Abstract—Patterns were investigated in juvenile fish use of unconsolidated sediments on the southeast United States continental shelf off Georgia. Juvenile fish and environmental data were sampled at ten stations along a 110-km cross-shelf transect, including four stations surrounding Gray's Reef National Marine Sanctuary (Gray's Reef NMFS). Cross-shelf stations were sampled approximately quarterly from spring 2000 to winter 2002. Additional stations were sampled on three transects inshore of Gray's Reef NMS and four transects offshore of the Sanctuary during three cruises to investigate along-shelf patterns in the juvenile fish assemblages. Samples were collected in beam trawls, and 121 juvenile taxa, of which 33 were reef-associated species, were identified. Correspondence analysis on untransformed juvenile fish abundance indicated a cross-shelf gradient in assemblages, and the station groupings and assemblages varied seasonally. During the spring, fall, and winter, three cross-shelf regions were identified: inner-shelf, mid-shelf, and outer-shelf regions. In the summer, the shelf consisted of a single juvenile fish assemblage. Water depth was the primary environmental variable correlated with cross-shelf assemblages. However, salinity, density, and water column stratification also correlated with the distribution of assemblages during the spring, fall, and winter, and along with temperature likely influenced the distribution of juvenile fish. No along-shelf spatial patterns were found in the juvenile fish assemblages, but the along-shelf dimension sampled was small (~60 km). Our results revealed that a number of commercially and recreationally important species used unconsolidated sediments on the shelf off Georgia as juvenile habitat. We conclude that management efforts would be improved through a greater recognition of the importance of these habitats to fish production and the interconnectedness of multiple habitats in the southeast U.S. continental shelf ecosystem.

Juvenile fish assemblages collected on unconsolidated sediments of the southeast United States continental shelf

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Fisheries management has been rapidly evolving for the southeast United States with the development of a formal stock assessment process (i.e., SEDAR[1]), and the identification of essential fish habitat (EFH; SAFMC, 1998). Single-species management plans have been used as the basis for fisheries management along the southeast United States for decades, and EFH is just beginning to be incorporated into management plans (e.g., *Sargassum* and *Oculina* bank habitat of particular concern: FR, 2000). Globally, as fish stocks continue to decline (Botsford et al., 1997) and harvest shifts to new species (Pauly et al., 1998), interest in ecosystem management and implementation of MPAs in many areas, including the southeast U.S. continental shelf, is growing (SAFMC, 2001). Understanding how juvenile fish use habitat is important for both single-species fishery management and ecosystem approaches to fishery management. A description of habitat needs at each life history stage for species that represent the "significant food web" are also a recognized part of fishery ecosystem plans (NOAA[2]; CFEPTAP, 2004).

Adult population variability, in most species, is caused by variability in the survival of the early-life stages: egg, larval, and juvenile (Sissenwine, 1984; Rothschild, 1986). Survival of these early stages is influenced by both habitat quantity and quality (Gibson, 1994; Peterson, 2003). One

approach to improving marine fisheries management is to incorporate habitat effects on early-life stage survival into stock assessments (Beck et al., 2001; Peterson, 2003). Determining how juvenile fish use habitat also benefits marine protected area (MPA) design and implementation. MPAs have been proposed to complement traditional fishery management practices by imposing site-specific rules to protect enclosed resources (Parrish, 1999; Dayton et al., 2000; Beck and Odaya, 2001). In some instances, MPAs provide benefits to outside areas through spillover effects (Roberts et al., 2001). MPAs may also provide a source of recruits to other nonprotected areas through planktonic transport (Cowen et al., 2000; Shanks et al., 2003). To be effective in protecting fishery resources, an MPA or a network of MPAs needs to encompass the habitats used by spe-

cies throughout their life cycle (Browman and Konstantinos, 2004).

Habitat use by juvenile fish has been studied extensively along the southeast United States, particularly for commercial and recreational species and structured habitats. For example, there is information available regarding the habitat use of specific estuarine (e.g., *Cynoscion nebulosus*: Thayer et al., 1999; paralichthid flounders: Walsh et al., 1999) and reef-associated species (e.g., *Mycteroperca microlepis*: Ross and Moser, 1995; *Lutjanus griseus*: Chester and Thayer, 1990; *Centropristis striata*: Lehnert and Allen, 2002). The importance of structural habitat to juvenile fish is also demonstrated by the consistent use of seagrass (Thayer et al., 1999), oyster reef (Meyer and Townsend, 2000), pelagic *Sargassum* (Moser et al., 1998), mangrove (Thayer et al., 1987), marsh (Hettler, 1989), and rocky reefs (Lindeman et al., 2000). Unconsolidated sediments in estuarine systems and from the surf-zone out into shallow coastal areas (<10 m) are also important juvenile habitat (estuarine: Burke et al., 1991; Walsh et al., 1999; surf-zone: Wenner and Sedberry, 1989; Ross and Lancaster, 2002).

Despite this large body of research, little is know about the use of unconsolidated sediments on the inner-, mid-, and outer-shelves of the southeast U.S. continental shelf. Unconsolidated sediment is not identified as EFH of the southeast U.S. (SAFMC, 1998), although it is identified in several fishery management plans (red drum, snapper-grouper, rock shrimp, royal red shrimp, coastal migratory pelagics, golden crab, spiny lobsters, and calico scallops). The only offshore habitats that currently have specific protection through their own fishery management plans are coral, coral reefs, live hard bottom, and pelagic *Sargassum* (Barnette[3]; FR, 2000). Research in other shelf ecosystems has identified unconsolidated sediments on the shelf as important juvenile habitat (Norcross et al., 1997; Steves et al., 2000; Sullivan et al., 2000; Johnson et al., 2001). Further, unconsolidated sediments on the southeast U.S. continental shelf cover a majority of the area (~60–80%; Parker et al., 1983), and likely serve as juvenile habitat for the more than 1200 fish species reported from the ecosystem (estimated from Kendall and Matarese, 1994). Thus, well-defined use of unconsolidated sediment habitat by juvenile fish is needed for sediment habitat to be incorporated into future fishery resource management on the southeast U.S. continental shelf.

Our purpose was to document juvenile fish habitat use and to examine the structure of juvenile fish assemblages in unconsolidated sediments off the Georgia coast region of the southeast U.S. continental shelf. Specific objectives were 1) to provide a list of species that

use unconsolidated sediments on the shelf as juvenile habitat; 2) to determine which reef-associated species use unconsolidated sediments as juvenile habitat; and 3) to describe the relationships between the juvenile assemblages and environmental factors. The focus on reef fish was motivated largely by the emphasis to protect reef areas by using MPAs, as part of the management of the reef-associated snapper-grouper complex (SAFMC, 2001). If species of the reef-associated snapper-grouper complex use unconsolidated sediments during the juvenile stage, then protection of these habitats should be incorporated into the larger MPA effort.

Materials and methods

Study site

The continental shelf off the Georgia coast is the widest part (200 km) of the southeast shelf. The shelf in this region is gently sloping and comprises four depth zones (Menzel, 1993); inner-shelf (0–20 m); mid-shelf (20–40 m), outer-shelf (40–70 m), and shelf-edge (70–200 m). Each zone has different physical dynamics (Atkinson et al., 1985), climate (Blanton et al., 2003), and larva1 fish assemblages (Marancik et al., 2005). Demersal habitat consists of unconsolidated sediments, primarily medium to coarse quartz and carbonate sands (Nelson et al., 1999) interspersed with rocky reefs (Parker et al., 1983). Reefs of the southeast U.S. shelf range from no relief patchy live-bottom communities, to high-relief ledges. On the shelf off Georgia, rocky-reefs cover about 30% of the bottom (Parker et al., 1983). Rocky-reef habitats have a high diversity of invertebrate (Wenner et al., 1983) and vertebrate faunas (Chester et al., 1984; Parker and Mays, 1998; Lindeman et al., 2000). Located within the continental shelf off Georgia is the 56-km^2 Gray's Reef National Marine Sanctuary (Gray's Reef NMS, Fig. 1). The sanctuary depth ranges from 18 to 22 m and the benthic macrohabitat is mainly (~75%) unconsolidated sand sediments interspersed with patchy live-bottom and moderate relief (≤2 m) hard-bottom ledges (Parker et al., 1994). The adult reef fish community of the sanctuary is typical of other inner-shelf (<30 m) reefs of the South and North Carolina shelves (Chester et al., 1984; Parker et al., 1994).

Collection of juvenile fish and environmental data

Sampling of juvenile fish was conducted approximately quarterly from April 2000 through February 2002 (Table 1). Ten cross-shelf stations (stations 1–7), approximately 18.5 km apart, were sampled during most cruises (Fig. 1). Stations were missed on some cruises owing to weather and equipment failure (Table 1). The cross-shelf transect was 110 km long and stations were sampled on the inner-, mid-, and outer-shelf (10 to 50 m water depth). To avoid sampling within Gray's Reef NMS, four stations were placed immediately adjacent to the four sides of the sanctuary (stations 2.1–2.4). Additional
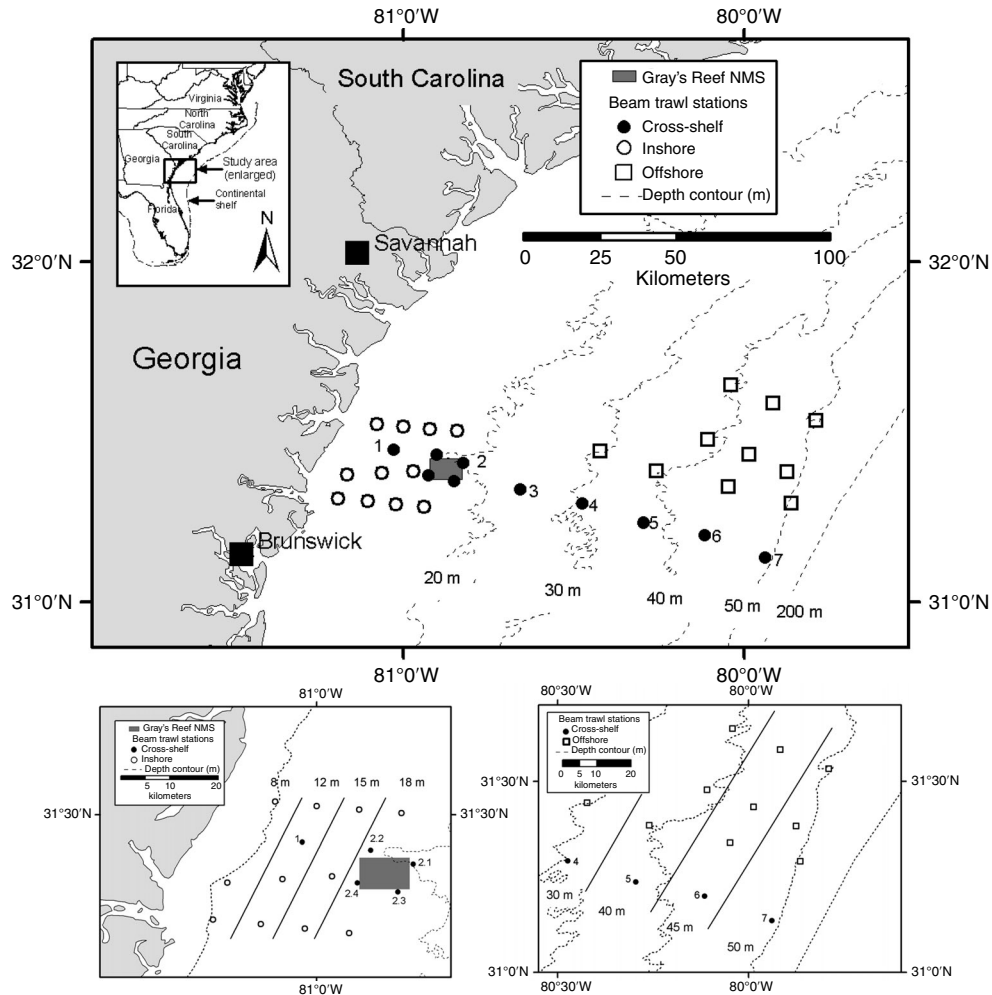

Figure 1

Maps of the study area showing cross-shelf beam trawl stations (black dots) at which juvenile fish and environmental sampling occurred quarterly from April 2000–February 2002 (see Table 1). Additional stations were sampled inshore (circles) and offshore (squares) of Gray's Reef NMS (see Table 1) (**A**). Station groups used in correspondence analysis of the inshore (**B**) and offshore (**C**) juvenile fish data sets are separated by solid lines and labeled.

stations were sampled along three transects inshore of Gray's Reef NMS and along four offshore transects during three cruises (Fig. 1 and Table 1). The benthic macrohabitat of the cross-shelf stations was determined by using a remotely operated vehicle (ROV, *Phantom* S2). The ROV was deployed off the starboard side of the ship. Approximately 30 m of the ROV tether was let out before the tether was attached to a 45-kg weight. The weight was lowered to 3 m above the bottom and the ship was allowed to drift. During April 2000, two 15-min drifts were made at eight of the ten cross-shelf stations. Because of inclement weather, no drifts were conducted at the inner- or outer-most stations. Video (HI-8 mm) was recorded of each drift.

