urophycis* sp.		X		WI	M
Ophidiidae	*Ophidion antipholus/holbrooki*		X		WA/WI	I/M
	Ophidion josephi		X		WA/WI	I/O
	Ophidion marginatum	Omar	X	X	WA	M
	Ophidion selenops		X		WA	M
	Otophidium omostigmum	Oomo	X	X	WA/WI	M
Holocentridae	Holocentridae		X		WA	O
Syngnathidae	*Hippocampus* sp.		X		WA	I
	Syngnathus fuscus/louisianae		X		WA	I
	Syngnathus louisianae		X		WA	I
Scorpaenidae	Scorpaenidae		X		WA/WI	M/O

continued

dance (Leis, 1989); excluding these taxa could remove data useful in defining larval assemblages. Thus, two taxa inclusion data sets were selected. The first data set comprised taxa that made up greater than one percent abundance at any one station, and the second data set included those taxa that made up at least 10 percent abundance at any one station (Table 2).

The data sets were further truncated by eliminating, with a few exceptions, all taxa not identified to genus or species level. Priacanthidae, Scaridae, Scorpaenidae, and Epinephalinae were included because, despite potential inclusion of multiple species, these larvae represent some of the only reef taxa collected, and larval assemblage data including these taxa would be useful

Table 2 (continued)

Family	Species	Taxonomic code	Included in 1% dataset	Included in 10% dataset	Season	Assemblage
Serranidae	Epinephalinae		X		WA/WI	M/O
	Serraninae		X		WA/WI	M/O
	Diplectrum spp.		X		WA/WI	I/M/O
	Hemanthias vivanus		X		WA	O
	Serraniculus pumilio		X		WA	M
Priacanthidae	Priacanthidae		X		WA	M/O
Pomatomidae	*Pomatomus saltatrix*		X		WA	O
Carangidae	*Elagatus bipinnulata*		X		WA	M/O
Coryphaenidae	*Coryphaena hippurus*		X		WA	I/O
Lutjanidae	*Lutjanus* sp.		X		WA	O
	Rhomboplites aurorubens		X		WA	O
Sparidae	*Lagodon rhomboides*	Lrho	X	X	WI	I
Sciaenidae	*Bairdiella chrysura*		X		WA	I
	Cynoscion nothus		X		WA	I/M
	Cynoscion regalis		X		WA	I
	Larimus fasciatus		X		WA	I/M
	Leiostomus xanthurus	Lxan	X	X	WI	I/M
	Menticirrhus americanus	Mame	X	X	WA	I
	Micropogonias undulatus	Mund	X	X	WA/WI	I/M
	Pogonias cromis		X		WA	I
	Sciaenops ocellatus		X		WA	I
Pomacentridae	*Abudefduf* sp.		X		WA	O
	Chromis spp.		X		WA	O
Mugilidae	*Mugil curema*		X		WI	M
Labridae	*Halichoeres* sp.		X		WA/WI	M
	Xyrichthys spp.	Xyr	X	X	WA	M/O
Scaridae	Scaridae		X		WA/WI	I/M/O
Dactyloscopidae	Dactyloscopidae type 1 (*D. moorei*)		X		WA	I
	Dactyloscopidae type 2		X		WA	M
	Dactyloscopidae type 3		X		WA/WI	O
Callionymidae	*Diplogrammus pauciradiatus*	Dpau	X	X	WA/WI	M
Scombridae	*Euthynnus alletteratus*		X		WA	O
	Scomberomorus cavalla		X		WA	O
	Scomberomorus maculatus		X		WA	I
	Auxis rochei	Aroc	X	X	WA	O
	Scomber japonicus		X		WA/WI	M/O
Stromateidae	*Ariomma* sp.		X		WA/WI	M/O
Bothidae	*Bothus ocellatus/robinsi*	Boce	X	X	WA/WI	M/O
Paralichthyidae	*Cyclopsetta* sp.		X		WA/WI	M/O
	Engyophrys spp.		X		WA	O
	Syacium spp.		X		WA	M/O
	Paralichthys albiguta/lethostigma		X		WI	O
	Citharichthys arctifrons		X		WI	I
	Citharichthys cornutus		X		WA	O
	Citharichthys gymnorhinus		X		WA/WI	I/M/O
	Citharichthys spilopterus	Cspi	X	X	WI	M
	Etropus crossotus	Ecro	X	X	WA	M
	Hippoglossina oblongatta		X		WA	M
	Paralichthys lethostigma		X		WI	M
Soleidae	*Trinectes maculatus*		X		WA	I
Balistidae	*Monocanthus hispidus*		X		WA	O

Table 3

Mean values for each station (station 2 is the average of stations 2.1–2.4) of the sixteen environmental variables used in canonical correspondence analysis to determine which environmental variables were most significantly linked to the larvae of the Georgia Bight. Temperature, salinity, and density gradients are horizontal gradients based on the difference between adjacent stations. Stratification of the water column was calculated by using Simpson's stratification parameter and is a measure of vertical change in density.

		Station						
Environmental variables	Code	1	2	3	4	5	6	7
Depth (m)	DEP	12.44	18.51	23.15	33.05	37.03	41.48	45.94
Average temperature (°C)	AVGTEM	19.51	20.76	21.67	22.33	21.97	22.73	23.10
Temperature gradient (°C)	TEMGRAD	–0.29	–0.67	–1.10	–0.82	–0.52	–1.33	–0.59
Average salinity	AVGSAL	34.78	35.70	36.11	36.32	36.35	36.30	36.24
Salinity gradient	SALGRAD	–0.88	–1.13	–0.56	–0.25	0.03	0.12	0.19
Average density (kg/m^3)	AVGDEN	24.56	24.97	25.04	25.05	25.18	24.92	24.79
Density gradient (kg/m^3)	DENGRAD	–0.64	–0.74	–0.18	0.01	0.16	0.44	0.31
Stratification	STRAT	3.10	1.47	3.37	6.19	13.41	42.41	98.44

for managing reef fish on the southeast United States continental shelf (see Powell and Robbins, 1994; 1998). Serraninae were also included because the majority of these larvae are likely one type: *Serranus subligarius*. In contrast, larvae identified to some genera were excluded because there are multiple species common in the area within each genus, and each species likely has different larval distributions: *Etropus* spp. (3 species), *Prionotus* spp. (14 species), *Sphoeroides* spp. (11 species), *Symphurus* spp., (22 species), and *Syngnathus* spp. (10 species). In summary, 86 taxa were included in the one percent data set, and 16 taxa were included in the ten percent data set (Table 2).

Preparation of environmental data

Season, water mass, and eight environmental variables (mostly derived from temperature and salinity data) were chosen in an attempt to explain variation in the ichthyoplankton data (Table 3). For subsequent use in multivariate analyses, all environmental variables were standardized to a mean of zero and a standard deviation of one.

CTD data were processed with the manufacturer's software (Seasave vers. 5.3, Seabird Electronics, Inc., Bellevue, WA) and averaged into 0.5-m bins. Two parameters were derived to describe each hydrographic variable (salinity, temperature, density): an average value through the entire water column and a horizontal gradient value (calculated as the difference in value between the two adjacent stations). Vertical stratification was estimated by using Simpson's stratification parameter (Simpson and James, 1986):

$$\Phi = 1/h \int_{-h}^{0} (\bar{\rho} - \rho) gz dz,$$

where h = water column depth;
$\bar{\rho}$ = average water column density;
ρ = water density;
g = acceleration due to gravity; and
z = depth.

The stratification parameter, Φ (jowles/m^3), is a measure of the resistance of water to mixing; higher numbers signify higher resistance to mixing.

Temperature and salinity data were further used to define water masses on the continental shelf off the coast of Georgia. Pietrafesa et al. (1994) defined four water masses on the southeast U.S. continental shelf: Georgia Bight Water, Carolina Capes Water, Virginia Coastal Water, and Gulf Stream Water. However, temperature data collected on the continental shelf off the coast of Georgia exhibited greater seasonal variability (10–29°C) than reported by Pietrafesa et al. (1994; 14–29°C). As a result, water mass definitions for our study, although based largely on the definitions of Pietrafesa et al. (1994), reflect the greater range of temperature and reflect the natural breaks in temperature, salinity, and stratification data. Specifically, two water masses (inner-shelf water and mid-shelf water) and two mixes (inner-shelf–mid-shelf mixed water and mid-shelf–Gulf Stream mixed water) were defined (Fig. 2). Inner-shelf water was characterized by salinities <35 ppt and seasonally variable temperatures. This water mass was found during winter and spring and was distributed inside the 20-m isobath (Fig. 3). Mid-shelf water, with salinities >36 (Fig. 2), was typically well mixed vertically (Simpson's stratification parameter value <10). Mid-shelf water was found year round over large sections of the shelf, particularly in the fall (Fig. 3). A mixture between inner-shelf and mid-shelf water was defined with salinities between 35 and 36 (Fig. 2). A mixture was also defined

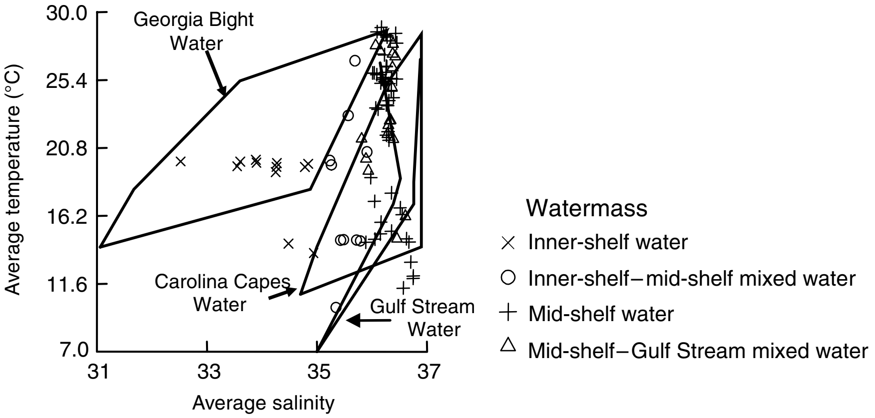


Figure 2

The average temperature and salinity for each station; symbols used represent the water mass designation for each station. The black polygons represent the temperature and salinity boundaries (data for all seasons bounded by one polygon) of three water masses defined by Pietrafesa et al. (1994; Georges Bight water; Carolina Capes water, and Gulf Stream water). Four water masses were defined in our study (inner-shelf water, inner-shelf–mid-shelf water, mid-shelf water, and mid-shelf–Gulf Stream mixed water).

as mid-shelf water and Gulf Stream water (Fig. 2). Gulf Stream water was not encountered, but its temperature and salinity properties are well documented (Churchill et al., 1993; Pietrafesa et al., 1994). Mid-shelf–Gulf Stream mixed water was highly stratified (Simpson's stratification parameter value >10), with warm highly saline water intruding on the surface during fall, winter, and spring and cool highly saline water intruding at depth during summer. Mid-shelf–Gulf Stream mixed water was encountered on most cruises and was found farthest offshore (Fig. 3).

