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LARGE SCALE PATTERNS IN FISH TROPHODYNAMICS OF ESTUARINE AND SHELF HABITATS OF THE SOUTHEAST UNITED STATES

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ABSTRACT

To describe the trophic structure of fishes on the southeast United States estuarine and shelf systems, published gut content data for 60 predator species were synthesized. Cluster analysis and correspondence analysis were used to define fish trophic guilds. On the shelf, three trophic guilds were defined: piscivores, carnivores (majority of diet consisting of fish and crustaceans), and browsers of attached invertebrate prey. In the estuary, six trophic guilds were defined: planktivores, carnivores that consumed mostly fish and crustaceans, a transitional *Sciaenops ocellatus* (Linneaus, 1766) group between the planktivorous larvae and carnivorous juveniles of the species, benthic invertebrate consumers from seagrass habitats, cnidarian and benthic invertebrate consumers, and benthic invertebrate consumers from non-seagrass habitats. In summary, the diets of most fish species were broad and not easily classified, with guild assignment largely defined by the inclusion of fish in the diet, location of prey (benthic vs pelagic), and mobility of prey (sessile vs mobile). Using trophic gradients instead of discrete guilds in the definition of trophic structure and improving diet data from which these gradients are derived will provide a better foundation for ecosystem-based approaches to management.

The ecosystem approach to fisheries management being adopted by the National Oceanic and Atmospheric Administration, regional fisheries management councils (e.g., the South Atlantic Fishery Management Council), and state agencies, is an attempt to manage fisheries by maintaining interactions among species, as well as between species and their environment (Latour et al., 2003; Pikitch et al., 2004). Due to the highly-interconnected nature of species interactions, marine ecosystems are complex (Menge, 1995), with multiple steady states (Link, 2002). Reducing our perception of this biological complexity and defining parameters describing ecosystem status and function are necessary first steps for the effective implementation of an ecosystem approach to fisheries management (May et al., 1979; Botsford et al., 1997; Link, 2002). Link (2002) suggested five such groups of parameters: systems analysis metrics, aggregate metrics, food web metrics, community metrics, and single species metrics. Based on these parameters, defining nodes, such as predator and prey guilds, and understanding links between them, provides a sound basis for describing ecosystem status, thereby leading to improved ecosystem management (Odum, 1969; Link, 2002). Additionally, trophic guilds are important nodes for network modeling such as Multispecies Virtual Population Analysis (MSVPA) and Ecopath with Ecosim (Luczkovich et al., 2002; Latour et al., 2003).

Several studies from the northeast United States continental shelf have described patterns in trophic structure at scales that are useful to ecosystem management. In a study spanning over 25 yrs of trophic data, Garrison and Link (2000b) found that the trophic structure of Georges Bank did not change, though the dominance of trophic guilds did. Heavy overexploitation of demersal fish appears related to a shift in structure from a primarily demersal to pelagic community. On shorter time scales,