Concurrent fish and hydrographic measurements were taken to examine the relationship between juvenile fish assemblages and the environment. At each sta-

tion, temperature, salinity, density, and water depth were measured from the water's surface to one meter above the bottom with a Seabird CTD (SBE19, Seabird Electronics, Inc., Bellevue, WA). Juvenile fish were collected at each station by using a 2-m beam trawl with a 6-mm mesh body and a 3-mm mesh tail bag. Two kilogram weights were added to each skid of a standard 2-m beam trawl (Kuipers, 1975) to ensure that the trawl stayed on the bottom. Three 5-min bottom tows were made at each station. Samples were sorted on deck and fish and invertebrates were preserved in 95% ethanol.

Preparation of fish data

All beam trawl samples were sorted and fish were identified to the lowest possible taxonomic level by using previously published descriptions (e.g., Able and Fahay,

Table 1

Number of beam trawl stations sampled off the coast of Georgia for juvenile fish. Station groups correspond to the station locations in Figure 1.

| Year | Month | Dates | Season | Station group | | |
				Cross-shelf	Inshore	Offshore
2000	April	24–27	spring	9		
	June	19–22	summer	9		
	August	15–17	summer	9		
	October	03–07	fall	10		
2001	Jan/Feb	30–01	wnter	10		
	March	21–23	winter	10		
	Apr/May	30–04	spring	10	11	
	June	04–09	summer	10		
	August	03–06	summer	10		
	September	07–09	fall			6
	October	11–13	fall	10		
2002	February	08–13	winter	10	10	10

1998; Munroe, 1998). Identification to species was not possible for all fish. Taxa were separated into larval, juvenile, and adult age classes according to life-history characteristics from the literature and standard length distributions (SL, mm) from the beam trawl collections. Fish were classified as larvae if fin development was not complete (and defined as "larvae at settlement stage" when fin formation was complete and pigmentation incomplete; fish were classified as juveniles when pigmentation was complete, and were classified as adults if they exceeded the reported minimum SL for sexual maturity. Because the mesh of the beam trawl is large enough to extrude larvae and less efficient at catching large (>150 mm SL) fish (Kuipers, 1975), analyses in this study were conducted only on settlement and juvenile stages, which were combined and referred to as juveniles. Taxa were also classified as not reef-associated, strongly reef-associated or weakly reef-associated based on habitat-use information (Chester et al., 1984; Humann, 1994; Parker et al., 1994; Parker and Mays, 1998; Lindeman et al., 2000). Taxa found predominantly on rocky-reefs (e.g., *Centropristis striata*) were classified as strongly reef-associated. Those that use rocky-reefs and other habitats (e.g., *Diplectrum formosum*) were classified as weakly reef-associated.

Standard catch per unit of effort (CPUE, fish/5-min bottom tow) was calculated for each taxon. CPUE for each taxon at each station was the average of all replicate tows. Three juvenile stage data sets (i.e., cross-shelf, inshore, and offshore) were compiled by using data from the station groups (Table 1, Fig. 1): the cross-shelf data set consisted of data from stations one through seven (Fig. 1A); the inshore data set consisted of data from stations predominately inside the 20-m isobath (Fig. 1B), and the offshore data set consisted of date from stations >30 m in depth (Fig. 1C).

For statistical analyses, the three data sets were subdivided into two groups so that rare taxa would not greatly influence the classification of assemblages. The first group consisted only of abundant taxa, and the second group included abundant and rare taxa. Cross-shelf and offshore data sets were subdivided into taxa that made up at least 10% (abundant) and 1% (abundant and rare) of the collections at any one station. The inshore data set was subdivided at 5% and 1% levels. The data sets were further condensed by eliminating all taxa not identified to species level with the exception of *Stenotomus* sp. and *Rypticus* sp. which were probably single species. Several abundant taxa were excluded from the analysis because they were only identified to genus and have multiple species common in the area, and each species may differ in distribution: i.e., *Etropus* spp. (4 species), *Prionotus* spp. (14 species), *Sphoeroides* spp. (11 species), *Microgobius* spp. (3 species), and *Bothus* spp. (3 species). As a result, the numbers of taxa in the rare and abundant data sets used in analyses were as follows: cross-shelf 82 (rare) and 28 (abundant) (Table 2); inshore 28 and 13 (Table 3), and offshore 51 and 17 (Table 4).

Preparation of environmental data

Season and five environmental (or hydrographic) variables were chosen in an attempt to explain variation in the juvenile fish data. Cruises were assigned to one of four seasons (Table 1) based on wind (Atkinson et al., 1985) and temperature regimes (Marancik et al., 2005). Environmental variables were calculated as in Marancik et al. (2005). Briefly, CTD measurements of temperature (°C) and salinity were used to derive density (σ_t, Kg/m^3). Bottom temperature, salinity, and density were used in the multivariate analyses with juvenile fish because benthic habitats were sampled and bottom values were

Table 2

Taxa collected by beam trawl during two years of sampling (April 2000–February 2002) at the cross-shelf stations (see Fig. 1A) off the coast of Georgia, and used in correspondence analysis. Mean and standard deviation (SD) of catch per unit of effort (CPUE) were calculated for the entire data set. Taxa that constituted one or ten percent of any one station were used in the analyses, and an asterisk next to a taxon indicates that it was in the 10% data set. Seasonal juvenile assemblages from correspondence analysis are shown (I= inner-shelf; I/M=inner-/mid-shelf; M=mid-shelf; O-outer-shelf; and S=entire shelf: S). Taxa in bold indicate reef-associated species.

Family	Taxon	CPUE		Seasonal juvenile assemblage			
		Mean	SD	Spring	Summer	Fall	Winter
Elopidae	*Elops saurus*	0.010	0.097		S		M
Ophichthidae	*Ophichthus gomesii*	0.003	0.056		S		
	Ophichthus ocellatus	0.021	0.155	I/M	S	M	M
Congridae	*Ariosoma balearicum**	0.163	0.479	I/M	S	M	M
Clupeidae	*Brevoortia tyrannus*	0.019	0.134				M
	Etrumeus teres	0.006	0.080				M
	Sardinella aurita	0.003	0.056		S		
Engraulididae	*Anchoa hepsetus**	0.303	1.313	I/M	S	M	
	Anchoa lamprotaena	0.013	0.237			M	
Argentinidae	*Argentina striata*	0.006	0.080				O
Synodontidae	*Synodus foetens**	0.746	1.626	I/M, O	S	M	M
	Synodus poeyi	0.048	0.487	O			
	Trachinocephalus myops	0.103	0.388	O	S	M,O	O
Gadidae	*Urophycis regia**	0.234	0.759	I/M			M
Ophidiidae	*Ophidion selenops**	2.185	4.844	I/M	S	M	M
	*Otophidium omostigmum**	0.364	1.190	O	S	O	M
Batrachoididae	*Porichtys plectrodon*	0.006	0.072			M	
Antennariidae	***Antennarius radiosus***	0.006	0.080				M, O
Ogcocephalidae	*Halieutichthys aculeatus*	0.019	0.137	O	S		
	Ogcocephalus nasutus	0.024	0.150	I/M	S		I
Exocoetidae	*Hemiramphus brasilieusis*	0.003	0.056		S		
	Hirundichthys affinis	0.022	0.169		S	M	
Syngnathidae	*Hippocampus erectus*	0.052	0.233	I/M	S	M	I,M,O
	*Syngnathus scovelli**	0.025	0.192		S	I	
	Syngnathus springeri	0.025	0.158	I/M	S		M
Scorpaenidae	***Scorpaena dispar***	0.019	0.161		**S**	M	
	Scorpaena plumieri*	0.080	0.332	I/M	S	M	M
Triglidae	*Bellator brachychir*	0.006	0.074		S	O	
	Bellator militaris	0.006	0.073	O	S		
	*Prionotus carolinus**	1.047	2.970	I/M	S	M	M
	Prionotus ophryas	0.003	0.056		S		
	Prionotus scitulus	0.022	0.146				M
Serranidae	***Centropristis ocyurus****	0.167	1.344	O	S		O
	Centropristis striata	0.022	0.186	I/M	S		
	Diplectrum formosum*	1.556	3.659	O	S	M,O	M
	Serraniculus pumilio	0.180	0.817	I/M	S	M	M
	Serranus phoebe*	0.085	0.466	O	S	O	O
Priacanthidae	***Priacanthus arenatus***	0.003	0.056		S		
Apogonidae	***Pristigenys alta***	0.016	0.123		S	M	
	Apogon pseudomaculatus	0.012	0.108		S		
Carangidae	*Caranx bartholomaei*	0.003	0.051	O			
	Chloroscombrus chrysurus	0.014	0.124		S	M	
	Decapterus macarellus	0.006	0.080	O			M
	*Decapterus punctatus**	0.022	0.218		S		M
	Trachurus lathami	0.003	0.054	I/M			
Lutjanidae	***Lutjanus analis***	0.003	0.056		S		

continued

		CPUE		Seasonal juvenile assemblage			
Family	Taxon	Mean	SD	Spring	Summer	Fall	Winter
Haemulidae	*Haemulon aurolineatum**	0.022	0.214		S	O	
Sparidae	*Stenotomus sp.**	0.119	0.811	I/M	S	M	M
	Lagodon rhomboides	0.016	0.149				M
Sciaenidae	*Cynosion nothus*	0.009	0.110			M	
	Cynosion regalis	0.011	0.118			M	
	*Larimus fasciatus**	0.036	0.363			I	
	*Leiostomus xanthurus**	0.621	3.752				I
	Menticirrhus americanus	0.013	0.185			I	
Mugilidae	*Mugil cephalus**	0.051	0.469				O
	Mugil curema	0.010	0.099				M
Labridae	*Halichoeres bivattatus*	0.006	0.113		S		
	Xyrichtys novacula	0.003	0.056		S		
Uranoscopidae	*Kathetostoma albigutta*	0.003	0.056				M
Dactyloscopidae	*Dactyloscopus moorei**	0.837	2.329	I/M	S	M	M
Blenniidae	*Hypleurochilus geminatus*	0.010	0.126	I/M	S		
	*Parablennius marmoreus**	0.006	0.080		S		
Callionymidae	*Diplogrammus pauciradiatus**	0.025	0.174		S		
Gobiidae	*Ioglossus calliurus*	0.003	0.047	O	S		
Stromateidae	*Peprilus triacanthus*	0.038	0.218	I/M			M
Bothidae	*Bothus lunatus*	0.006	0.080	O			O
	Bothus ocellatus	0.021	0.155		S	M	O
	*Bothus robinsi**	0.497	1.643	O	S	M	O
Paralichthyidae	*Ancylcopsetta quadrocellata*	0.063	0.300				M
	Citharichthys macrops	0.096	0.475	I/M	S	M	M
	Cyclopsetta fimbriata	0.031	0.184	O	S	M	
	*Syacium papillosum**	0.042	0.282	I/M	S	O	
Soleidae	*Gymnachirus melas**	0.019	0.134	O	S		
Cynoglossidae	*Symphurus diomedeanus*	0.010	0.126	O			
	*Symphurus minor**	0.519	1.801	O	S	O	O
	Symphurus parvus	0.016	0.125	O	S		
	Symphurus plagiusa	0.006	0.113		S		
	*Symphurus urospilus**	0.324	0.806	I/M	S	M	M
Balistidae	*Aluterus schoepfi*	0.006	0.076		S	M	
	*Monocanthus hispidus**	0.504	1.424	I/M	S	M	O
	Monocanthus setifer	0.003	0.047			O	
Ostraciidae	*Lactophyrs quadricornis*	0.005	0.068		S		

Table 2 (continued)

highly correlated with the average water column and surface variables (Marancik et al., 2005). Vertical stratification was estimated by using Simpson's stratification parameter (Simpson and James, 1985), Φ (joules/m^3), which is a measure of the resistance of water to mixing (higher numbers signify higher resistance to mixing).