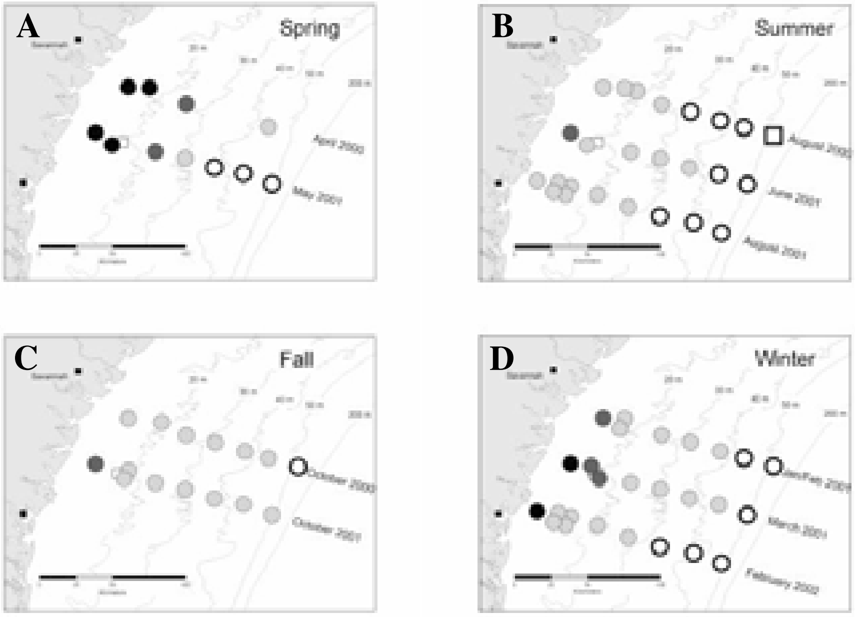
Cruises were assigned to one of four seasons (Table 1) based on wind and temperature regimes. Although Blanton et al. (1985) identified five seasons for the southeast United States based on wind regimes (Spring [March–May], summer [June–July], transition [August], autumn [September–October], and winter [November–February]), the temperature data collected in our study supported classifying both August cruises as summer and the March cruise as winter.

Data analyses

Multivariate analyses were used to define larval assemblages and to explore the factors that influence distribution of larval assemblages on the continental shelf off the coast of Georgia. Multivariate analyses arrange sites and species along environmental gradients creating a low dimensional map (an ordination). Analyses can be conducted for samples where the distance between points in the ordination represents the similarity of species abundance between samples. Analyses also can be conducted for species where the distance between points in the ordination represents the similarity in the sample distribution between species. Ordinations, then, can be analyzed in two ways: with regard to proximity and dimensionality. Points that occur in close proximity can be considered similar based on similar composition. Points that occur on the same dimension define gradients in the data.

The effects of data transformation (untransformed, square root transformed, and fourth root transformed) and species inclusions (1% and 10% data sets) on the ordination of community and environmental data by two multivariate ordination techniques, multidimensional scaling and correspondence analysis (CA), were compared to determine which method was more effective at analyzing the larval fish data collected on the continental shelf off the coast of Georgia (Marancik, 2003). Overall, the two analytical methods produced similar ordinations and were robust to the inclusion of rare species and to the type of data transformation.

Correspondence analysis on untransformed larval fish concentration data was used to define larval assemblages in relation to season and the entire two-year data set. One of the strengths of CA is that it allows one to plot analyses of species and station data simultaneously on one ordination, thereby, allowing immediate comparisons between those stations that occur in close proximity in ordination space and those taxa that influence that proximity. Eigenvalues are a measure of the importance of each CA dimension (ter Braak and Smilauer, 2002). Thus, the dimensions needed to describe patterns in the data can be determined by an abrupt drop in the magnitude of eigenvalues from one dimension to the next.



Water masses	Salinity	Stratification
● Inner-shelf water	<35	-----
● Inner-shelf–mid-shelf mixed water	35–36	-----
● Mid-shelf water	>36	<10
○ Mid-shelf–Gulf Stream mixed water	-----	>10
☐ No data collected		

Figure 3

Water mass designations for each station for each cruise. Cruises within a season were put together in one map with transects offset from center: (**A**) spring, (**B**) summer, (**C**) fall, and (**D**) winter. Inner-shelf water was the least saline and found farthest inshore. Mid-shelf–Gulf Stream mixed water was a highly stratified mix of Gulf Stream water and mid-shelf water and was found farthest offshore.

Canonical correspondence analysis (CCA), which incorporates environmental variables by aligning species and station data along environmental gradients, was used to explore the relationship between larval assemblages and the environment. The species-environment correlation is a measure of the strength of the relation between the species data and the environmental data for each CCA dimension (ter Braak and Smilauer, 2002). The product of the species-environment correlation and the eigenvalue can be used to describe the variance in the data. CA and CCA were performed by using the statistical package CANOCO (Ter Braak, 1988).

Multivariate analyses were used to determine which fish species spawn on the continental shelf off the coast of Georgia, to examine what environmental factors influence larval distribution, and to explore the physical factors affecting the transport of larvae spawned on the shelf. Specifically, six objectives were addressed: 1) cross-shelf patterns in the larval fish community; 2) larval assemblages associated with cross-shelf patterns in the larval fish community; 3) the relation among cross-shelf patterns in the larval fish community, larval assemblages, and environmental variables; 4) the relation between water mass and larval assemblages; 5) seasonal patterns in the larval fish community and larval assemblages; and 6) the relation between seasonal larval assemblages and environmental variables.

In addition to addressing the six specific objectives, the implications for larval transport were considered. By comparing the distributions of specific taxa to the patterns discerned by addressing the objectives above, some insights were gained into larval transport processes. The distribution of taxa representative of each larval assemblage was examined for patterns through space and time. Mechanisms driving larval transport were then explored by linking these patterns to water mass and other environmental variables.

Results

Two dimensions were sufficient to explain the majority of the variance in the larval concentration data (Table 4). The winter data eigenvalues indicated the relevance of a third dimension; yet, inspection of three dimensions did not define any patterns not indicated by the first two dimensions. Thus, two dimensions were analyzed for each season in both the CA and CCA analyses.

Cross-shelf patterns in the larval fish community

A cross-shelf pattern in the larval community was observed. In spring, summer, and fall, the inshore stations (stations 1–3) were in close proximity, forming an inner-shelf station group in the ordination resulting from the CA (Fig. 4). Along the same dimension (axis) as the inner-shelf group was a mid-shelf station group of stations 3–6 (stations 2.1–2.4 were also included in this group in spring, summer, and winter). An outer-shelf group composed of offshore stations (stations 5–7) was distributed along a nearly perpendicular dimension, and the mid-shelf group was at the intersection of the two dimensions (Fig. 4). Analysis of the one-percent species data set revealed an identical pattern for each season (not shown).

The winter station ordination resulted in a less distinct cross-shelf pattern (Fig. 4D). In January 2001, stations 1, 2, 3, and 6 were in the inner-shelf group; whereas, stations 4 and 7 from the same cruise were in the mid-shelf group, and station 5 was in the outer-shelf group. Some of this blurring of the cross-shelf pattern in the ordination may be explained by a lower total catch, giving the taxa found across the shelf (*Brevoortia tyrannus* and *Leiostomus xanthurus*) more influence over the data. In addition, most of the variance was explained by the first dimension (Table 4), meaning that the separation of the outer-shelf group (stations 5 and 6) from the mid- and inner-shelf groups is based on a weak relationship among the stations.