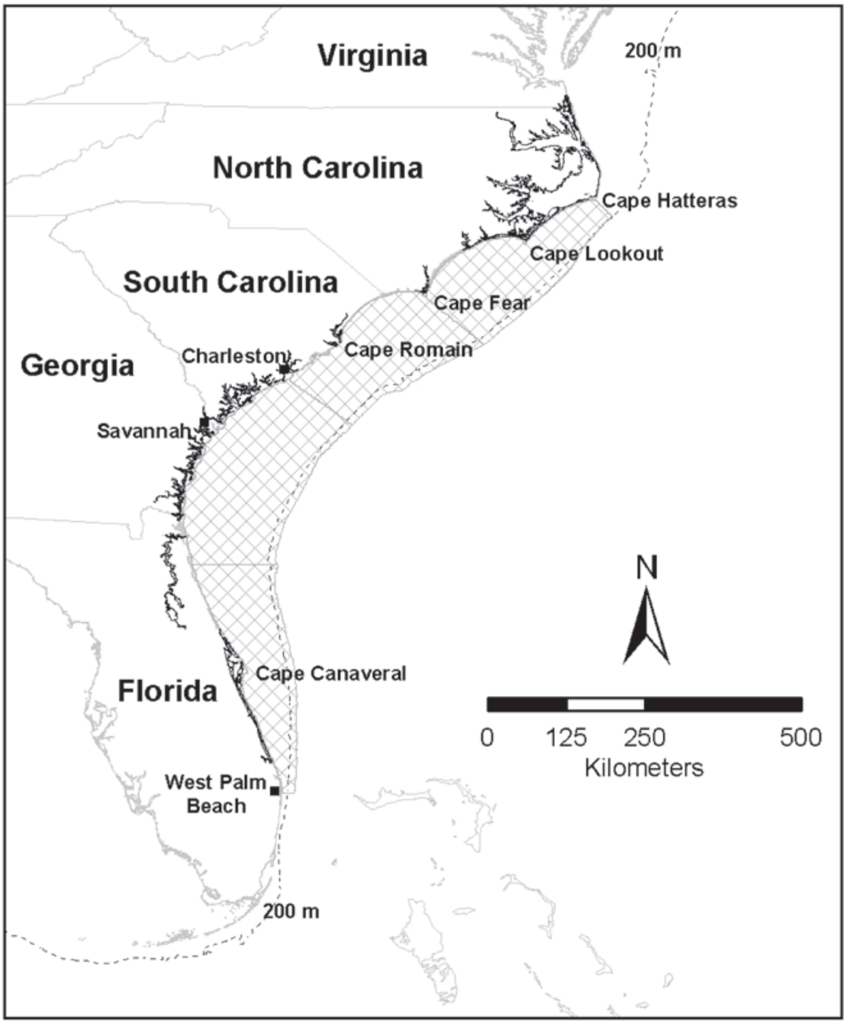

Figure 1. Map of southeast United States highlighting the area of the shelf and the estuaries included and showing the location of five capes of the region.

seasonal and ontogenetic shifts in trophic structure have been described (Garrison, 2000 and Garrison and Link, 2000a), and in conjunction with spatial separation and prey switching, appear to minimize competition within guilds due to dietary overlap (Garrison and Link 2000a).

The southeast United States Atlantic continental shelf ecosystem extends from Cape Hatteras, North Carolina to West Palm Beach, Florida (Fig. 1). The landward side of the ecosystem contains many interconnected, shallow estuarine areas, and the offshore side of the ecosystem is dominated by the Gulf Stream, a strong poleward flowing western boundary current. In total, ~1200 fish species from ~140 families inhabit the ecosystem (Kendall and Matarese, 1994). Many of these species support economically important recreational and commercial fisheries, including reef fish (e.g., *Mycteroperca microlepis, Pagrus pagrus*), ground fish in estuaries and on the inner-shelf (e.g., *Paralichthys dentatus, Micropogonias undulatus*), and pelagic fishes including industrial fisheries for *Brevoortia tyrannus* and commercial and recreational fisheries for *Coryphaena hippurus*, scombrids, and istiophorids (Manooch, 1998). The South Atlantic Fisheries Management Council is embarking on ecosystem fisheries management, and an early step in this process is the definition of trophic guilds to reduce the biological complexity found in the ecosystem (SAFMC, 2004).

There have been numerous diet studies for individual species and small groups of sympatric species of fish from the southeast United States [see Marancik and Hare (2005) for review]. These studies, which have emphasized small-scale patterns in trophodynamics (i.e., within species and within habitats), show that individuals of a species can go through marked changes in diet due to ontogenetic, seasonal, or habitat shifts. For example, at least four trophic stages of *Lagodon rhomboides* occur due to ontogenetic shifts: planktivorous, carnivorous, omnivorous, and herbivorous (Stoner, 1980; Stoner and Livingston, 1984; Gallagher et al., 2001). Seasonal shifts in diet have also been examined in several species. The diet of king mackerel, *Scomberomorus cavalla*, in the southeast U.S. is dominated by clupeids (*B. tyrannus* and *Opisthonema oglinum*) in spring, but becomes more diverse in fall, including a wider variety of fish (i.e., exocoetids and scombrids; DeVane, 1978; Saloman and Naughton, 1983a). Few studies have directly examined trophodynamics at medium scales (i.e., within species among habitats or among species within habitats). Since many fish species move from one habitat to another ontogenetically (e.g., from nearshore to reefs), many species exhibit different diets between habitats (e.g., Cocheret de la Moriniere et al., 2003). Yet even the same ontogenetic states can have different diets in different habitats; for example, *Archosargus probatocephalus* appears to eat more attached sessile prey in inner- and mid-shelf reef habitats (Sedberry, 1987) compared to estuarine habitats (Overstreet and Heard, 1982).