Data Analyses

Correspondence analysis (CA) and canonical correspondence analysis (CCA) were performed by using the statistical package CANOCO (ter Braak and Smilauer, 2002). Using the cross-shelf, inshore, and offshore data sets, we had seven objectives: 1) to describe the cross-shelf patterns in the juvenile fish assemblages; 2) to identify the species associated with the assemblages including the reef-associated species that contribute to these assemblages; 3) to describe the relationship among cross-shelf patterns in the assemblages and environmental variables; 4) to describe the seasonal patterns in the assemblages; 5) to determine the relation between seasonal assemblages and environmental variables; 6) to describe the along-shelf and cross-shelf patterns in the inshore data set; and 7) to describe the along-shelf and cross-shelf patterns in the offshore data set.

Correspondence analysis was used to define juvenile fish assemblages and to explore the factors that influence distribution of assemblages on the shelf off

Table 3

Taxa collected by beam trawl during spring and winter sampling at stations inshore of Gray's Reef National Marine Sanctuary (see Fig. 1B), and used in correspondence analysis. Mean and standard deviation (SD) of catch per unit of effort (CPUE) were calculated for the entire data set. Taxa that constituted one or five percent of any one station were used in the analyses, and an asterisk next to a taxon indicates that it was in the 5% data set. Station depth groups for each season for juvenile assemblages, as determined from correspondence analysis, are shown. Taxa in bold indicate reef-associated species.

Family	Taxon	CPUE		Juvenile assemblage	
		Mean	SD	Spring	Winter
Congridae	*Ariosoma balearicum**	0.022	0.147	12–15 m	
Clupeidae	*Sardinella aurita*	0.011	0.105	12–15 m	
Engraulididae	*Anchoa hepsetus**	0.613	5.135	8 m	8 m
	Anchoa lamprotaena	0.022	0.147	8 m	8 m
Synodontidae	*Synodus foetens**	0.416	1.525	12–15 m	12–15 m
Gadidae	*Urophycis regia**	0.718	1.176	12–15 m	12–15 m
Ophidiidae	*Ophidion selenops**	0.794	1.867	12–15 m	12–15 m
Ogcocephalidae	*Ogcocephalus nasutus*	0.011	0.105	12–15 m	
Syngnathidae	*Hippocampus erectus*	0.098	0.333	12–15 m	12–15 m
Scorpaenidae	***Scorpaena plumieri***	0.044	0.206	12–15 m	12–15 m
Triglidae	*Prionotus carolinus**	2.227	2.939	12–15 m	12–15 m
	Prionotus scitulus	0.122	0.332	12–15 m	
Serranidae	***Centropristis ocyurus***	0.022	0.147	12–15 m	
	Diplectrum formosum*	0.099	0.366	12–15 m	12–15 m
Sparidae	***Stenotomus* sp.***	0.261	0.949	12–15 m	12–15 m
Sciaenidae	*Leiostomus xanthurus**	14.053	46.103	8 m	
	Stellifer laceolatus	0.022	0.210	8 m	
Mullidae	*Upeneus parvus*	0.011	0.105	12–15 m	
Dactyloscopidae	*Dactyloscopus moorei**	0.545	1.108	12–15 m	12–15 m
Gobiidae	*Gobiosoma bosci*	0.053	0.303	12–15 m	
Stromateidae	*Peprilus triacanthus**	0.076	0.370	12–15 m	
Bothidae	*Bothus ocellatus*	0.010	0.095	12–15 m	
Paralichthyidae	*Ancylopsetta quadrocellata*	0.344	0.604	8 m	12–15 m
	Citharichthys macrops	0.088	0.353	8 m	12–15 m
Cynoglossidae	*Symphurus plagiusa**	0.112	0.538	8 m	
	Symphurus urospilus	0.109	0.403	12–15 m	12–15 m
Balistidae	*Monocanthus hispidus**	0.154	0.445	12–15 m	12–15 m
Ostraciidae	***Lactophyrs quadricornis***	0.011	0.105	8 m	

the coast of Georgia. CA arranges stations and species along gradients (Greenacre, 1984), creating a low-dimensional map (an ordination). Points that occur in close proximity can be considered to have similar species composition and abundance. Points that occur on the same dimension define gradients in the data. The eigenvalues, which are a relative measure of the amount of variance explained by each CA dimension (ter Braak and Smilauer, 2002), were used to determine the number of dimensions that best described the data. CA on untransformed CPUE data was used to define assemblages for the cross-shelf, inshore, and offshore data sets in relation to season.

Canonical correspondence analysis, which incorporates environmental variables by aligning species and station data along environmental gradients, was used to explore the relationship between juvenile 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. CCA on untransformed CPUE data and standardized environmental data was used to explore the relation between the assemblages and environment for the cross-shelf, inshore, and offshore data sets in relation to season. Environmental data were standardized to a mean of zero and a standard deviation of one.
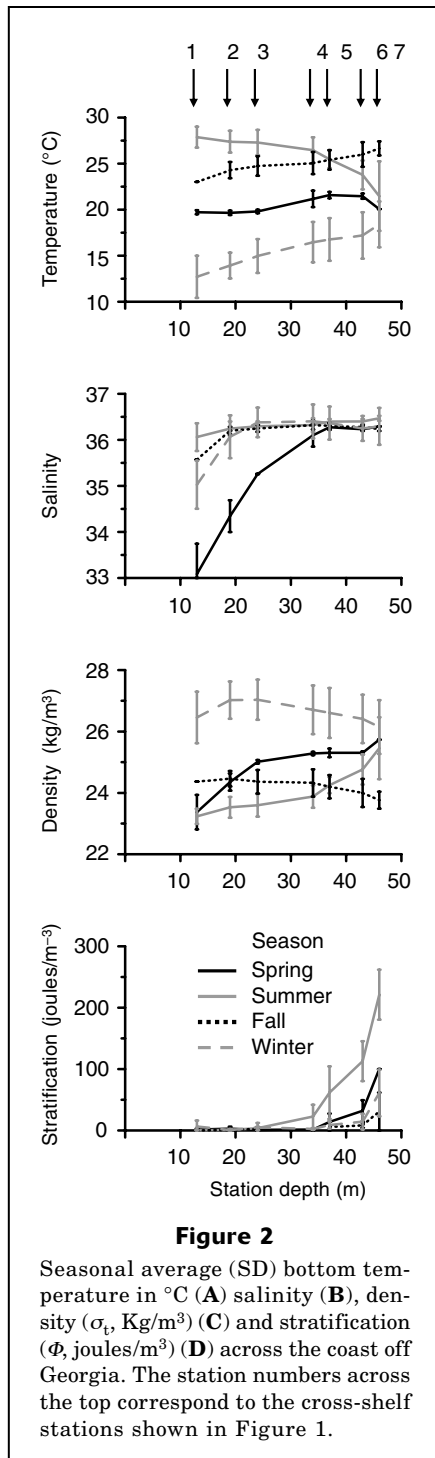
Results

Habitat characterization

The environmental variables showed the typical seasonal and depth patterns across the shelf (Fig. 2). During the spring, bottom water temperature was near 20°C

Table 4

Taxa collected by beam trawl during fall and winter sampling at stations offshore of Gray's Reef National Marine Sanctuary (see Fig. 1C), and used in correspondence analysis. Mean and standard deviation (SD) of catch per unit of effort (CPUE) were calculated for the entire data set. Taxa that constituted one or ten percent of any one station were used in the analyses, and an asterisk next to a taxon indicates that it was in the 10% data set. Station depth groups for each season for juvenile assemblages, as determined from correspondence analysis, are shown. Taxa in bold indicate reef-associated species.

		CPUE		Juvenile assemblage	
Family	Taxon	Mean	SD	Spring	Winter
Muraenidae	*Gymnothorax saxicola*	0.024	0.155	50 m	
Ophichthidae	*Ophichthus gomesii*	0.036	0.246	30–45 m	
Congridae	Ariosoma balearicum	0.183	0.485	30–45 m	50 m
Synodontidae	*Synodus foetens**	0.410	0.980	30–45 m	30–45 m
	Trachinocephalus myops	0.147	0.391	30–45 m	30–45 m
Ophidiidae	*Ophidion selenops**	0.813	2.289	30–45 m	30–45 m
	*Otophidium omostigmum**	0.957	1.401	50 m	30–45 m
Batrachoididae	*Porichtys plectrodon*	0.012	0.105	50 m	
Antennariidae	**Antennarius ocellatus**	0.012	0.109	50 m	
	Antennarius radiosus	0.039	0.203	50 m	
Ogcocephalidae	*Ogcocephalus nasutus*	0.059	0.233	30–45 m	
	Ogcocephalus parvus	0.024	0.154	50 m	
Syngnathidae	*Hippocampus erectus*	0.024	0.154	50 m	50 m
Scorpaenidae	**Scorpaena dispar**	0.152	0.989	50 m	50 m
	Scorpaena plumieri	0.137	0.510	30–45 m	50 m
Triglidae	*Bellator brachychir*	0.012	0.109	30–45 m	
	*Prionotus carolinus**	0.360	0.785	30–45 m	30–45 m
	Prionotus scitulus	0.024	0.153	30–45 m	
Serranidae	**Centropristis ocyurus**	0.998	2.381	50 m	50 m
	Diplectrum formosum	2.305	4.132	30–45 m	30–45 m
	Epinephelus niveatus	0.024	0.155	50 m	30–45 m
	Serraniculus pumilio	0.206	0.579	50 m	30–45 m
	Serranus phoebe	0.857	3.515	50 m	50 m
	Serranus subligarius	0.037	0.331	50 m	
Grammistidae	**Rypticus sp.**	0.239	1.330	50 m	50 m
	Rypticus bistrispinus	0.280	1.336	50 m	
Priacanthidae	**Pristigenys alta**	0.049	0.217	50 m	
Apogonidae	**Apogon maculatus**	0.314	1.525	50 m	
	Apogon pseudomaculatus	0.107	0.439	30–45 m	50 m
Haemulidae	**Haemulon aurolineatum**	0.035	0.233	30–45 m	
Sparidae	**Stenotomus sp.**	0.049	0.267	30–45 m	
Mugilidae	*Mugil cephalus*	0.024	0.221	30–45 m	
	Mugil curema	0.037	0.192	30–45 m	
Labridae	**Halichoeres bivittatus**	0.015	0.133	50 m	
Dactyloscopidae	*Dactyloscopus moorei*	0.049	0.266	30–45 m	
Blenniidae	*Hypleurochilus geminatus*	0.073	0.262	50 m	50 m
	Parablennius marmoreus	0.024	0.221	30–45 m	
Callionymidae	*Diplogrammus pauciradiatus*	0.048	0.212	50 m	30–45 m
Bothidae	*Bothus ocellatus**	0.143	0.701	30–45 m	50 m
	*Bothus robinsi**	0.665	1.145	30–45 m	30–45 m
Paralichthyidae	*Ancylopsetta quadrocellata*	0.060	0.284	30–45 m	
	Citharichthys macrops	0.024	0.152	30–45 m	
	Cyclopsetta fimbriata	0.095	0.394	30–45 m	
	Syacium papillosum	0.087	0.329	30–45 m	
Cynoglossidae	*Symphurus minor**	2.047	3.593	30–45 m	30–45 m
	*Symphurus urospilus**	0.194	0.501	30–45 m	30–45 m
Balistidae	**Cantherhines pullus**	0.061	0.287	50 m	
	Monocanthus ciliatus	0.012	0.110	50 m	
	*Monocanthus hispidus**	0.891	2.057	30–45 m	30–45 m
	Monocanthus setifer	0.012	0.110	50 m	
Ostraciidae	**Lactophyrs quadricornis**	0.012	0.108	30–45 m	

Figure 2

Seasonal average (SD) bottom temperature in °C (**A**) salinity (**B**), density (σ_t, Kg/m^3) (**C**) and stratification (Φ, joules/m^3) (**D**) across the coast off Georgia. The station numbers across the top correspond to the cross-shelf stations shown in Figure 1.

across the entire shelf (Fig. 2A). In the summer, bottom waters were warmest on the inner-shelf and cooler on the outer-shelf (Fig. 2A). Average fall bottom water temperature was intermediate between that of spring and summer and was warmest on the outer-shelf (Fig. 2A). The lowest bottom water temperatures were measured during the winter on the inner-shelf (Fig. 2A). Bottom salinity was lowest on the inner-shelf during

all seasons (Fig. 2B). Bottom salinity was also low on the inner- and mid-shelves during the spring and rose to near 36 psu on the outer-shelf (Fig. 2B). During the summer, fall, and winter the mid- and outer-shelf bottom salinities remained near 36 psu (Fig. 2B). Bottom water density reflected the seasonal and cross-shelf patterns in temperature and salinity (Fig. 2C). Bottom water density was greatest during the winter when water temperatures were the lowest (Fig. 2C). In the spring, a cross-shelf pattern occurred and density was lowest inshore (Fig. 2C). During summer bottom water density was lowest inshore, where the water temperatures were low (Fig. 2C). There was no cross-shelf density pattern in the fall (Fig. 2C). Water column stratification was greatest during the summer and Simpson's stratification numbers were always higher on the outer-shelf (Fig. 2D). The low stratification numbers on the inner- and mid-shelves (Fig. 2D) indicated that there was a high probability of vertical mixing in all seasons.