Larval assemblages associated with cross-shelf patterns in the larval fish community

Three larval assemblages were defined that corresponded to the three station groups (Fig. 5). The inner-shelf assemblage was composed of species that spawn in coastal and estuarine habitats. Larvae in this assemblage were distributed within the 20-m isobath and confined largely to stations classified as inner-shelf (Fig. 6). The inner-shelf assemblage was primarily represented by *Menticirrhus americanus* during spring, summer, and fall, and by *Micropogonius undulatus* and *Lagodon rhomboides* during winter (Table 5). Taxa included in the mid-shelf assemblage were generally found between the 20- and 40-m isobaths. Some mid-shelf taxa, however, were found across the shelf (stations 1–7) and a large percentage of the larvae occurring in each region were mid-shelf taxa (Fig. 6). The outer-shelf assemblage comprised offshore or deepwater spawned taxa and was

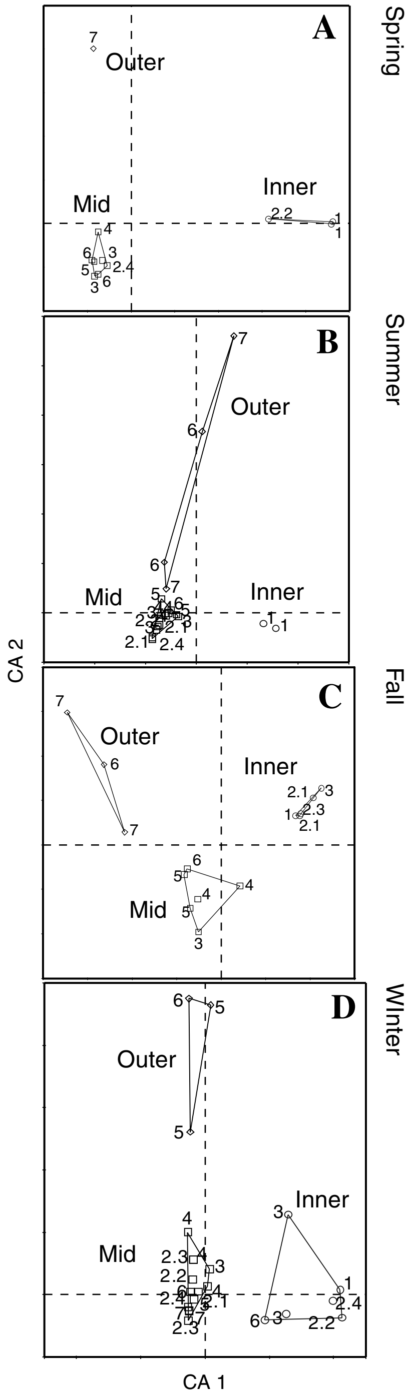


Figure 4

Correspondence analysis ordinations (portraying the first and second dimension scores) of the larval fish community data showing station groups in each season (**A**) spring, (**B**) summer, (**C**) fall, and (**D**) winter. Three cross-shelf station groups were identified within each season. Solid lines enclose the boundary of each station group with three or more stations. Station groups comprising one or two stations are not enclosed by a solid line. Each station group is labeled and portrayed with a different symbol. The dashed lines intersect at the origin of the plot. Analyses were conducted with larval concentration data only. Data from each cruise within a season are shown together.

Table 4

Eigenvalues and species-environment correlations (r^2) for each axis analyzed (correspondence analysis [CA] and canonical correspondence analysis [CAA]) by season and the entire year. A sharp drop in the eigenvalue marks the axes that explain most of the data. Species and environment correlations represent the strength of the relation between the species data and the environmental data for each axis within each season. Values of zero denote no relation; values of one denote a perfect relation. The product of the species-environment correlation and the eigenvalue explains the variance in the data for CCA. Eigenvalues alone explain the variance in the data for CA.

	CA axis				CCA axis			
Season	1	2	3	4	1	2	3	4
Spring								
Eigenvalue	0.932	0.674	0.348	0.107	0.89	0.631	0.329	0.068
r^2					0.98	0.969	0.969	0.796
Summer								
Eigenvalue	0.792	0.621	0.537	0.292	0.703	0.564	0.409	0.159
r^2					0.959	0.959	0.889	0.799
Fall								
Eigenvalue	0.738	0.544	0.273	0.106	0.707	0.443	0.228	0.053
r^2					0.983	0.909	0.935	0.946
Winter								
Eigenvalue	0.526	0.287	0.197	0.165	0.42	0.104	0.059	0.041
r^2					0.894	0.665	0.645	0.496
Year								
Eigenvalue	0.937	0.788	0.607	0.54	0.773	0.61	0.319	0.276
r^2					0.923	0.899	0.8	0.735

Table 5

Three cross-shelf larval assemblages (inner-shelf, mid-shelf, and outer-shelf) were persistent in the Georgia Bight with seasonal changes in membership. Shown are the assemblages from the ten-percent data set. "*Bothus ocellatus/robinsi*" means *B. ocellatus* and *B. robinsi* or one of either of them.

Season	Inner	Mid	Outer
Spring	*Menticirrhus americanus*	*Diplogrammus pauciradiatus* *Otophidium omostigmum* *Bothus ocellatus/robinsi* *Xyrichthys* spp. *Micropogonias undulatus* *Etropus crossotus* *Anchoa hepsetus*	*Auxis rochei* *Opisthonema oglinum*
Summer	*M. americanus* *O. oglinum*	*D. pauciradiatus* *O. omostigmum* *Ophidion marginatum* *Xyrichthys* spp. *E. crossotus* *M. undulatus* *A. hepsetus*	*A. rochei* *B. ocellatus/robinsi*
Fall	*M. americanus* *A. hepsetus* *O. marginatum* *Leiostomus xanthurus*	*D. pauciradiatus* *M. undulatus* *E. crossotus* *O. omostigmum*	*Xyrichthys* spp. *B. ocellatus/robinsi*
Winter	*M. undulatus* *L. rhomboides*	*B. tyrannus* *M. punctatus* *C. spilopterus* *D. pauciradiatus* *O. omostigmum* *L. xanthurus*	*B. ocellatus/robinsi*

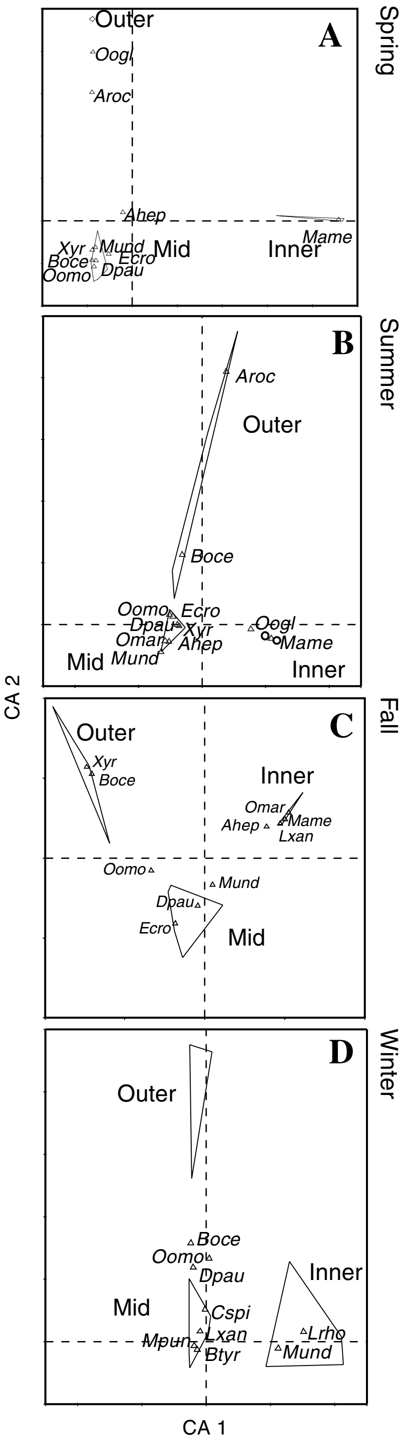


Figure 5

Correspondence analysis (CA) ordinations (portraying the first and second dimension scores) of the larval fish community data showing species in each season: (**A**) spring, (**B**) summer, (**C**) fall, and (**D**) winter. A larval fish assemblage was associated with each cross-shelf station group. Each station group is outlined and labeled as in Figure 4. The dashed lines intersect at the origin of the plot. Analyses were conducted by using larval concentration data only. Refer to table 2 for definitions of larval taxa codes. Three larval fish assemblages were defined based on species association with station groups (see table 5).

found primarily at outer-shelf stations (Fig. 6). *Auxis rochei* and *Bothus ocellatus/robinsi* [where the slash (/) means "*B. ocellatus* and *B. robinsi*" or one of these species] represented the outer-shelf assemblage (Table 5).

The region of the shelf with the highest species richness depended on the inclusion of rare taxa and season. With the exception of fall, species richness was highest in the mid-shelf group when only abundant taxa were included in analyses (Table 5, Fig. 7A). When rare taxa were included (the 1% data set), species richness was highest in the mid-shelf group during spring and summer and highest in the outer-shelf group during fall and winter (Fig. 7B).

Relationship among cross-shelf patterns in the larval fish community, larval assemblages, and environmental variables

Five environmental variables were correlated to the cross-shelf pattern in station groups and larval assemblages. Water density, salinity, temperature, depth, and stratification of the water column had a significant relation to the structure of larval assemblages and the grouping of stations in the CCA ($P<0.05$ for each variable, Monte Carlo permutation test; Table 6). The species-environment correlation for the first two axes of the ordination was greater that 0.79, indicating a strong association between the environment and larval assemblages (Table 6). Although the portrayal of station groups and larval assemblages in ordination space was not identical when environmental data were included (compare Figs. 4 and 5 to 8), the cross-shelf pattern in station groups and larval assemblages was maintained (Fig. 8).

The first CCA dimension, in all seasons, was most highly influenced by the depth, temperature, salinity, and density of the water (Fig. 8). In spring, summer, and winter, the mid- and outer-shelf stations were aligned along CCA 1 and separated from the inner-shelf stations along this gradient (Fig. 8). Similarly, in fall, the three station groups were arranged separately along this gradient with the mid-shelf groups intermediate to the inner- and outer-shelf stations. Thus, the separation between inner-shelf and mid- and outer-shelf stations is related to a gradient in depth, temperature, salinity, and density.

The second dimension separated outer-shelf stations from inner- and mid-shelf station groups. In spring and summer, the second dimension (CCA 2) was clearly influenced by stratification (Fig. 8). The outer-shelf stations experienced a higher degree of stratification, separating them from the inner- and mid-shelf stations. During fall and winter, stratification still impacted the second dimension, but less dramatically. In summary, outer-shelf stations were distinguished from mid- and inner-shelf stations by increased stratification of the water.