Video analysis of the ROV tows indicated that the cross-shelf bottom on the continental shelf off the coast of Georgia consisted predominately of unconsolidated sand sediments. Hard-bottom (rock rubble) was seen in one video frame at station 2.3, on the southern edge of the Gray's Reef NMS. No ROV data were collected at the inner- or outermost stations; however, no hard-bottom has been reported from either station (SEAMAP-SA, 2001). These data indicate that unconsolidated sediments were sampled.

Cross-shelf patterns in the juvenile fish assemblages

One hundred eighty one taxa were collected with the beam trawl, and of these, 121 were classified as juveniles (Appendix). Twelve strongly reef-associated species and 21 weakly reef-associated species were collected. The assemblages exhibited a cross-shelf gradient and the station groupings varied seasonally (Fig. 3). CA of both the 10% and 1% data sets resulted in the same overall patterns; however, rare species frequently were found between station groups in the ordination. During the spring, there were two cross-shelf station groups that overlapped at station 4 (Fig. 3A), an inner and mid-shelf group (stations 1–4), mainly inshore of the 30-m isobath, and an outer-shelf group (stations 4–7). Eigenvalues of the CA showed that the separation of the two groups was mainly along the first dimension (Table 5). During the summer, there was little cross-shelf pattern in the assemblages. The only exception was station 2.3, which was distinct from all other stations because live bottom was sampled at that station (Fig. 3B). When this station was removed from the analysis, there was no cross-shelf pattern in the summer data set (Fig. 3C). Three cross-shelf station groups were present in the fall (Fig. 3D): inner-shelf (station 1), mid-shelf (stations 2–5), and outer-shelf (stations 6–7). Separation of the groups was predominately along the first dimension (Table 5), which separated the inner- and mid-shelf station groups from the outer-shelf station group. During the winter, there was a cross-shelf gradient in the juvenile fish assem-

blages and the three overlapping groups were not as distinct as they were in spring or fall (Fig. 3, E and F). The species composition and abundance at station 7 from January 2001 was dissimilar from the rest of the winter samples (Fig. 3E) and generated a high eigenvalue for the second dimension (Table 5). The cross-shelf gradient along the first dimension had the highest eigenvalue (Table 5) in the winter; the first dimension showed three cross-shelf groups (Fig. 3F): an inner-shelf group (stations 1–2), a mid-shelf group (stations 2–5), and an outer-shelf group (stations 4–7).

Species composition of juvenile fish assemblages

Five seasonal juvenile fish assemblages were associated with the cross-shelf station groups (Fig. 4, Table 2). The cross-shelf distribution of juveniles was related to adult distribution patterns and habitat use (Appendix). During the spring, the inner- and mid-shelf assemblage comprised species that are found in estuarine, coastal, and open-shelf habitats as adults (Fig. 4A, Appendix). *Synodus foetens* fell between the two station groups on the ordination, and was found in the both assemblages (Fig 4A). The outer-shelf assemblage was predominately coastal and open-shelf species (Fig. 4A, Appendix). Three reef-associated species were present in both assemblages (Table 2).

Eighteen juvenile reef-associated species were collected during the summer (Table 2). Six species (*Centropristis striata, Apogon pseudomaculatus, Haemulon aurolineatum, Stenotomus* sp., *Halichoeres bivittatus,* and *Parablennius marmoreus*) were collected in June 2001 at station 2.3, when sampling was conducted over live-bottom. Sixteen of the 56 species from the summer sampling were collected solely during this season, and overall, the entire shelf was considered a single assemblage (Table 2).

Only estuarine and coastal species were observed in the inner-shelf assemblage during the fall (Fig. 4B, Table 2). The greatest number of species was observed in the mid-shelf assemblage (Fig. 4B, Table 2), which consisted of a mixture of estuarine, coastal, and open-shelf species (Fig. 4B, Appendix). *Diplectrum formosum* was collected from stations 2 to 7 and was in both the mid- and outer-shelf assemblages (Fig 4B). The outer-shelf assemblage consisted of only coastal and open-shelf species (Fig. 4B, Appendix). Seven reef-associated species were present in mid- to outer-shelf assemblages during the fall (Table 2).

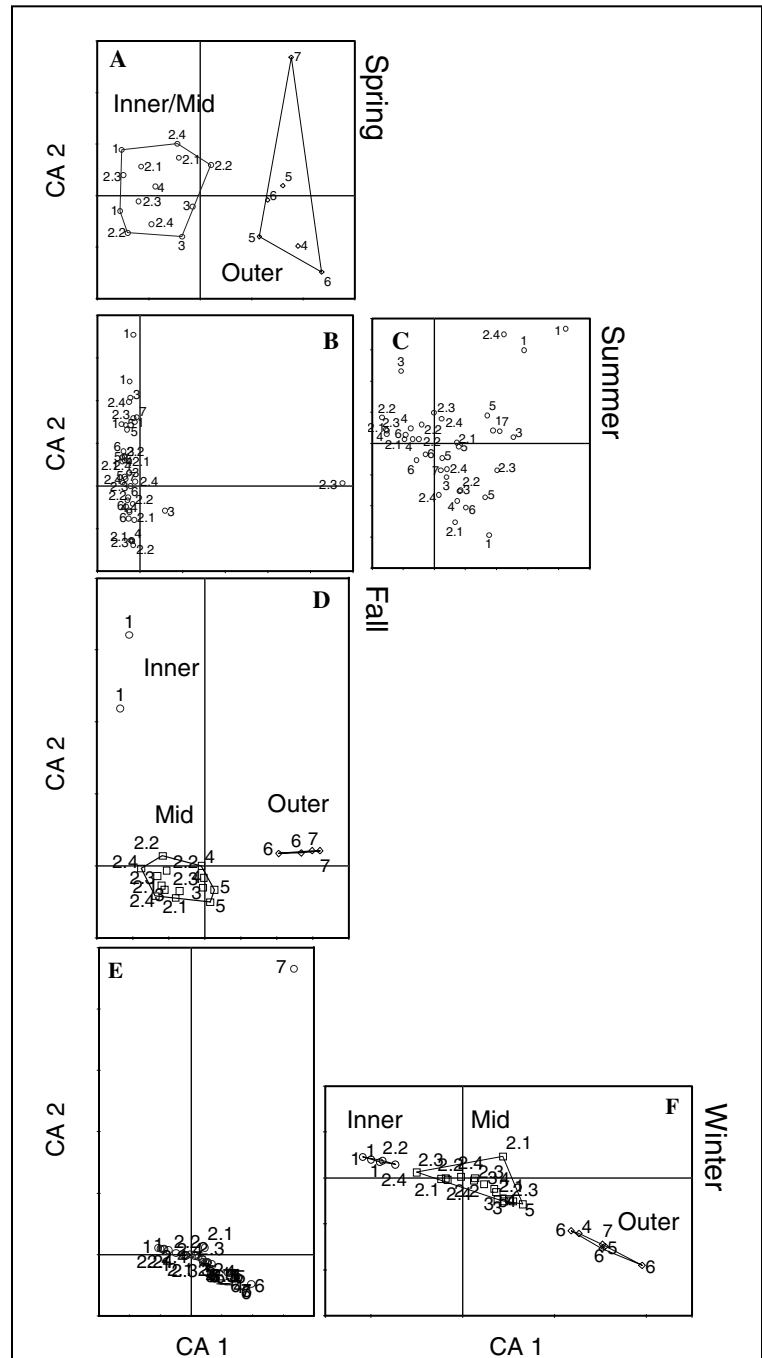There was a cross-shelf gradient in the winter juvenile fish assemblages that was in-

Figure 3

Correspondence analysis (CA) ordinations (portraying the first and second dimension scores) of the 10% cross-shelf data set showing station groups in each season; spring (**A**), summer (**B**), summer without station 2.3 (**C**), fall (**D**), winter (**E**), and winter without station 7 (**F**). The 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 identified by a different symbol. The dashed lines intersect at the origin of the plot. Analyses were conducted by using juvenile fish abundance data only. Data from each cruise within a season are shown together.

Table 5

Eigenvalues and species–environment correlations ($r2$) for each axis analyzed (correspondence analysis [CA] and canonical correspondence analysis [CCA]) by season and the entire year. A sharp drop in the eigenvalue marks the axes that explain most of the data. Eigenvalues alone explain the variance in the data for CA. The product of the species-environment correlation and the eigenvalue explains the variance in the data for CCA.

Season		CA axis				CCA axis			
		1	2	3	4	1	2	3	4
Spring	Eigenvalue	0.574	0.326	0.273	0.251	0.538	0.292	0.172	0.052
	r^2					0.971	0.962	0.959	0.577
Summer	Eigenvalue	0.461	0.389	0.350	0.303	0.248	0.160	0.123	0.049
	r^2					0.857	0.742	0.684	0.422
Fall	Eigenvalue	0.604	0.376	0.275	0.224	0.447	0.301	0.121	0.090
	r^2					0.910	0.899	0.846	0.765
Winter	Eigenvalue	0.669	0.644	0.492	0.414	0.531	0.306	0.181	0.118
	r^2					0.930	0.862	0.669	0.625
Year	Eigenvalue	0.698	0.507	0.499	0.394	0.169	0.125	0.102	0.089
	r^2					0.606	0.628	0.615	0.522

Table 6

The P values from a Monte Carlo permutation test on the environmental variables for each season. Significant P values ($P<0.05$) are in bold.

	Season			
Variable	Spring	Summer	Fall	Winter
Depth (m)	**0.002**	0.918	**0.002**	**0.002**
Stratification	**0.002**	**0.002**	0.622	0.178
Bottom temperature	0.410	0.138	0.094	0.070
Bottom salinity	1.000	0.160	**0.020**	0.316
Bottom density	**0.034**	0.848	0.102	**0.020**

fluenced by the single station 7 (Fig. 3E), which had a high abundance of *Monacanthus hispidus*. *Bothus ocellatus* and *B. lunatus* were also collected only at this station (Table 2). The inner-shelf consisted of one dominant species (Fig. 4C), and the mid-shelf had the greatest number of species (Fig. 4C, Table 2). The outer-shelf assemblage consisted of estuarine, coastal, and open-shelf species (Fig. 4C). Six reef-associated species were found in the mid- and outer-shelf assemblages. The distributions of species in all three winter assemblages indicated cross-shelf mixing. An open-shelf species, *Ogcocephalus nasutus*, was present in the inner-shelf assemblage and *Mugil cephalus*, which uses estuaries as adults, was present in the outer-shelf assemblage (Table 2, Appendix). Finally, two slope species (*Argentina striata* and *Antennarius radiosus*) were present in the mid- and outer-shelf assemblages (Table 2, Appendix).

Cross-shelf patterns in juvenile fish assemblages and environmental variables

The juvenile fish assemblages and environmental variables all showed a cross-shelf gradient, which was correlated with depth during three of the four seasons (Table 6). The relationship between the other environmental variables and assemblages varied with season. In spring, the gradient in the inner- and mid-shelf and outer-shelf was mainly along the first dimension (Table 5) and was influenced by depth, bottom salinity, and bottom density (Fig. 5A). Inner- and mid-shelf stations were shallower and had less saline and dense bottom water than outer-shelf stations (Fig. 2). The spread along the second dimension in the outer-shelf group was less important (Table 5) and was influenced by the higher stratification of the outer stations (Fig. 2). A Monte Carlo permutation test of the environmental variables for spring indicated that depth, stratification, and bottom density were significantly related to the juvenile assemblages and the grouping of stations in the CCA (Table 6).

The summer juvenile assemblage was not related to these environmental variables. The ordination of the station and species data changed with the inclusion of environmental data to the analyses, indicating a poor relationship between the juvenile data and the environment (Fig. 5B) The low eigenvalues also indicated that very little of the observed variation in the data was explained by the environment (Table 5). These results agree with the results from the CA, both of which indicate that the entire shelf is a single assemblage.

The fall cross-shelf patterns in the juvenile fish assemblages were related to depth and bottom salinity (Fig. 5C). The first dimension had the highest eigenvalue and species-environment correlation (Table 5)
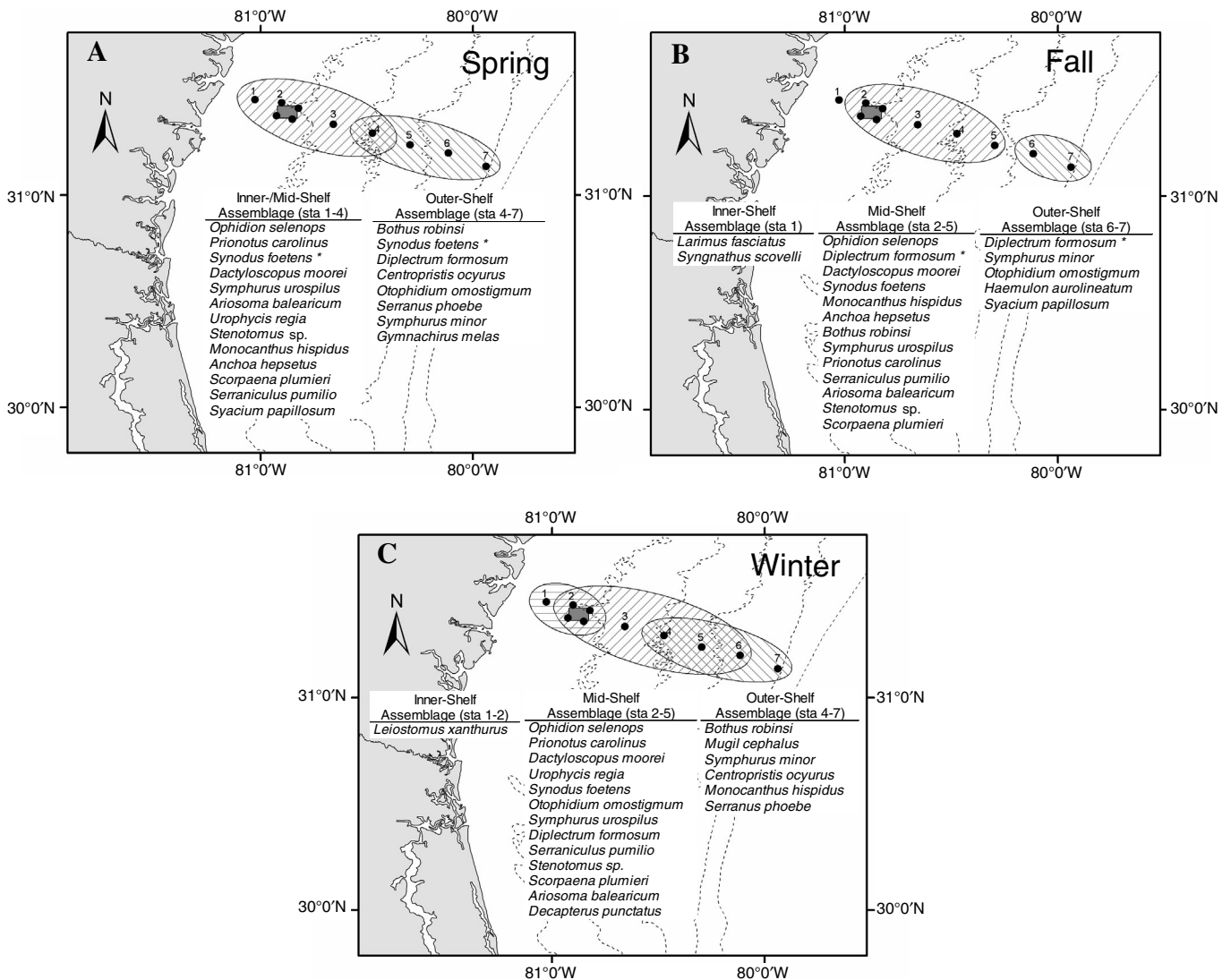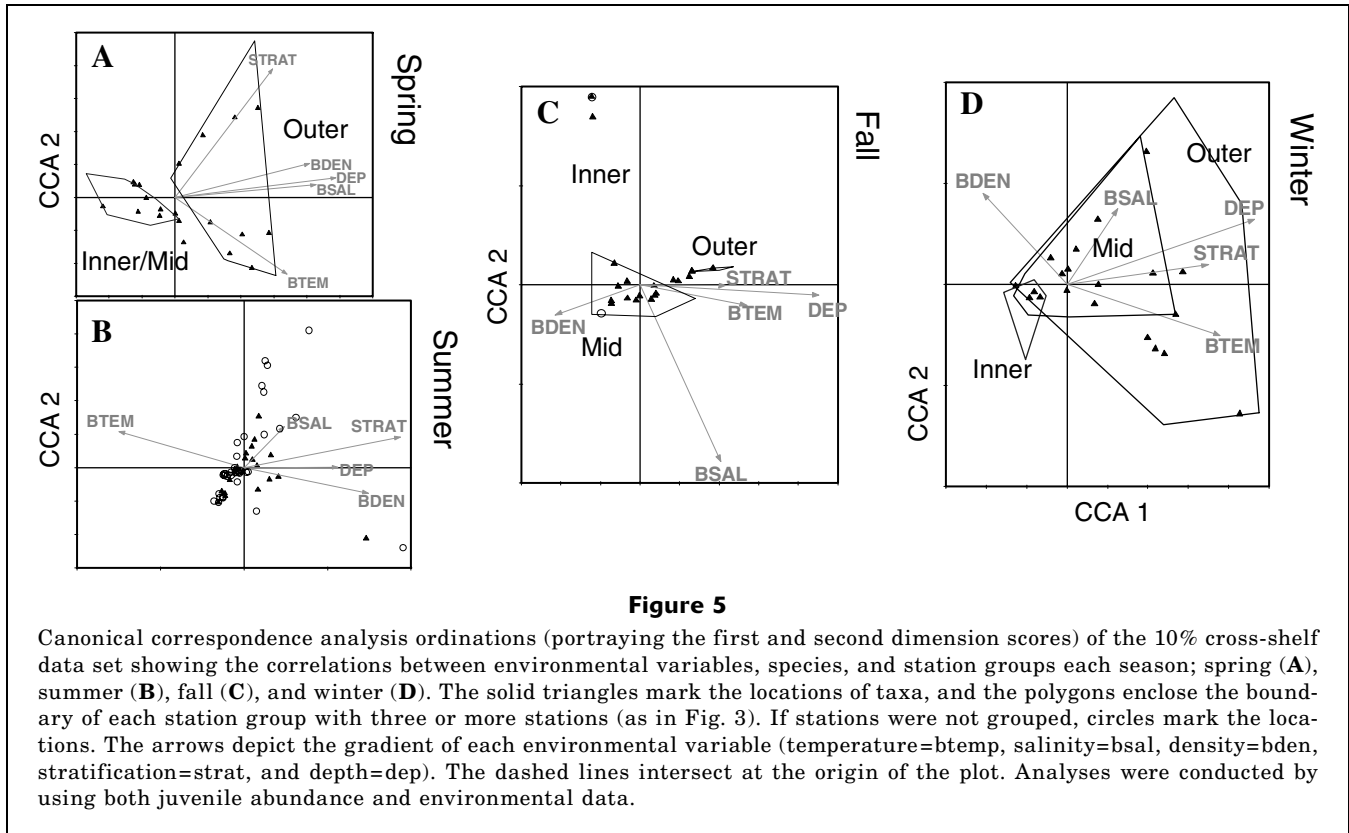
Figure 4

Cross-shelf juvenile fish assemblages identified from correspondence analysis for spring (**A**), fall (**B**), and winter (**C**). Summer was not plotted because there was only one summer assemblage. Hatched circles enclose stations that grouped together each season. Taxa from the 10% cross-shelf data set, in order of abundance, for each assemblage are shown in the tables. Asterisks indicate species that were found in multiple assemblages.

and was mainly influenced by depth; the shallower inner- and mid-shelf stations were separate from the outer-shelf stations. The second dimension was related to bottom salinity (Fig. 5C) and correlated with the separation of the inner-shelf station from the higher saline mid- and outer-shelf stations (Fig. 2). A Monte Carlo permutation test of the relationships between the assemblages and environmental data for the fall indicated that depth and bottom salinity were significantly related to the juvenile assemblages and cross-shelf station groups (Table 6).

The inclusion of environmental variables in the analysis of winter juvenile assemblage showed a weak relationship with the cross-shelf groups and juvenile assemblages, as indicated by the CCA correlation (Table 5).

The addition of the environmental data also changed the ordination of the stations (Fig. 5D); yet there was still a cross-shelf gradient. Along the first dimension, depth, bottom temperature, and stratification were related to the juvenile assemblages and cross-shelf groups (Fig. 5D). The shallow inner- and mid-shelf groups were lower in bottom temperature and stratification, whereas bottom density was lowest on the inner- and outer-shelves and highest on the mid-shelf (Fig. 2). A Monte Carlo permutation test for the winter relationships indicated that depth and bottom density were significantly correlated with the fish assemblages and station groups (Table 6), although the bottom density did not appear to have any relation to the patterns described (Fig. 5D).

Figure 5

Canonical correspondence analysis ordinations (portraying the first and second dimension scores) of the 10% cross-shelf data set showing the correlations between environmental variables, species, and station groups each season; spring (**A**), summer (**B**), fall (**C**), and winter (**D**). The solid triangles mark the locations of taxa, and the polygons enclose the boundary of each station group with three or more stations (as in Fig. 3). If stations were not grouped, circles mark the locations. The arrows depict the gradient of each environmental variable (temperature=btemp, salinity=bsal, density=bden, stratification=strat, and depth=dep). The dashed lines intersect at the origin of the plot. Analyses were conducted by using both juvenile abundance and environmental data.

Seasonal patterns in juvenile fish assemblages

Many of the species (>68%) were present on the shelf in more than one season, which resulted in a large overlap of the seasonal assemblages (ordination not shown), including 12 of the 23 reef-associated species (Table 2). The assemblage data could be explained in three dimensions (as determined by CA of the 10% cross-shelf data set [Table 5]) and portrayed seasonal and cross-shelf patterns. Along the first dimension, there was separation between the winter inner-shelf assemblage and all other assemblages. The second and third dimensions portrayed a cross-shelf gradient in the spring, fall, and winter juvenile assemblage data. The summer assemblage overlapped all the cross-shelf groups from the other seasons except the winter inner-shelf assemblage. High abundances of *Larimus fasciatus* in the fall and *Leiostomus xanthurus* and *Mugil cephalus* in the winter (Table 2) caused these two seasons to be more dissimilar than were spring and summer, which were very similar. Many of the juveniles were found in the same cross-shelf assemblages during each season, whereas others shifted assemblages (Fig. 4).

Relation between seasonal juvenile assemblages and environmental variables

There appeared to be no relationship between the seasonal juvenile assemblages and environmental variables. The products of the CCA eigenvalues and species-environment correlations were extremely low (Table 5), and the CCA ordination of seasonal juvenile assemblages and environmental variables was different from the CA ordination. Thus, over the entire year, environmental variables did not help explain among-season variation in the juvenile assemblage data.