Relation between larval assemblages and water mass distributions

When hydrographic variables were combined to define water mass, a possible explanation for the cross-shelf

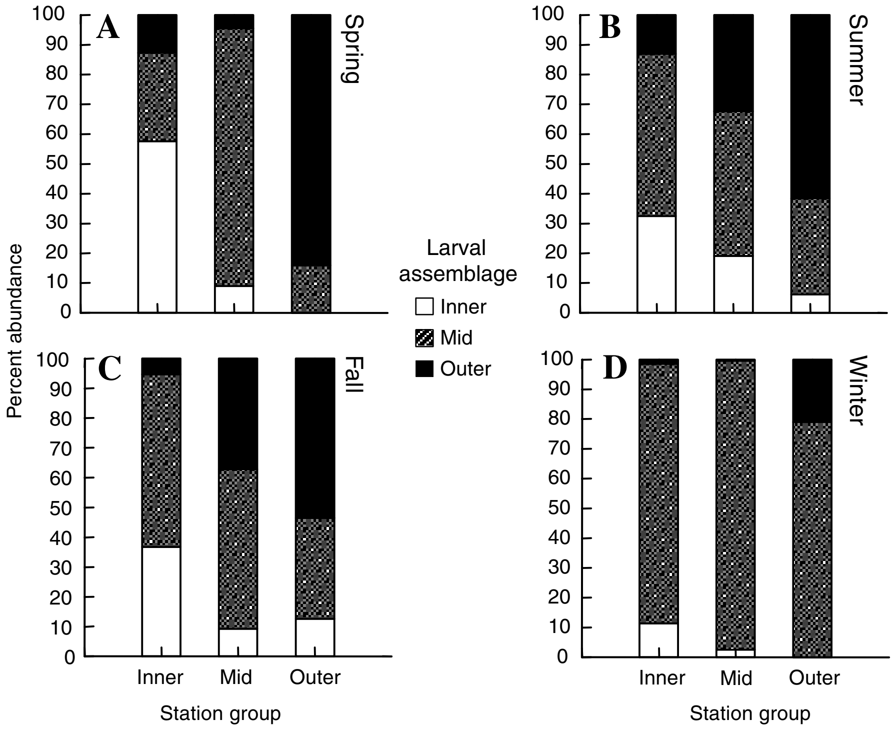


Figure 6

Percent abundance of taxa in larval assemblages associated with each station group (inner-, mid-, and outer-shelf) in (**A**) spring, (**B**) summer, (**C**) fall, and (**D**) winter.

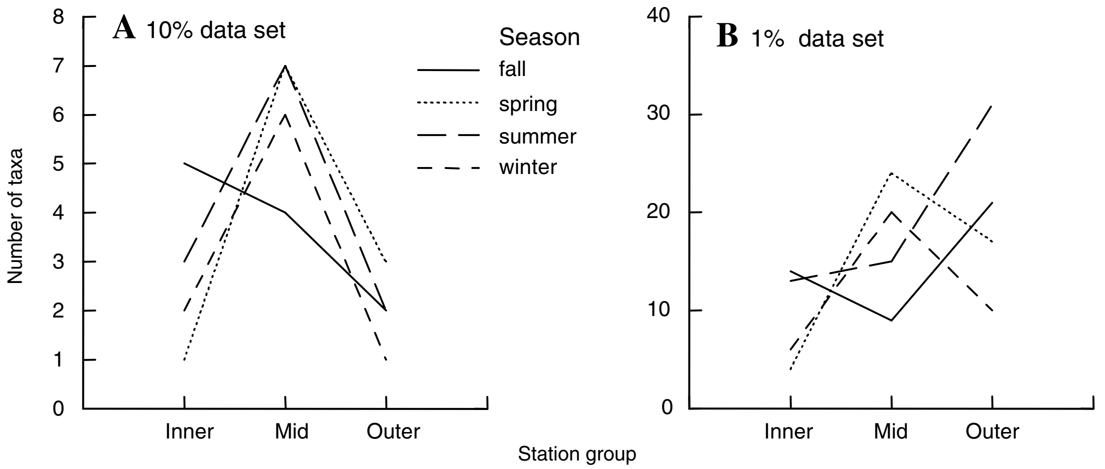


Figure 7

The number of taxa collected in each station group during each season for the (**A**) ten-percent and (**B**) one-percent data sets.

pattern in the larval community was revealed. Physical data delineated four water masses (Fig. 3). Larval fish assemblages differentiated only three of these water masses. Stations associated with inner-shelf water (the inshoremost water mass) and mid-shelf–Gulf Stream mixed water (the offshoremost water mass) formed distinct groups in the ordination of larval community data (Fig. 9). Stations associated with mid-shelf water also

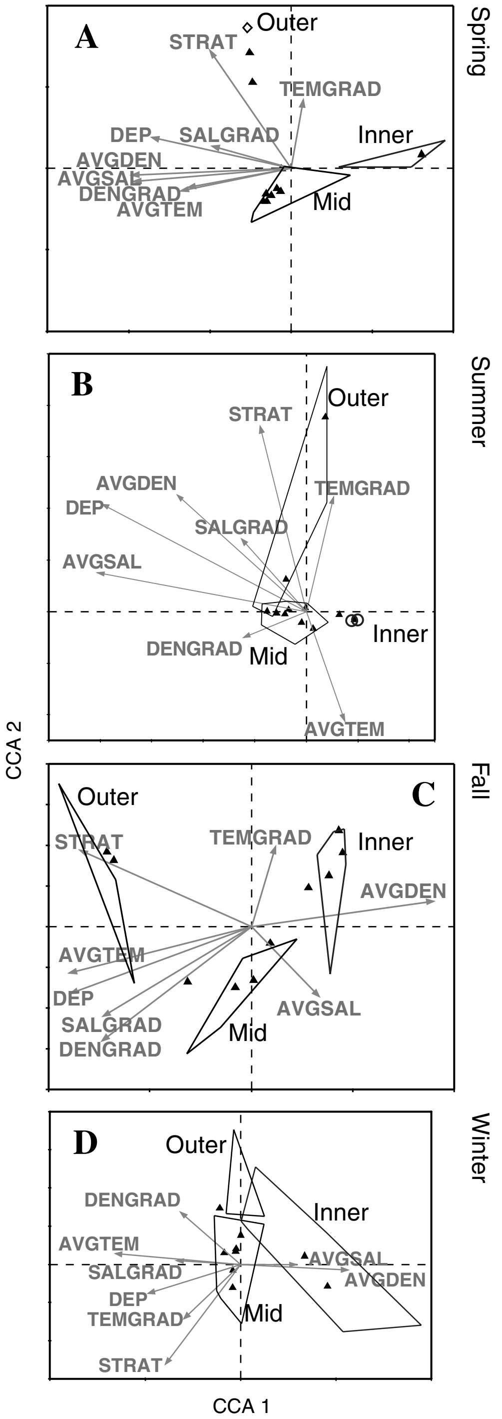


Figure 8

Canonical correspondence analysis (CCA) ordinations (portraying the first and second dimension scores) of the larval fish community data showing the correlations between environmental variables, species, and station groups: (**A**) spring, (**B**) summer, (**C**) fall, and (**D**) winter. The solid triangles mark the location of taxa (as in Fig. 5), and the polygons surround the three cross-shelf station groups (as in Fig. 4). The arrows depict the gradient of each environmental variable. The dashed lines intersect at the origin of the plot. Analyses were conducted with both larval and environmental data. Refer to Table 3 for definitions of environmental variable codes.

Table 6

The *P* values from a Monte Carlo permutation test on the environmental variables for each season. Significant values ($P<0.05$) are shown in bold font. See Table 3 for definitions of variable codes.

	Season			
Variable code	Spring	Summer	Fall	Winter
AVGDEN	**0.002**	**0.01**	0.34	0.494
AVGSAL	**0.002**	**0.022**	**0.016**	**0.004**
AVGTEM	0.152	0.1	**0.04**	**0.016**
DENGRAD	0.836	0.076	0.466	0.958
SALGRAD	0.456	0.086	0.78	0.634
TEMGRAD	0.074	0.076	0.38	0.574
DEP	0.468	**0.002**	**0.002**	0.68
STRAT	**0.036**	**0.014**	**0.012**	0.504

formed distinct groups. The fourth water mass, inner-shelf–mid-shelf mixed water overlapped with either inner-shelf or mid-shelf water depending on season. In summary, the cross-shelf distribution and assemblages of water masses coincided with the three cross-shelf regions described: inner-shelf, mid-shelf, and outer-shelf characterized by inner-shelf water, mid-shelf water, and mid-shelf–Gulf Stream mixed water, respectively.

Seasonal patterns in the cross-shelf distributions of the larval fish community

The ten percent data set revealed two distinct seasonal station groups (Fig. 10). The winter stations occurred in close proximity and were separate from stations sampled during the rest of the seasons (Fig. 10A). However, inner-shelf stations sampled during fall overlapped with the winter stations because of the presence of winter and fall spawning species (*L. xanthurus* and *M. undulatus*). There was also overlap of the winter and the warm weather outer-shelf stations (Fig. 10, A and B).

Similarly, the ten percent data set revealed two seasonal assemblages in the larval community data (Fig. 10, C and D). The warm weather assemblage comprised taxa associated with the warm weather station group and were collected during spring, summer, and fall. The winter assemblage was associated with the winter station group and comprised taxa collected during winter. Taxa from the warm weather inner- and mid-shelf assemblages were different from those representing the winter inner- and mid-shelf assemblages (Table 5). The outer-shelf assemblage, however, was less seasonally distinct, represented by *Bothus ocellatus/robinsi* in summer, fall, and winter and by *Auxis rochei* in spring, summer, and fall (Table 5).

Relation between seasonal larval assemblages and environmental variables

The seasonal pattern in the larval concentration data described above was maintained when constrained by environmental variables in the CCA. The community data clearly showed a seasonal influence on the first dimension in ordination space; winter taxa were separate from taxa collected during the rest of the seasons. This seasonal pattern was also reflected in the environmental data (Fig. 11). Salinity, density, temperature, depth, and stratification of the water column were again the most significant environmental variables for explaining variance in the species data ($P<0.05$, Monte Carlo permutation test, Table 6). The warm weather stations and taxa coincided with higher water temperature, lower density, and a lower density gradient. In addition, the cross-shelf pattern evident in the second and third dimensions of the full larval concentration data (Fig. 10, A and B) appeared to correlate with depth of the water column, the degree of stratification in the water column, and salinity (Fig. 11).