Along-shelf and cross-shelf patterns in the inshore juvenile fish data set

The inshore data set was made up of estuarine, coastal, and open-shelf species (Table 3, Appendix). There was a cross-shelf gradient in the spring and winter (Fig. 6). The innermost station group (8-m) separated from the other station groups along the first dimension (Fig. 7A) in spring. Most taxa from the 8-m assemblage (5 of 7) were not collected in high enough abundance to be included in the cross-shelf data set (Tables 2 and 3). In winter there was also a gradient from shallow to deeper stations (Fig. 6C). The assemblage nearest the origin in the winter (8-m assemblage) included estuarine species that were abundant at all the inshore stations (Table 3, Appendix). The coastal species, however, were more abundant at the deeper (12-m, 15-m, and 18-m) station groups (Table 3). There was no pattern in the along-shelf transects, from north to south, during either season (Fig. 6, B and D).

Along-shelf and cross-shelf patterns in the offshore juvenile fish data set

The offshore juvenile fish data set included primarily (76%) coastal, open-shelf, and slope species (Table 4, Appendix) and patterns in the data set varied with season. During the fall, there were both cross-shelf (Fig. 7A) and along-shelf patterns (Fig. 7B). Along the first dimension, there was a cross-shelf gradient (Fig. 7A) from the shallow stations (30–45 m depth; Fig. 1C) to the 50-m station group. The juvenile assemblage at the 50-m station group had high abundances of reef-associated species (Table 4). The stations on the northern most transect (Fig. 1C) also separated from the others along the second dimension, and had higher abundances of reef-associated species. The cross-shelf pattern was present in the winter, with greater abundances of reef-associated species at the 50-m station group (Fig. 7C), but there was no along-shelf pattern (Fig. 7D).

Discussion

One hundred and twenty-one taxa of juvenile fish were collected on unconsolidated sediments on the continental shelf off Georgia. The actual number of species was higher, but taxonomic problems limited species identification (e.g., identification of *Etropus* spp., *Prionotus* spp., *Sphoeroides* spp., and *Microgobius* spp.). With concurrent ichthyoplankton sampling of the cross-shelf stations (Fig. 1), we collected 161 taxa (Marancik et al., 2005); the larval community had more pelagic species, including several scombrids (e.g., *Auxis rochei, Scomberomorus cavalla,* and *S. maculatus*) and 17 myctophids. The large juvenile and adult fish communities of the shallow coastal zone (<10 m) and continental shelf (9–180 m) comprised about 150 species, including both pelagic and demersal species (Wenner et al.[4,5,6,7]; Wenner and Sedberry, 1989). A maximum of 164 species were reported from rocky-reefs in the region (Chester et al., 1984; Parker et al. 1994;

Figure 6

Correspondence analysis ordinations (portraying the first and second dimension scores) of the inshore juvenile fish community data showing cross-shelf and along-shelf station groups in spring (**A** and **B**) and winter (**C** and **D**). 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 by using juvenile fish abundance data only.

Baron et al., 2004). Fewer species inhabit estuaries than shelf habitats of the southeast (<90), particularly

[4] Wenner, C. A., C. A. Barans, B. W. Stender, and F. H. Berry. 1979a. Results of MARMAP otter trawl investigations in the South Atlantic Bight. II, spring 1974, 78 p. [Available from Marine Resources Division, South Carolina Department of Natural Resources, 217 Ft. Johnson Rd., P.O. Box 12559, Charleston, SC 29412.]
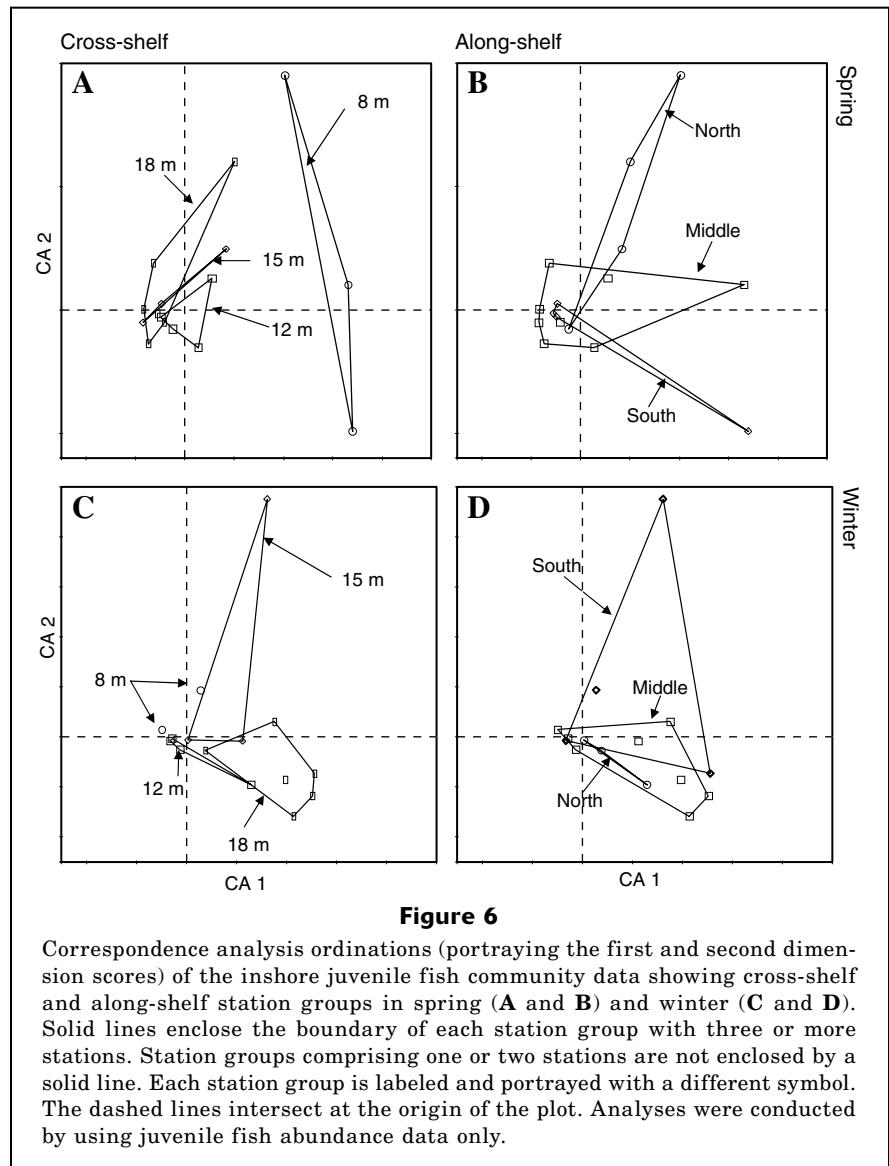
[5] Wenner, C. A., C. A. Barans, B. W. Stender, and F. H. Berry. 1979b. Results of MARMAP otter trawl investigations in the South Atlantic Bight. III, summer 1974, 62 p. [Available from Marine Resources Division, South Carolina Department of Natural Resources, 217 Ft. Johnson Rd., P.O. Box 12559, Charleston, SC 29412.]

[6] Wenner, C. A., C. A. Barans, B. W. Stender, and F. H. Berry. 1979c. Results of MARMAP otter trawl investigations in the South Atlantic Bight. IV, winter-early spring 1975, 59 p. [Available from Marine Resources Division, South Carolina Department of Natural Resources, 217 Ft. Johnson Rd., P.O. Box 12559, Charleston, SC 29412.]

[7] Wenner, C. A., C. A. Barans, B. W. Stender, and F. H. Berry. 1980. Results of MARMAP otter trawl investigations in the South Atlantic Bight. V, summer 1975, 57 p. [Available from Marine Resources Division, South Carolina Department of Natural Resources, 217 Ft. Johnson Rd., P.O. Box 12559, Charleston, SC 29412.]

if different habitat types are considered (Ross and Epperly, 1985; Hettler, 1989; Nelson et al., 1991). Thus, unconsolidated sediments are as rich a habitat in terms of the number of species, as are pelagic, rocky reef, and estuarine habitats in the southeast U.S. continental shelf ecosystem.

Cross-shelf regions were defined on the Georgia shelf from spatial patterns in juvenile fish distributions. The number and extent of cross-shelf regions varied seasonally, but in general, three regions were identified: inner-shelf, mid-shelf, and outer-shelf regions. Juvenile assemblages were associated with the regions, yet some individual species were distributed across regions. Juveniles of year-round residents (e.g., *Ophidion selenops, Diplectrum formosum,* and *Prionotus carolinus*) were usually the most abundant species, although transient juveniles (e.g., *Leiostomus xanthurus, Lagodon rhomboides*, and *Brevoortia tyrannus*) were seasonally abundant. Cross-shelf gradients in species distribution have been found for other organisms and life stages of fish on the southeast U.S. shelf (macroinfauna: Atkinson et al., 1985; larval fish: Marancik et al., 2005; adult reef fish: Chester et al., 1984; adult demersal fish: Wenner et al.[4,5,6,7]). Cross-shelf gradients also are common in demersal juvenile fish distribu-

Figure 7

Correspondence analysis ordinations (portraying the first and second dimension scores) of the offshore juvenile fish community data showing cross-shelf and along-shelf station groups in fall (**A** and **B**) and winter (**C** and **D**). 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 by using juvenile fish abundance data only.

tions in other continental shelf ecosystems (northwest U.S.: Norcross et al., 1997; Toole et al., 1997; Abookire and Norcross, 1998; Bailey et al., 2003; Johnson et al., 2003; northeast U.S.: Steves et al., 2000; Sullivan et al., 2000; southwest U.S.: Johnson et al., 2001).

The cause of cross-shelf gradients in juvenile fish distribution is difficult to determine. The primary environmental variable correlated with cross-shelf juvenile fish assemblages is often depth (Table 6; Norcross et al., 1997; Steves et al., 2000; Sullivan et al., 2000; Johnson et al., 2001; Johnson et al., 2003), although temperature, salinity, and sediment grain size also are correlated with depth (Norcross et al., 1997; Steves et al., 2000; Sullivan et al., 2000). On the Georgia shelf, salinity, density, and stratification correlated with the distribution of juvenile assemblages during the spring, fall, and winter (Table 6), and along with temperature (Figs. 2 and 6) likely influenced the distribution of juvenile fish, but the causative mechanisms remain unresolved. On the northeast U.S. shelf, cold bottom water left from winter resides on the mid-shelf during summer
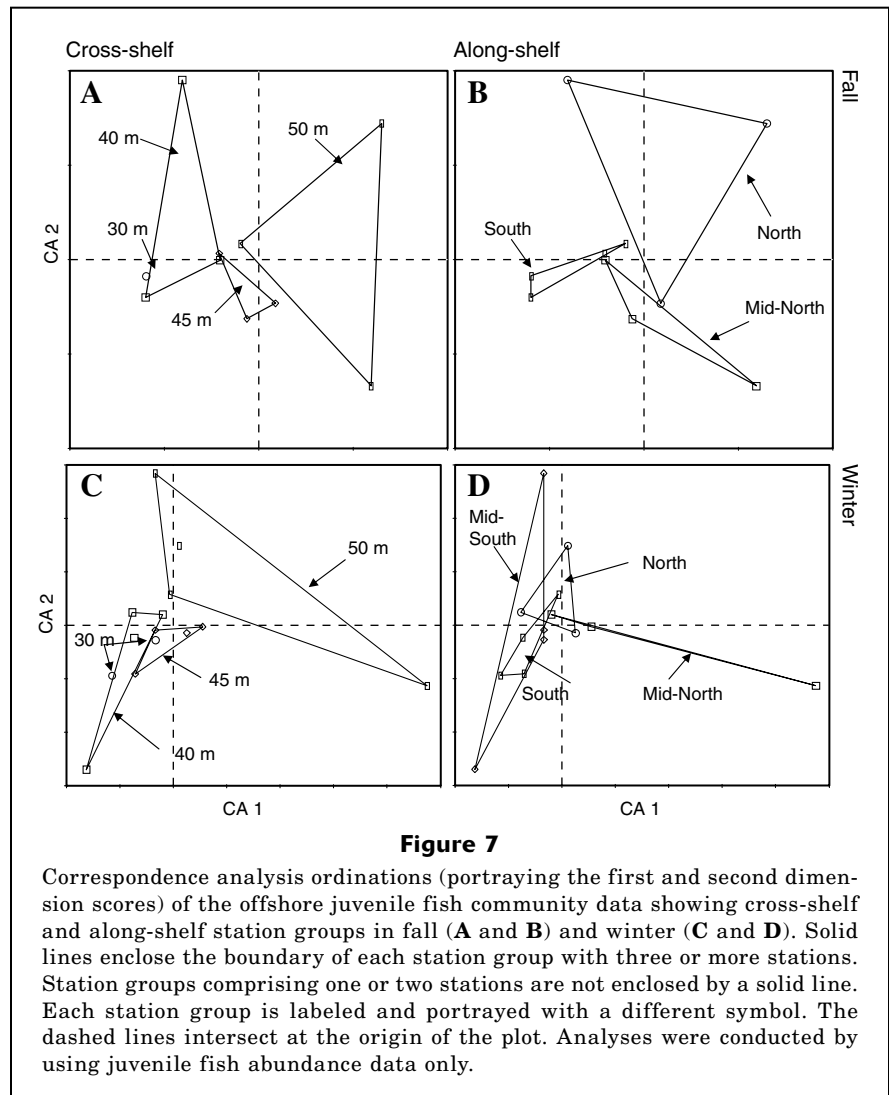
and fall (cold pool; Ketchum and Corwin, 1964). Steves et al. (2000) and Sullivan et al. (2000) hypothesized that cross-shelf patterns in settlement and juvenile fish distributions were caused by cross-shelf temperature gradients related to the presence of the cold pool on the mid-shelf. Similarly, juvenile flatfish species in Alaska exhibited cross-shelf gradients in habitat use that were influenced by temperature-depth interactions (Norcross et al., 1997). *Hippoglossoides elassodon* were most abundant in the colder, deeper locations, and *Hippoglossus stenolepis* were more abundant in the warmer, shallow locations (Norcross et al., 1997). On the Georgia shelf, juvenile assemblages were less distinct during summer, when environmental gradients were weakest, providing some support for the hypothesis that cross-shelf patterns in juvenile distribution were caused by environmental factors. Alternatively, in other studies it has been hypothesized that juvenile distribution results from selection of specific habitat characteristics within large-scale environmental gradients (Stoner and Abookire, 2002). For example, laboratory and field

studies have found that some fish species select specific sediment characteristics or biogenic structures (Stoner and Abookire, 2002; Diaz et al., 2003; Stoner and Titgen, 2003), and spatial patterns in these habitat characteristics may cause spatial patterns in juvenile fish distribution. We did not stratify sampling by sediment characteristics or biogenic structures and thus we could draw no conclusion regarding the role of habitat characteristics in influencing juvenile fish distribution on the Georgia shelf.

No along-shelf spatial patterns were found in the juvenile fish community on the continental shelf off the Georgia coast; however, the along-shelf dimension sampled (~60 km) was relatively small compared to the along-shelf dimension of the southeast U.S. continental shelf ecosystem (~1000 km). Consistent patterns in along-shelf gradients in oceanographic features (Atkinson et al., 1985; Lee et al., 1991) and adult fish communities (Chester et al., 1984; Wenner and Sedberry, 1989) exist on the southeast U.S. shelf, but over larger along-shelf dimensions than sampled in the present study (200–400 km). Consistent patterns of juvenile use of along-shelf habitat over smaller dimensions (~100 km) have been reported for other shelf ecosystems (northwest U.S.: Norcross et al., 1997; Abookire and Norcross, 1998; northeast U.S.: Steves et al., 2000; Sullivan et al., 2000), but the relation to along-shelf environmental and habitat characteristics is unclear. Along-shelf patterns in juvenile fish distribution on unconsolidated sediments may occur on the southeast U.S. shelf, but at dimensions larger than 60–100 km.

Seasonal patterns in settlement and postsettlement movement both defined and blurred classification of juvenile fish assemblages on the Georgia shelf. Many of the resident shelf species were consistently collected in the same cross-shelf regions (i.e., inner and mid-shelf: *Ophidion selenops, Prionotus carolinus, Dactyloscopus moorei, Stenotomus* sp., and *Serraniculus pumilio*; outer-shelf: *Symphurus minor, Serranus phoebe, Centropristis ocyurus,* and *Bothus lunatus*), and the consistent collection of these species helped form a definition of juvenile assemblages. Other resident species shifted juvenile assemblages (e.g., *Diplectrum formosum, Monacanthus hispidus, Bothus robinsi, Otophidium omostigmum,* and *Bothus ocellatus*), possibly because of seasonal changes in settlement patterns or ontogenetic postsettlement movements, with the result that some classifications were blurred. Four scieanid species, present during the spring, summer, and fall as larvae (Marancik et al., 2005), were collected during the fall as juveniles and contributed to defining the fall inner-shelf (*Larimus fasciatus* and *Menticirrhus americanus*) and mid-shelf (*Cynosion nothus* and *C. regalis*) juvenile assemblages. These species may shift settlement or juvenile habitat (or both) between estuaries and the coastal ocean; this shift has been shown to occur off the coast of New Jersey (Able et al., 2003; Neuman and Able, 2003). Further, a number of species in the ecosystem spawn on the shelf yet use estuarine habitats as juvenile nurseries (Warlen and Burke, 1990; Able and Fahay, 1998).

In our study, settlement stage *L. xanthurus, Brevoortia tyrannus,* and *Lagodon rhomboides* were collected on the shelf, and contributed to the definition of the inner- and mid-shelf assemblages. Some individuals of these estuarine-dependent species may not settle directly into estuarine habitats as has been demonstrated for *Centropristis striata* off the coast of New Jersey (Able and Fahay, 1998).

Only a few reef-associated species collected during the study used unconsolidated sediments consistently. *Centropristis ocyurus, Diplectrum formosum,* and *Stenotomus* sp. were the most common reef fishes collected on unconsolidated sediments, and made up >1% of the total catch (Appendix). Other less frequently occurring juveniles of important reef-associated species that were collected were *Centropristis striata, Epinephelus niveatus, Pristigenys alta, Priacanthus arenatus,* and *Lutjanus analis*.

Reef-associated species were collected across the entire shelf. *Centropristis ocyurus* and *Stenotomus* sp. were commonly collected on the outer-, inner-, and mid-shelves, respectively (Table 2, Appendix). *Centropristis striata*, which uses habitats in estuaries and coastal regions as juveniles (Able and Fahay, 1998), was collected on the inner- and mid-shelf in the spring and summer, during periods of high settlement (Able and Hales, 1997). The presence of many reef-associated species at the deeper (50 m) stations (Table 4) may indicate greater use of offshore unconsolidated sediments by reef-associated species or that sampling was done in an area closer to rocky-reefs. Several species of the South Atlantic Fishery Management Council snapper-grouper complex have been reported to use a variety of nonreef habitats as newly settled juveniles, including unconsolidated sediments on the shelf (Lindeman et al., 2000). Many coral reef fish also use several types of nearshore nonreef habitat as juveniles (de la Moriniere et al., 2002; Nagelkerken and van der Velde, 2002). These nonreef habitats are assumed to be important nursery habitats; however, strong evidence of movement from juvenile to adult habitats has been documented only for a few reef-associated fishes (Gillanders et al., 2003). The fact that reef-associated species also use unconsolidated sediments indicates there is an interdependence between reef habitats and unconsolidated sediments; yet the function of each habitat remains unquantified.

In addition to reef species, a number of commercially and recreationally important demersal species used unconsolidated sediments on the shelf off Georgia as juvenile habitat. Juvenile *Cynoscion nothus, C. regalis* and *Menticirrhus americanus* were collected on the inner- and mid-shelves in the fall, and settlement-size *Leiostomus xanthurus* were collected in the winter. However, small noncommercial demersal species were the most abundant juveniles collected during beam trawl sampling.

Much of the southeast U.S. continental shelf is impacted by trawl fisheries that can adversely impact unconsolidated sediments (Barnette[3]). Current manage-

ment concerns focus primarily on bycatch reduction, impacts on stock assessments of commercially and recreationally important finfish, and destruction of coral, live hard-bottom, and SAV habitat (NOAA[8]; Barnette[3]). The presence of reef-associated and sciaenid species in our samples indicate that the unconsolidated sediments of the shelf are potentially important habitats for early life stages, and that trawl fisheries on the shelf may impact the population dynamics of these species. Equally important may be the ecological effects on the small noncommercial demersal species that dominate the catch on unconsolidated sediments and that are abundant in the shrimp trawl bycatch (SAFMC, 1996).

Unconsolidated sediments serve as juvenile habitat for a number of species in the southeast U.S. shelf ecosystem. Some species use unconsolidated sediments throughout their life history, but for a number of species, unconsolidated sediments serve as only one of a mosaic of habitats through the life history (see Browman and Konstantinos, 2004). Additionally, there is growing recognition of the importance of unconsolidated sediments in the trophic ecology of the southeast U.S. shelf. Benthic primary production of the shelf has been shown to be 4–6 times greater than water-column production at specific locations (Nelson et al., 1999). Unconsolidated sediments are areas of reef fish feeding (Sedberry, 1985, 1990) and several important fish predators inhabit unconsolidated sediments (triglids, synodontids, Ross, 1976; Richards et al., 1979). Current ecosystem approaches to fisheries (see Sissenwine and Murawski, 2004) in the region largely ignore unconsolidated sediments (SAFMC, 1998, 2001), and although the importance of this habitat to juvenile fish production remains unquantified (sensu Beck et al., 2001), management efforts would be improved through a greater recognition of the potential importance of these habitats to fisheries production and the interconnectedness of multiple habitats in the southeast U.S. continental shelf ecosystem.

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Appendix

Juvenile taxa collected in beam trawl collections from the continental shelf off the coast of Georgia, USA. Seasonal catch per unit of effort (CPUE, fish/5 min) was calculated from cross-shelf stations (see Fig. 1 and Table 1). Mean (SD) of the total CPUE and standard length (SL, mm) was calculated from all stations. Adult distributions (AD) and whether species are reef-associated (RA) was determined from the literature. E = estuarine, C = coastal (0–20 m), O = open-shelf (20–70 m), Sl = slope (>70 m), W = weakly reef-associated, and S = strongly reef-associated.

| Family | Species | Cross-shelf stations Mean | | | | All stations CPUE | All stations SL (mm) | | |
		Spring	Summer	Fall	Winter	Mean (SD)	Mean (SD)	AD	RA
Elopidae	*Elops saurus*		0.02		0.01	0.007 (±0.084)	46.7 (±15.9)	E, C	
Muraenidae	*Gymnothorax saxicola*					0.005 (±0.069)	69.5 (±0.7)	C, O	
Ophichthidae	*Ophichthus gomesii*		0.01			0.009 (±0.119)	103.3 (±20.1)	E, C, O	
	Ophichthus ocellatus	0.05		0.03	0.02	0.016 (±0.133)	160.9 (±59.2)	E, C, O	
Congridae	*Ariosoma balearicum*	0.39	0.10	0.30	0.02	0.135 (±0.431)	126.5 (±44.2)	E, C, O	
Clupeidae	*Brevoortia tyrannus*				0.07	0.014 (±0.116)	24.5 (±1.8)	E, C, O	
	Etrumeus teres	0.02			0.01	0.005 (±0.069)	31.8 (±1.1)	C, O	
	Sardinella aurita		0.01			0.005 (±0.069)	36.0 (±2.8)	C, O	
Engraulididae	*Anchoa hepsetus*	0.09	0.19	1.14		0.355 (±2.631)	31.3 (±10.2)	E, C, O	
	Anchoa lamprotaena			0.07		0.015 (±0.215)	44.5 (±5.8)	C	
Argentinidae	*Argentina striata*				0.02	0.005 (±0.069)	52.0 (±1.4)	Sl	
Synodontidae	*Synodus foetens*	1.00	0.45	1.55	0.39	0.643 (±1.570)	65.8 (±40.1)	E, C, O	
	Synodus poeyi	0.26				0.035 (±0.420)	33.1 (±3.5)	O	
	Trachinocephalus myops	0.13	0.06	0.22	0.06	0.091 (±0.354)	92.3 (±47.6)	O	
Gadidae	*Urophycis regia*	0.28			0.68	0.302 (±0.867)	69.7 (±21.3)	C, O	
Ophidiidae	*Ophidion grayi*	0.02				0.002 (±0.049)	39.0	C, O	
	Ophidion holbrooki	0.70				0.121 (±1.226)	98.8 (±47.3)	C, O	
	Ophidion marginatum	0.11	0.03	0.01	0.03	0.050 (±0.270)	94.8 (±43.0)	C, O	
	Ophidion selenops	3.63	0.35	4.92	1.49	1.823 (±4.373)	56.1 (±19.7)	O	
	Ophidion welshi	0.12		0.02		0.019 (±0.194)	107.9 (±27.1)	C, O	
	Otophidium omostigmum	0.60	0.09	0.69	0.38	0.392 (±1.192)	60.0 (±21.8)	O	
Batrachoididae	*Porichthys plectrodon*			0.03		0.007 (±0.078)	56.3 (±13.7)	C, O	
Antennariidae	*Antennarius ocellatus*					0.002 (±0.048)	47.0	O, Sl	W
	Antennarius radiosus				0.02	0.010 (±0.102)	24.0 (±4.1)	O, Sl	W
Ogcocephalidae	*Halieutichthys aculeatus*	0.02	0.04			0.014 (±0.118)	14.4 (±1.5)	C, O	
	Ogcocephalus nasutus	0.02	0.05		0.01	0.025 (±0.154)	29.0 (±17.8)	C, O	
	Ogcocephalus parvus				0.02	0.012 (±0.108)	75.6 (±34.1)	O	