Implications for larval transport

The structure of larval assemblages was linked to water mass distributions and the cross-shelf zonation of physical circulation processes. Three cross-shelf zones of physical dynamics have been defined previously (Atkinson and Menzel, 1985; Pietrafesa et al., 1985a, 1985b; Lee et al., 1991; Boicourt et al., 1998). Three analogous cross-shelf zones were delineated in the larval community data. The cross-shelf larval assemblages were linked to three water masses with cross-shelf structure, and to the physical-chemical characteristics of the region (temperature, salinity, density, and stratification of the water column). The three cross-shelf zones identified previously in terms of physical dynamics coincided with the station groups and larval assemblages identified in our study. Thus, larval distribution and physical properties of the ocean are linked and indicate a strong influence of physical properties and processes on the distribution of larval fish on the southeast United States continental shelf.

Retention on the inner-shelf was a clear larval transport pattern identified in the analyses. *Menticirrhus americanus* represents the inner-shelf group (Table 5) and were always found inshore of the 20-m isobath in inner-shelf water, in inner-shelf–mid-shelf mixed water, or in mid-shelf water, (Fig. 12). Spawning likely occurs on the inner-shelf (Cowan and Shaw, 1988), and larvae are retained in the inner-shelf region.

The analyses also demonstrated that transport from offshore onto the shelf is limited on the continental shelf off the coast of Georgia. *Ceratoscopelus maderensis* and *Auxis rochei* were found only at offshore stations (Fig. 13), representing the outer-shelf group (Table 5) and the mid-shelf–Gulf Stream mixed water mass. The presence of *C. maderensis* identified transport of a mesopelagic fish to waters inshore of the shelf break; how-

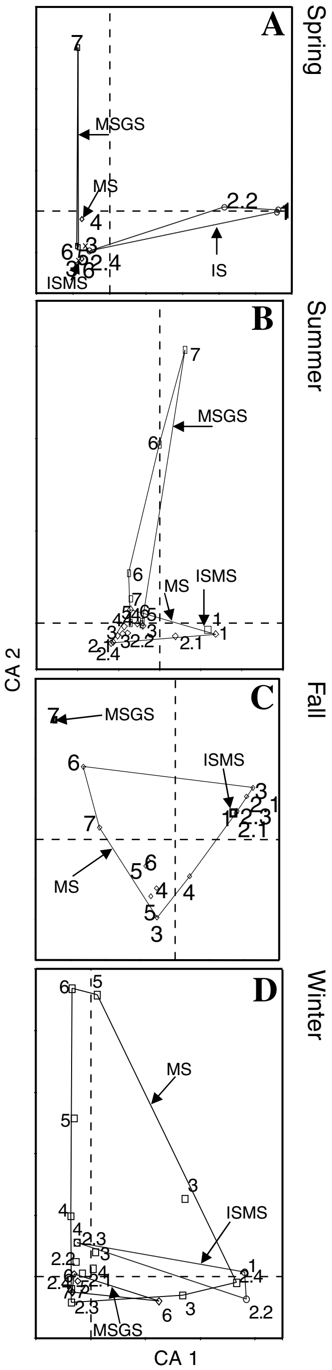


Figure 9

Correspondence analysis (CA) ordinations (portraying the first and second dimension scores) of the larval fish community data showing the full ten-percent data set: (**A**) spring, (**B**) summer, (**C**) fall, and (**D**) winter. The points represent stations classified by water mass. Solid lines enclose the boundary of each station group with three or more stations. Station groups comprising one or two stations are not enclosed by a solid line. Each station group is labeled and portrayed with a different symbol. Stations with inner-shelf water are labeled with IS (inner-shelf), inner-shelf–mid-shelf mixed water with ISMS, mid-shelf water with MS, and mid-shelf–Gulf Stream mixed water with MSGS. The dashed lines intersect at the origin of the plot. Analyses were conducted using larval data only.

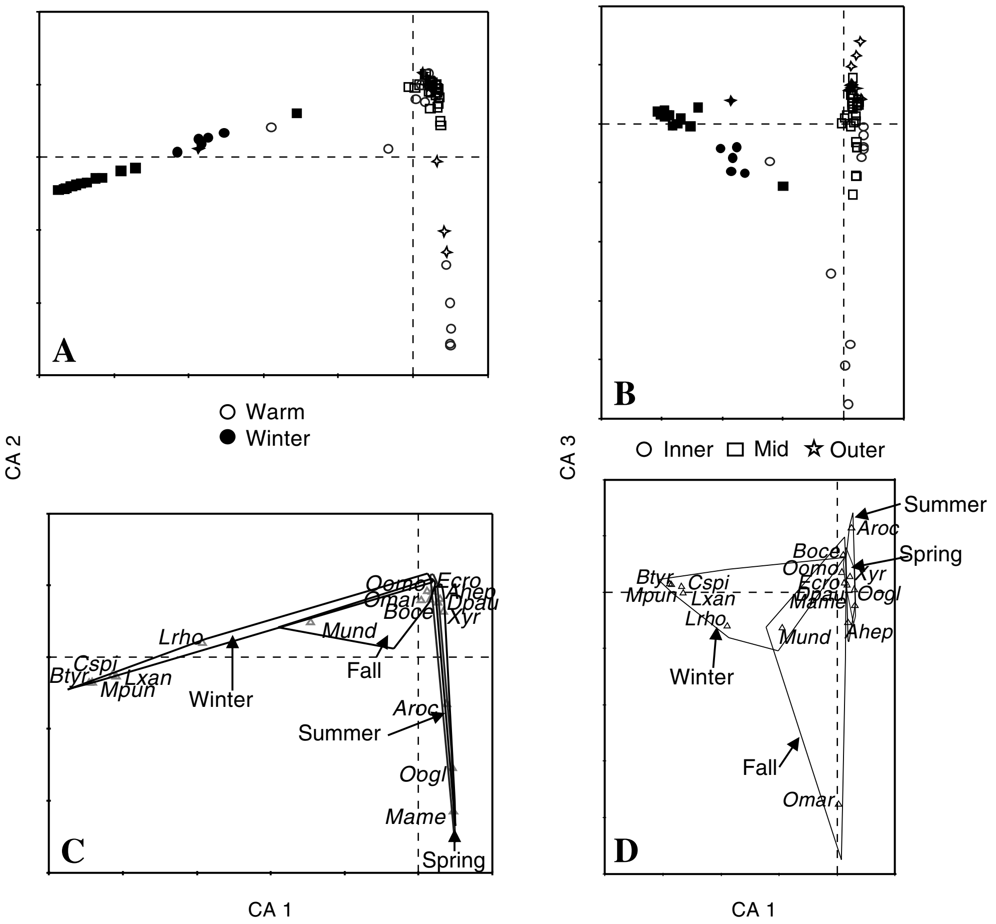


Figure 10

Correspondence analysis (CA) ordinations of the larval fish community data showing (**A**) the first and second dimension scores and (**B**) the first and third dimension scores of the station groups (inner, mid, and outer) defined within each season when the 10% data set was used. Open symbols denote stations sampled during the warm weather season and filled symbols denote stations sampled during the winter season. (**C**) The first and second dimensions and (**D**) the first and third dimensions of the station and species groups in the full data set are shown without the incorporation of the environmental data. The dashed lines intersect at the origin of the plot.

ever, the rarity of this species on the continental shelf off the coast of Georgia provides evidence for relatively limited onshore transport from off the shelf. Powell and Robins (1994, 1998) and Govoni and Spach (1999) also collected tropical and deepwater taxa inshore of the shelf break. The presence of these taxa was likely due to frequent but variable exchange of larvae across the Gulf Stream front (Govoni and Spach, 1999). Less is known about spawning of *A. rochei* but the species' larval distribution represents restriction to offshore waters (always collected offshore of the 40-m isobath).

During winter, when *B. tyrannus* was found across the shelf (Fig. 14), *Bothus ocellatus/robinsi* was collected only on the outer part of the shelf (Fig. 14). Both *B. tyrannus* and *B. ocellatus/robinsi* likely spawn on the outer shelf. However, unlike *B. tyrannus, Bothus ocellatus/robinsi* was never collected inshore of station 3 (the boundary between the inner- and mid-shelf zones), indicating that the two taxa may experience different transport pathways or different seasonal spawning patterns (see "Discussion" section).

Discussion

Three cross-shelf regions were defined on the continental shelf off the coast of Georgia based on the distribution and abundance of larval fish: inner-shelf, mid-shelf, and outer-shelf. Each region was dominated by a distinct group of species (i.e., larval assemblage). The inner-shelf

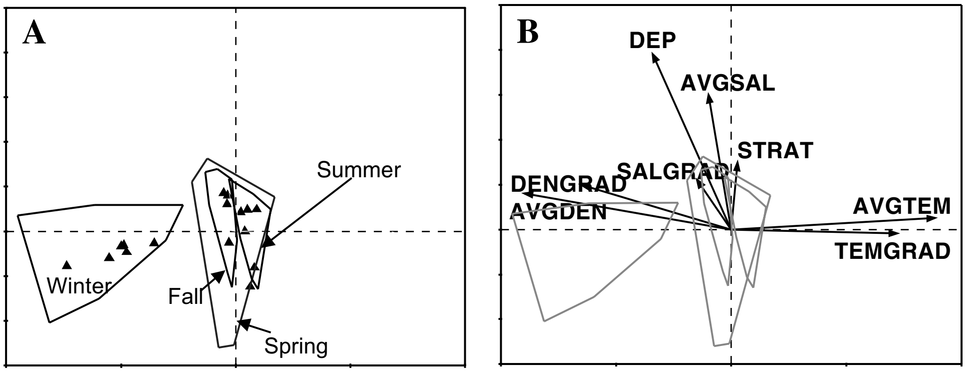


Figure 11

The correlation between environmental variables and station groups portrayed by canonical correspondence analysis (Fig. 10). (**A**) The proximity of seasonal station groups (black polygons) and taxa (black triangles) when environmental and larval concentration data were analyzed. (**B**) The relationship between the environmental variables (black arrows) and the seasonal station groups (gray polygons). The direction of the arrows depicts the gradient of each environmental variable. The dashed lines intersect at the origin of the plot.

region was defined inshore of the 20-m isobath (Figs. 4, 5, 12). The inner-shelf larval assemblage was the least diverse taxonomically (Table 2, Fig. 7B), and most taxa in the assemblage were nearshore or estuarine spawning species (e.g., *Cynoscion regalis*, *Menticirrhus americanus*, Table 2). Gradients in salinity and density were associated with the separation of the inner-shelf region but the direction of the gradient varied among seasons; in the spring and summer the inner-shelf region was characterized by lower salinity and density, whereas in the fall and winter, the inner-shelf region was characterized by higher salinities and densities (Fig. 8). The restricted inshore distribution of the assemblage indicated mechanisms of larval retention in the inner-shelf zone.

The mid-shelf region was defined between the 20- and 40-m isobaths (Figs. 4, 5, 12). The mid-shelf larval assemblage was distributed over the widest area (Figs. 4, 5, 12) and species in the assemblage were found in all three regions defined (Fig. 6). The mid-shelf region and larval assemblage were related to the average environmental parameters encountered on the shelf (Fig. 8), which varied seasonally. The broad distribution of the assemblage indicated either broad spawning distributions of member species or mechanism of larval transport to both the inner- and outer-shelf regions.

The outer-shelf region was defined as the area offshore from the 40-m isobath (Figs. 4, 5, 12). The outer-shelf region was related to increased stratification of the water column, which was likely a result of Gulf Stream waters mixing onshore. These periodic intrusions would help explain the higher species richness of rare taxa found on the outer-shelf during fall and winter (Fig. 7B). Taxa in the outer-shelf assemblage were either spawned on the outer-shelf (e.g., *Hemanthias vivanus*), spawned offshore of the shelf break and transported onto the shelf (e.g., *Ceratoscopelus maderensis*), or spawned south of the study area and transported onto the shelf (e.g., *Abudefduf* sp.). Most outer-shelf taxa, however, were restricted to outer-shelf stations indicating limited onshore exchange between the outer- and mid-shelf regions.

Larval assemblages on the continental shelf off the coast of Georgia are derived from a combination of spawning distributions and larval transport; *Brevoortia tyrannus* and *Bothus ocellatus/robinsi* provide an example. *Brevoortia tyrannus* spawn in water temperatures between 16° and 23°C during winter (Checkley et al. 1999); these temperatures were experienced in the mid- and outer-shelf regions during winter. *Bothus ocellatus/robinsi* adults also occur on the mid- and outer-shelf of the continental shelf off the coast of Georgia (Gutherz, 1967). Thus, during winter the spawning distribution of these two species are likely similar. The larval distributions, however, are different: *B. tyrannus* larvae were collected in all three regions of the shelf during winter, whereas *B. ocellatus/robinsi* were collected on the mid- and outer-shelf (Fig. 14). The vertical distributions of the two species also are different. *B. tyrannus* larvae occur higher in the water column than do *B. ocellatus/robsini* (Hare and Govoni[1]). The observed differences in horizontal distribution could result from the differences in vertical distributions. Alternatively, the distributional differences could result from physiological differences that allow *B. tyrannus* larvae to survive cooler inshore waters or could result from seasonal cross-shelf spawning patterns that result

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[1] Hare, J. A., and J. J. Govoni. 2004. In review. Vertical distribution and the outcome of larval fish transport along the southeast US continental shelf during winter.

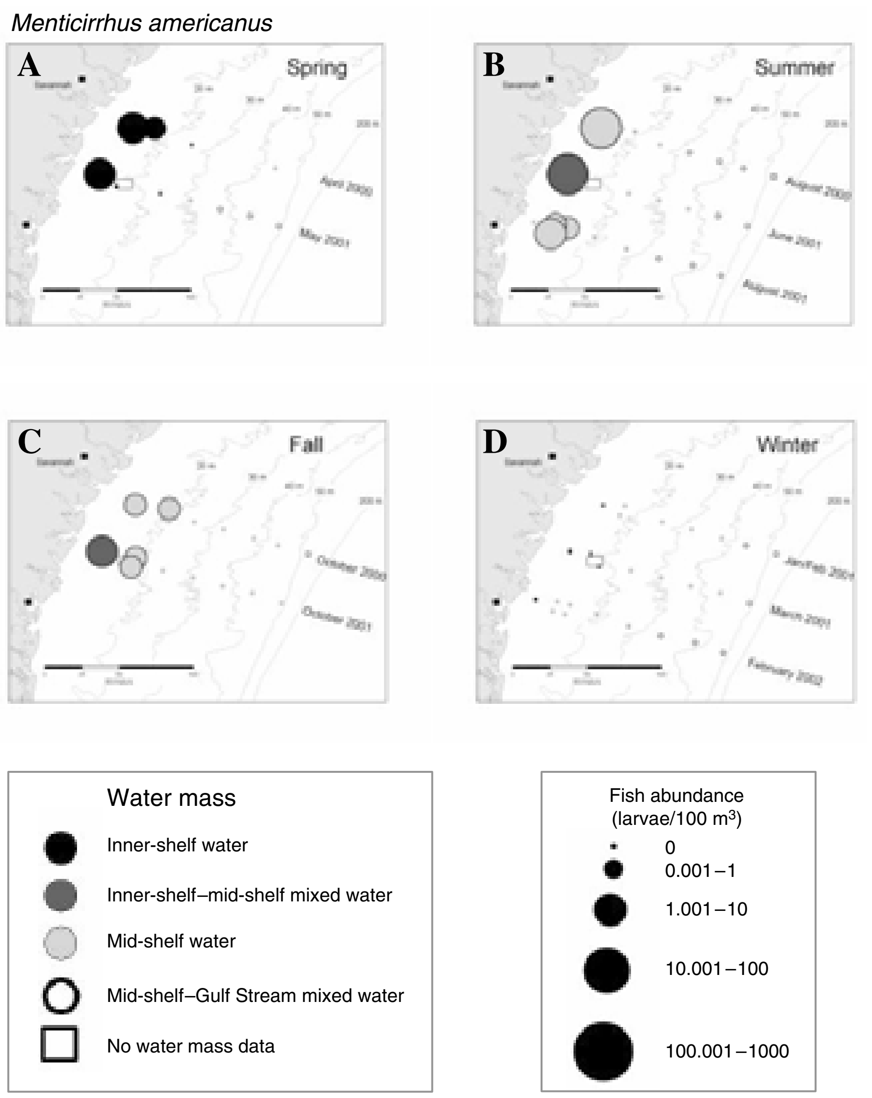

Figure 12

Distribution of *Menticirrhus americanus* in (**A**) spring, (**B**) summer, (**C**) fall, and (**D**) winter. Transects for each cruise within a season are offset from one another. The size of the circle for each station varies with larval fish concentration (larvae/100 m^3). The fill color for each circle varies with water mass.

in *B. tyrannus* spawning inshore during the fall. This example demonstrates that there are multiple mechanisms or pathways that affect the transport of larval fish, and that each species may be subject to different transport regimes. Therefore, to understand larval transport, many factors, including physical forcing mechanisms, the horizontal and vertical distributions of larvae, seasonal patterns, and the physiology of a species, need to be considered.

Temporal larval assemblages were defined in addition to the spatial assemblages. Larvae clearly separated into two seasonal spawning groups: winter and warm seasons (Fig. 10). The winter assemblage was associated with cool, denser water, whereas the warm water assemblage was associated with warmer, less dense water (Fig. 11). The cross-shelf structure in larval assemblages was still evident in the two seasonal assemblages, but there was overlap in the winter and warm-weather outer-shelf assemblages (Fig. 10). This overlap occurred in waters with the least seasonal variability in temperature and salinity and likely results from year-round spawning by species in the outer-shelf assemblage or year-round supply of larvae to the outer-shelf region by the Gulf Stream.

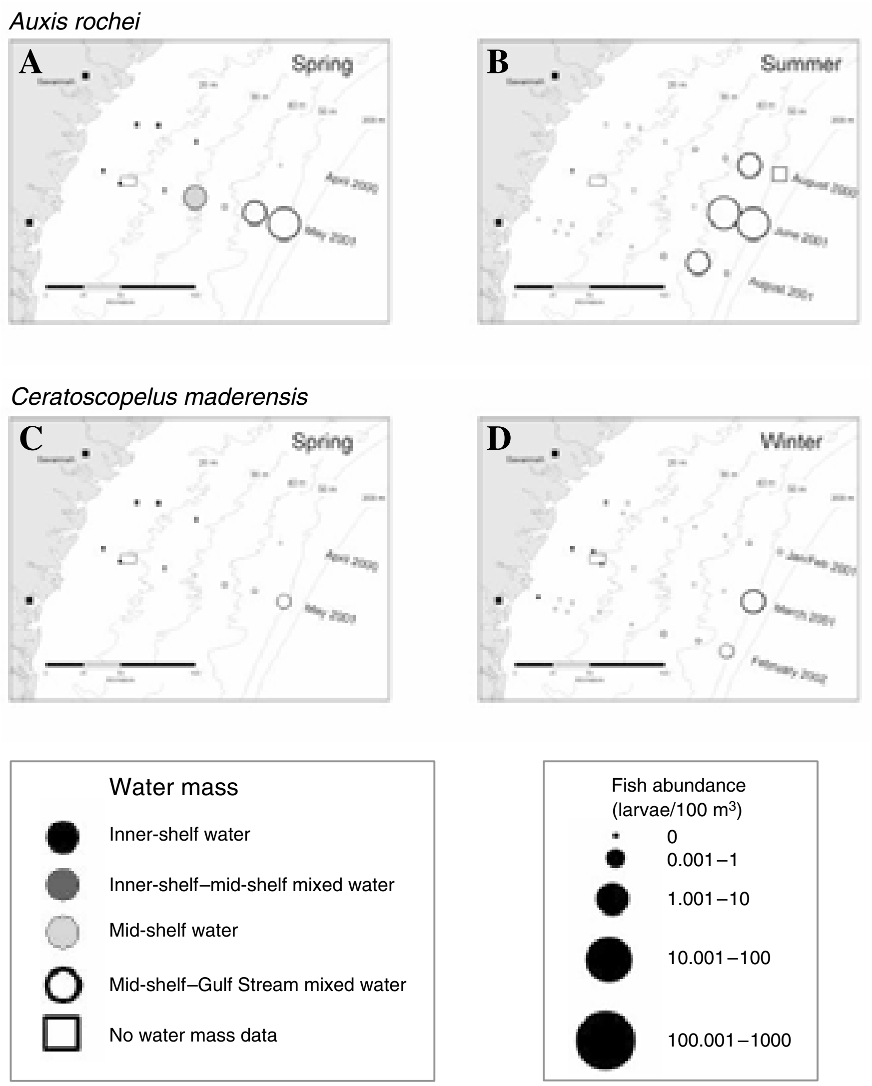

Figure 13

Distribution of *Auxis rochei* in (**A**) spring, (**B**) summer, and distribution of *Ceratoscopelus maderensis* in (**C**) spring (**D**) winter, across the shelf and across water masses. Transects for each cruise within a season are offset from one another. The size of the circle for each station varies with fish concentration (larvae/100 m^3). The fill color for each circle varies with water mass.