continued

Appendix (continued)

| Family | Species | Cross-shelf stations Mean | | | | All stations CPUE | SL (mm) | | |
		Spring	Summer	Fall	Winter	Mean (SD)	Mean (SD)	AD	RA
Exocetidae	*Hemiramphus balao*			0.02		0.003 (±0.052)	80.0	C, O	
	Hemiramphus brasilieusis		0.01			0.002 (±0.049)	97.0	C, O	
	Hirundichthys affinis		0.05	0.02		0.017 (±0.146)	35.4 (±13.8)	C, O	
	Parexocoetus brachypterus			0.02		0.002 (±0.048)	34.0	O	
Syngnathidae	*Hippocampus erectus*	0.12	0.04	0.01	0.04	0.055 (±0.236)	60.8 (±19.9)	E, C	
	Syngnathus scovelli		0.06	0.02		0.019 (±0.166)	56.3 (±11.8)	E, C	
	Syngnathus springeri	0.02	0.01		0.07	0.021 (±0.144)	64.3 (±6.9)	C, O	
Scorpaenidae	*Scorpaena dispar*		0.02	0.07		0.043 (±0.458)	39.4 (±21.6)	C, O	W
	Scorpaena plumieri	0.07	0.13	0.08	0.02	0.078 (±0.335)	43.5 (±31.0)	C, O	W
Triglidae	*Prionotus* spp.	0.73	0.17	15.31	0.52	2.700 (±9.684)	11.6 (±3.3)	C, O	
	Bellator brachychir		0.01	0.01		0.007 (±0.079)	27.0 (±13.2)	O	
	Bellator militaris	0.01	0.01			0.004 (±0.063)	17.5 (±12.0)	O	
	Prionotus carolinus	3.04	0.32	0.42	1.08	1.127 (±2.801)	53.5 (±27.9)	E, C, O	
	Prionotus evolans	0.03				0.004 (±0.081)	90.0 (±62.2)	E, C, O	
	Prionotus ophryas		0.01			0.002 (±0.049)	16.0	C, O	
	Prionotus scitulus				0.08	0.033 (±0.180)	133.3 (±19.4)	C, O	
Serranidae	*Centropristis ocyurus*	0.73	0.04		0.08	0.313 (±1.592)	31.0 (±12.0)	O	W
	Centropristis striata	0.07	0.04			0.017 (±0.161)	33.1 (±14.8)	E, C, O	S
	Diplectrum formosum	0.96	2.50	2.39	0.16	1.360 (±3.378)	28.2 (±23.8)	C, O	W
	Epinephelus niveatus					0.005 (±0.069)	29.0 (±7.1)	Sl	S
	Serraniculus pumilio	0.03	0.21	0.34	0.12	0.155 (±0.734)	22.5 (±7.5)	C, O	W
	Serranus phoebe	0.31	0.04	0.02	0.04	0.220 (±1.618)	21.6 (18.1)	C, O	W
	Serranus subligarius					0.007 (±0.146)	30.7 (±9.3)	C, O	S
Grammistidae	*Rypticus* spp.			0.01		0.046 (±0.590)	41.8 (±12.9)	C, O	S
	Rypticus bistrispinus					0.054 (±0.596)	42.5 (±5.2)	C, O	S
Priacanthidae	*Priacanthus arenatus*		0.01			0.002 (±0.049)	15.0	O	S
	Pristigenys alta		0.02	0.05		0.016 (±0.126)	17.7 (±8.6)	O	S
Apogonidae	*Apogon* sp.	0.01	0.03			0.011 (±0.125)	20.9 (±11.0)	O	W
	Astrapogon spp./*Epigonus* spp.		0.01			0.002 (±0.049)	9.2		
	Apogon maculatus					0.061 (±0.680)	17.6 (±3.5)	O	W
	Apogon pseudomaculatus		0.04			0.028 (±0.213)	18.6 (±14.1)	O	W
Carangidae	Carangidae				0.02	0.005 (±0.068)	18.5 (±6.4)		
	Decapterus spp.		0.14			0.031 (±0.278)	24.8 (±5.7)	O	
	Caranx bartholomaei	0.02				0.002 (±0.044)	12.0	C, O	
	Caranx crysos			0.02		0.002 (±0.049)	101.0	C, O	W
	Chloroscombrus chrysurus		0.01	0.06		0.010 (±0.107)	15.1 (±3.6)	C, O	W
	Decapterus macarellus	0.02			0.01	0.005 (±0.069)	23.0 (±4.2)	O	
	Decapterus punctatus		0.05	0.01		0.017 (±0.188)	27.6 (±5.8)	C, O	
	Trachurus lathami	0.02				0.002 (±0.046)	16.0	C, O	
Lutjanidae	*Lutjanus analis*		0.01			0.002 (±0.049)	18.0	C, O	S
Haemulidae	*Haemulon aurolineatum*		0.05	0.05		0.016 (±0.185)	45.3 (±26.8)	C, O	W
Sparidae	*Stenotomus* sp.	0.18	0.16	0.14	0.08	0.135 (±0.823)	46.1 (±28.4)	C, O	W
	Lagodon rhomboides				0.06	0.012 (±0.128)	27.1 (±27.9)	E, C, O	W
Sciaenidae	*Cynoscion nothus*		0.04			0.006 (±0.095)	9.8 (±0.9)	E, C	
	Cynoscion regalis		0.06			0.008 (±0.102)	10.3 (±0.8)	E, C	
	Larimus fasciatus		0.19			0.027 (±0.313)	14.7 (±4.7)	E, C	
	Leiostomus xanthurus			2.27		3.361 (22.193)	16.2 (±1.7)	E, C, O	

Appendix (continued)

Family	Species	Cross-shelf stations Mean				All stations CPUE	SL (mm)	AD	RA
		Spring	Summer	Fall	Winter	Mean (SD)	Mean (SD)		
Sciaenidae (cont.)	Menticirrhus americanus		0.07			0.010 (±0.159)	13.3 (±9.1)	E, C	
	Stellifer laceolatus					0.005 (±0.097)	75.0 (±0.0)	E, C	
Mullidae	Upeneus parvus					0.002 (±0.049)	48.0	C, O	
Mugilidae	Mugil cephalus				0.18	0.047 (±0.422)	21.7 (±2.3)	E, C, O	
	Mugil curema		0.01		0.02	0.027 (±0.214)	21.8 (±1.5)	E, C, O	
Labridae	Halichoeres bivittatus		0.02			0.010 (±0.152)	71.0 (±5.0)	O	S
	Xyrichtys novacula		0.01			0.002 (±0.049)	41.5	O	
Scaridae	Scaridae		0.03			0.009 (±0.093)	41.3 (±31.8)		
Uranoscopidae	Kathetostoma albigutta				0.01	0.002 (±0.049)	26.0	O	
Dactyloscopidae	Dactyloscopus moorei	0.80	0.17	2.09	0.80	0.689 (±2.073)	22.1 (±5.1)	O	
Blenniidae	Chasmodes/Parablennius marmoreus		0.04			0.007 (±0.109)	19.0 (±2.6)	E, C	S
	Hypleurochilus geminatus	0.04	0.01			0.021 (±0.160)	43.6 (±17.2)	E, C	
	Parablennius marmoreus		0.02			0.009 (±0.119)	20.3 (±4.3)	E, C	S
Callionymidae	Diplogrammus pauciradiatus		0.07			0.025 (±0.170)	9.5 (±1.0)	O	
Gobiidae	Microgobius spp.	0.06	0.82	1.42	0.01	0.454 (±1.424)	16.7 (±1.9)		
	Gobiosoma bosci				0.01	0.014 (±0.150)	19.5 (±1.5)	E, C	
	Gobiosoma ginsburgi				0.02	0.005 (±0.068)	22.5 (±3.5)	E, C	W
	Ioglossus calliurus	0.01				0.002 (±0.041)	14.7	C, O	
Stromateidae	Peprilus triacanthus	0.07	0.01		0.08	0.042 (±0.250)	25.3 (±11.7)	C, O	
Bothidae	Bothus ocellatus/robinsi	0.07	0.08	0.07		0.041 (±0.254)	15.9 (±2.6)		
	Bothus spp.	0.86	0.41	4.50	0.33	0.971 (±3.728)	18.4 (±3.0)	O	
	Bothus lunatus	0.02			0.01	0.005 (±0.069)	79.0 (±9.9)	E, C, O	
	Bothus ocellatus		0.03	0.04	0.01	0.046 (±0.341)	33.4 (±23.5)	C, O	
	Bothus robinsi	1.21	0.23	0.52	0.34	0.435 (±1.464)	37.3 (±35.7)	C, O	
Paralichthyidae	Citharichthys spp.	0.19	0.03		0.41	0.132 (±0.671)	13.7 (±6.0)		
	Etropus spp.	8.89	1.31	2.96	15.97	10.563 (20.936)	18.3 (±8.2)		
	Ancylopsetta quadrocellata				0.22	0.114 (±0.386)	38.1 (±17.7)	C, O	
	Citharichthys gymnorhinus	0.03				0.004 (±0.063)	18.5 (±7.8)	O	
	Citharichthys macrops	0.20	0.04	0.02	0.13	0.090 (±0.441)	76.9 (±44.8)	C, O	
	Cyclopsetta fimbriata	0.03	0.04	0.05		0.037 (±0.226)	28.9 (±14.5)	O	
	Syacium papillosum	0.02	0.09	0.04		0.040 (±0.269)	16.5 (±17.2)	C, O	
Scopthalmidae	Scopthalmus aquosus				0.01	0.002 (±0.049)	14.0	E, C, O	
Soleidae	Gymnachirus melas	0.04	0.03			0.014 (±0.115)	17.1 (±7.5)	O	
Cynoglossidae	Symphurus spp.		0.01	0.02		0.005 (±0.067)	18.0 (±9.9)		
	Symphurus diomedeanus	0.05				0.007 (±0.109)	22.5 (±17.7)	O	
	Symphurus minor	0.26	0.25	1.87	0.15	0.552 (±1.878)	23.8 (±4.2)	O	
	Symphurus parvus	0.05	0.02			0.012 (±0.108)	15.9 (±1.7)	O	
	Symphurus plagiusa		0.02			0.029 (±0.270)	59.9 (±16.5)	E, C, O	
	Symphurus urospilus	0.42	0.24	0.43	0.28	0.257 (±0.717)	55.5 (±20.8)	O	
Balistidae	Aluterus schoepfi		0.01	0.02		0.005 (±0.066)	18.0 (±11.3)	C, O	W
	Cantherhines pullus					0.012 (±0.128)	18.5 (±1.5)	S	
	Monacanthus ciliatus	0.02				0.005 (±0.069)	41.0 (±26.9)		
	Monacanthus hispidus	0.18	0.54	1.36	0.06	0.460 (±1.314)	34.4 (±22.6)	C, O	
	Monacanthus setifer			0.01		0.004 (±0.063)	91.0 (±0.0)	O	
Ostraciidae	Lactophrys quadricornis		0.01			0.009 (±0.090)	67.8 (±83.6)	O	W
Tetraodontidae	Sphoeroides spp.	0.03	0.13		0.01	0.126 (±0.600)	15.9 (±4.0)		
Diodontidae	Chilomycterus schoepfi	0.02				0.002 (±0.049)	17.0	E, C	