Winter-spawning species that use estuaries are frequently grouped together as "estuarine-dependent" taxa (*sensu* Warlen and Burke, 1990). However, Hare and Govoni[1] found that vertical distributions of these winter taxa are different. In addition, our study demonstrated that the horizontal distributions of these species are distinct: *Lagadon rhomboides* and *Micropogonias undulatus* were members of the inner-shelf assemblage and *Leiostomus xanthurus*, *Myrophis punctatus*, and *Brevoortia tyrannus* were members of the mid-shelf assemblage. These findings imply that often grouped "estuarine-dependent" species have different spawning locations or experience different larval transport processes (or both) and may not reflect a single group.

The definition of three regions based on larval fish distributions is consistent with the division of the shelf into three cross-shelf zones based on physical dynamics. The inner-shelf (0–20 m) is dominated by freshwater discharge, tides, and winds; the mid-shelf (20–40 m) is influenced by wind and tides; and the outer-shelf (40–75 m) is affected by the Gulf Stream and wind (Atkinson and Menzel, 1985; Pietrafesa et al., 1985a, 1985b; Lee et al., 1991; Boicourt et al., 1998). Thus, the physical dynamics of the shelf appear to be closely linked to spa-

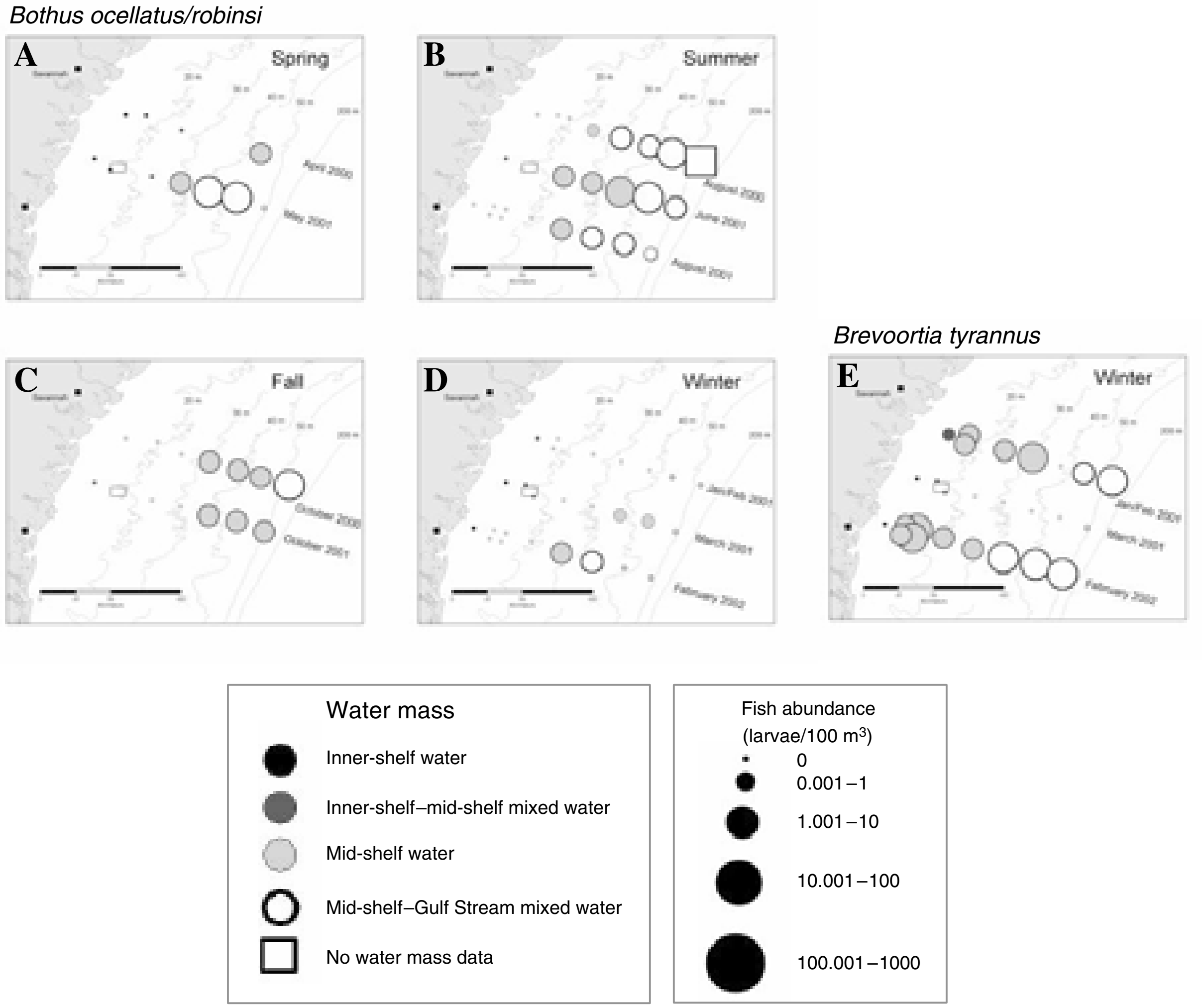

Figure 14

Distribution of *Bothus ocellatus/robinsi* in (**A**) spring, (**B**) summer, (**C**) fall, and (**D**) winter, and *Brevoortia tyrannus* (**E**) in winter, across the shelf and across water masses. Transects for each cruise within a season are offset from one another. The size of the circle for each station varies with fish concentration (larvae/100 m^3). The shading for each circle varies with water mass.

tial patterns in the distribution of larval fish. Further physiochemical characteristics of the environment (e.g., temperature, salinity, water masses) are highly associated with the structure of larval assemblages (Tables 4, 6, Fig. 9), again indicating a strong link between physical dynamics and larval distribution. However, patterns in spawning and behaviorally modified vertical distributions also have an influence on larval distributions and thus a simple two-dimensional passive model will not adequately explain the distribution of larval fish on the continental shelf off the coast of Georgia.

The three regions defined in our study have important implications for the consideration of MPAs on the southeast United States shelf. The described cross-shelf zones (inner-, mid-, or outer-shelf) provide information needed to protect spawning habitat of specific species (e.g., *Rhomboplites aurorubens* spawns on the outer-shelf; Table 2). Conversely, the species included in an area under consideration for protection can also be derived (e.g., Gray's Reef National Marine Sanctuary potentially protects species spawning at the interface between the inner- and mid-shelf, Table 2). Further, spawning location information can be derived for several species protected under the South Atlantic Fisheries Management Council's coastal migratory pelagics management plan (e.g., *Rachycentron canadum*, *Scomberomorus cavalla*, *Scomberomorus maculatus*, or *Coryphaena hippurus*, Table 2), but individuals of these species range so widely (Sutter et al., 1991), only very large MPAs would afford protection from fishing (Parrish 1999, Beck and Odaya 2001). Unfortunately, many species in the snapper-grouper complex, a more sedentary group of species of particular importance in the southeast United States, were not collected. Either these taxa do not spawn on the continental shelf off the coast of Georgia and their larvae are rarely transported into the area, or snapper-grouper spawning on the continental shelf off the coast of Georgia is at a very low level and larvae are quite rare.

Another aspect of MPAs designed for fisheries management is production of individuals in the MPA and their supply to surrounding areas; larval transport is a major mechanism of supply. On the continental shelf off the coast of Georgia, larval assemblages suggest that the supply of larvae from the south (by the Gulf Stream) and even between cross-shelf zones is limited. Members of the outer-shelf assemblage rarely occurred on the mid- and inner-shelf, and members of the inner-shelf assemblage rarely occurred on the mid- and outer-shelf. Thus, larvae spawned on the inner-shelf and to a lesser degree on the mid-shelf likely remain on the continental shelf off the coast of Georgia and appear to be subject to local retention. MPAs in the region, therefore, could provide a local benefit by supplying recruits to nonprotected areas on the continental shelf off the coast of Georgia.

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Literature cited

Atkinson, L. P., and D. W. Menzel.
1995. Introduction: Oceanography of the southeast United States continental shelf. *In* Oceanography of the southeastern U.S. continental shelf (L. P. Atkinson, D. W. Menzel, and K. A. Bush, eds.), p 1–9. Am Geophysical Union, Washington, D. C.

Beck, M. W., and M. Odaya.
2001. Ecoregional planning in marine environments: identifying priority sites for conservation in the northern Gulf of Mexico. Aquat. Conserv.: 11:235–242

Blanton, J. O., F. B. Schwing, A. H. Weber, L. J. Pietrafesa, and D. W. Hayes.
1985. Wind stress climatology in the south Atlantic Bight. *In* Oceanography of the Southeastern U.S. continental shelf (L. P. Atkinson, D. W. Menzel, and K. A. Bush, eds.). p. 10–22. American Geophysical Union, Washington, D.C.

Boicourt, W. C., W. J. Wiseman Jr., A. Valle-Levinson, and L. P. Atkinson.
1998. Chapter 6. Continental shelf of the southeastern United States and the Gulf of Mexico: in the shadow of the western boundary current. *In* The sea, vol. 11 (A. R. Robinson and K. H. Brink, eds.), p. 135–182. John Wiley and Sons, Inc., New York, NY.

Checkley, Jr., D. M., P. B. Ortner, F. E. Werner, L. R. Settle, and S. R. Cumming.
1999. Spawning habitat of the Atlantic menhaden in Onslow Bay, North Carolina. Fish. Oceanogr. 8:22–36.

Churchill, J. H., E. R. Levine, D. N. Connors, and P. C. Cornillon.
1993. Mixing of shelf, slope and Gulf Stream water over the continental slope of the Middle Atlantic Bight. Deep-Sea Res. 40:1063–1085.

Clarke, K. R., and R. M. Warwick.
2001. Change in marine communities: an approach to statistical analysis and interpretation. PRIMER-E, 2nd ed., 144 p. Plymouth Marine Laboratory, Plymouth, Cornwall, UK.

Collins, M. R., and B. W. Stender.
1987. Larval king mackerel (*Scomberomorus cavalla*), Spanish mackerel (*S. maculates*), and bluefish (*Pomatomus saltatrix*) off the southeast coast of the United States, 1973–1980. Bull. Mar. Sci. 41:822–834.
1987. Larval striped mullet (*Mugil cephalus*) and white mullet (*Mugil curema*) off the southeastern United States. Bull. Mar. Sci. 45:580–589.

Cowan, J. H., and R. F. Shaw.
1988. The distribution, abundance, and transport of larval sciaenids collected during winter and early spring from the continental shelf waters off west Louisiana. Fish. Bull. 86:129–142.

Cowen, R. K. , J. A. Hare, and M. P. Fahay.
1993. Beyond hydrography: can physical processes explain larval fish assemblages within the Middle Atlantic Bight? Bull. Mar. Sci. 53:567–587.

Crowder, L. B., S. J. Lyman, W. F. Figueira, and J. Priddy.
2000. Source-sink population dynamics and the problem of siting marine reserves. Bull. Mar. Sci. 66:799–820.

Fahay, M. P.
1975. An annotated list of larval and juvenile fishes captured with surface-towed meter net in the South Atlantic Bight during four RV *Dolphin* cruises between May 1967 and February 1968. NOAA/NMFS Technical Report SSRF 685, 39 p
1983. Guide to the early stages of marine fishes occurring in the western North Atlantic Ocean, Cape Hatteras to the southern Scotian Shelf. Northwest Atl. Fish. Sci. 4:1–423.

Federal Register.
2000. Presidential documents. Executive Order 13158 of

May 26, 2000. Volume 65, number 105, May 31 2000. U.S. Government Printing Office, Washington, D.C.

Govoni, J. J., and H. L. Spach.
1999. Exchange and flux of larval fishes across the western Gulf Stream front south of Cape Hatteras, USA, in winter. Fish. Oceanogr. 8(suppl. 2):77–92.

Gutherz, E. J.
1967. Field guide to the flatfishes of the family Bothidae in the Western North Atlantic, 47 p. United States Department of the Interior, Washington, D.C.

Hare, J. A., J. A. Quinlan, F. E. Werner, B. O. Blanton, J. J. Govoni, R. B. Forward, L. R. Settle, and D. E. Hoss.
1999. Larval transport during winter in the SABRE study area: results of a coupled vertical larval behavior-three-dimensional circulation model. Fish. Oceanogr. 8:57–76.

Hare, J. A., M. P. Fahay, and R. K. Cowen.
2001. Springtime ichthyoplankton of the Slope Sea: larval assemblages, relation to hydrography and implications for larval transport. Fish. Oceanogr. 10:164–192.

Hoss, D. E., H. L. Spach, L. R. Settle, J. A. Hare, and E. H. Laban.
1997. The growth and behaviour of two species of clupeid larvae and how it affects their oceanic transport. *In* Ichthyoplankton ecology (A. J. Geffen, J. M. Fives, J. E. Thorpe, eds.), 22 p. Fisheries Society of the British Isles, Galway, Ireland.

Johnson, G. D., and P., Keener.
1984. Aid to the identification of American grouper larvae. Bull. Mar. Sci. 34:106–134.

Judy, M. H., and R. M. Lewis.
1983. Distribution of eggs and larvae of Atlantic menhaden, *Brevoortia tyrannus* along the Atlantic coast of the United States. U. S. National Marine Fisheries Service, Special Scientific Report—Fisheries 774, 23 p.

Kendall, A. W., Jr., and A. C. Materese.
1994. Status of early life history descriptions of marine teleosts. Fish. Bull. 92:725–36.

Kendall, A. W., Jr, and L. A. Walford.
1979. Sources and distribution of bluefish, Pomatomus saltatrix, larvae and juveniles off the east coast of the United States. Fish. Bull. 77:213–27.

Lee, T. N., J. A. Yoder, and L. P. Atkinson.
1991. Gulf Stream frontal eddy influence on productivity of the southeast U.S. continental shelf. J. Geophy. Res. 96:22191–2205.

Leis, J. M.
1989. Larval biology of butterflyfishes (Pisces, Chaetodontidae): what do we really know? Environ. Biol. Fishes 25:87–00.

Marancik, K. E.
2003. Larval fish assemblages of the Georgia Bight. M.S. thesis, 149 p. East Carolina Univ., Greenville, NC.

Parrish, R.
1999. Marine reserves for fisheries management: why not. CalCOFI Rep. 40:77–6

Pietrafesa, L. J., J. O. Blanton J. D. Wang, V. Kourafalou, T. L. Lee, and K. A. Bush.
1985a. The tidal regime in the South Atlantic Bight. *In* Oceanography of the southeastern U.S. continental shelf (L. P. Atkinson, D. W. Menzel, K. A. Bush, eds.), p. 63–6. American Geophysical Union, Washington, D.C.

Pietrafesa, L. J., G. S. Janowitz, and P. A. Wittman.
1985b. Physical oceanographic processes in the Carolina Capes. *In* Oceanography of the southeastern U.S. continental shelf (L. P. Atkinson, D. W. Menzel, K. A. Bush, eds.), p. 23–32. American Geophysical Union, Washington, D.C.

Pietrafesa, L. J., J. M. Morrison, M. P. McCann, J. Churchill, E. Bohm, and R. W. Houghton.
1994. Water mass linkages between the Middle and South Atlantic Bights. Deep-Sea Res. II 41:365–89.

Plan Development Team.
1990. The potential of marine fishery reserves for reef fish management in the U.S. southern Atlantic. NOAA Tech. Memo. NMFS-SEFC-261, 40 p.

Powell, A. B., D. G. Lindquist, and J. A. Hare.
2000. Larval and pelagic juvenile fishes collected with three types of gear in Gulf Stream and shelf waters in Onslow Bay, North Carolina, and comments on ichthyoplankton distribution and hydrography. Fish. Bull. 98:427–38.

Powell, A. B., and R. E. Robbins
1994. Abundance and distribution of ichthyoplankton along an inshore-offshore transect in Onslow Bay, North Carolina. NOAA Tech. Report NMFS 120, 28 p.
1998. Ichthyoplankton adjacent to live-bottom habitats in Onslow Bay, North Carolina. NOAA Tech. Report NMFS 133, 32 p.

Powles, H., and B. W. Stender.
1976. Observations on composition, seasonality and distribution of ichthyoplankton from MARMAP cruises in the South Atlantic Bight in 1973. South Carolina Marine Resources Center, Technical Report Series Number 11, Charleston, SC.

Rakocinski, C. F., J. Lyczkowski-Shultz, and S. L. Richardson.
1996. Ichthyoplankton assemblage structure in Mississippi Sound as revealed by canonical correspondence analysis. Estuar. Coast. Shelf Sci. 43:237–57.

Richards, W. J. (ed.).
2001. Preliminary guide to the identification of the early life history stages of fishes of the Western Central Atlantic. (http://www4.cookman.edu/noaa). [Accessed 12 May 2004.]

Simpson, J. H., and I. D. James.
1986. Coastal and estuarine fronts. *In* Baroclinic processes on continental shelves (C. N. K. Mooers, ed.), p. 63–93. American Geophysical Union, Washington, D.C.

Smith, W., P. Berrien, and T. Potthoff.
1994. Spawning patterns of bluefish, Pomatomus saltatrix in the northeast continental shelf ecosystem. Bull. Mar. Sci. 54:8–6.

Smith, K. A., M. T. Gibbs, J. H. Middleton, and I. M. Suthers.
1999. Short term variability in larval fish assemblages of the Sydney shelf: tracers of hydrographic variability. Mar. Ecol. Prog. Ser. 178:1–5.

Stephenson, R. L.
1999. Stock complexity in fisheries management: A perspective of emerging issues related to population sub-units. Fish. Res. 43:247–249

Sutter, F. C., III, R. I. Williams, and M. F. Godcharles.
1991. Movement patterns and stock affinities of king mackerel in the southeast United States. Fish. Bull. 89:315–324

ter Braak, C. F. J.
1988. CANOCO—a FORTRAN program for canonical community ordination by correspondence analysis, principal components analysis and redundancy analysis. Technical Report: LWA-88-02. Groep Landbouw-wiskunde, Wageningen, The Netherlands.

ter Braak, C. F. J., and P. Smilauer.
2002. CANOCO Reference manual and CanoDraw for Windows User's guide: software for canonical community ordination (vers. 4.5), 500 p. Microcomputer Power Ithaca, New York, NY.

Warlen, S. M., and J. S. Burke.
1990. Immigration of larvae of fall/winter spawning marine fishes into a North Carolina estuary. Estuaries 13:453–61.

Warner, R. R., S. E. Swearer, and J. E. Caselle.
2000. Larval accumulation and retention: Implications for the design of marine reserves and essential fish habitat. Bull. Mar. Sci. 66:821–830.