For ecosystem management, however, trophodynamic relationships should be examined at larger scales (i.e., among species and among habitats). Many fish stocks require large-scale consideration. Individuals of migratory pelagic species can range great distances during the course of a year or season (Sutter et al., 1991). Many fish also utilize multiple habitat types during the course of their life, such as many estuarine-dependent species that spawn offshore, mature in estuaries, and then return to the shelf as adults (Ross and Moser, 1995). Further, in complex ecosystems, general patterns in trophic structure are often used rather than consideration of specific species (Link, 2002). Despite a growing need to understand trophodynamics of the southeast United States among species and among habitats, few large-scale studies of trophic structure have been conducted in the region (e.g., Okey and Pugliese, 2001). Therefore, the overall objectives of this study were to identify predator and prey guilds among fishes in the southeast United States continental shelf and estuarine ecosystems at medium (within habitats) and large-scales (among habitats). By using multivariate statistical techniques to analyze the data, trophic guilds were defined objectively based on the reported diets of fish.

Materials and Methods

Data Collection.—Fish diet data were collected from published literature of fishes found in the southeast United States continental shelf and estuaries (Table 1). To maximize the number of species included, actual study sites ranged from Long Island, New York, through the Caribbean and northern Gulf of Mexico to Belize, but most studies were conducted with-

Table 1. Predator species used in analyses and reference to original study. *Full citation can be found in Marancik and Hare, 2005. †Full citation can be found in the Literature Cited section of this paper. Predator codes used in correspondence analyses also are shown. Members of each trophic guild are labeled for each habitat: benthic/demersal carnivores (BCAR); pelagic carnivores (PCAR); structure-associated carnivores (SCAR); benthic invertebrate consumers (BIN); cnidarian and benthic invertebrate consumers (CBI); benthic and epibenthic seagrass invertebrate consumers (BSI); planktivores (PLA); transitional *Sciaenops ocellatus* guild (SOCE2); benthic/demersal piscivores (BPISC); pelagic piscivores (PPISC); structure associated piscivores (SPISC); browsers (BROW).

					Trophic Guild	
Family	Species	Study of Origin	Predator Code	Size	Estuary	Shelf
Albulidae	*Albula vulpes* (Linnaeus, 1758)	Crabtree et al., 1998*	AVUL	228–702 mm FL	BCAR	
Muraenidae	*Gymnothorax moringa* (Cuvier, 1829)	Young and Winn, 2003*	GMOR	379–808 mm TL		SCAR
Muraenidae	*Gymnothorax vicinus* (Castelnau, 1855)	Young and Winn, 2003*	GVIC	403–947 mm TL		SPISC
Clupeidae	*Harengula jaguana* Poey, 1856	Motta et al., 1995*	HJAG	82–122 mmSL	BSI	
Engraulidae	*Anchoa hepsetus* (Linnaeus, 1758)	Motta et al., 1995*	AHEP	86–100 mm SL	BSI	
Ariidae	*Arius felis* (Linnaeus, 1766)	Motta et al., 1995*	AFEL	280–377 mm SL	BIN	
Gadidae	*Urophycis floridana* (Bean and Dresel, 1884)	Sikora et al., 1972*	UFLO	50–224 mm TL	BCAR	
Gadidae	*Urophycis regia* (Walbaum, 1792)	Sikora et al., 1972*	UREG	56–200 mm TL	BCAR	
Cyprinodontidae	*Floridichthys carpio* (Günther, 1866)	Motta et al., 1995*	FCAR	46–87 mm SL	BSI	
Cyprinodontidae	*Fundulus similis* (Baird and Girard, 1853)	Motta et al., 1995*	FSIM	73–114 mm SL	BSI	
Syngnathidae	*Syngnathus scovelli* (Evermann and Kendall, 1896)	Motta et al., 1995*	SSCO	91–149 mm SL	BSI	
Triglidae	*Bellator militaris* (Goode and Bean, 1896)	Ross, 1977*	BMIL	28.1–108.2 mm SL		BCAR
Triglidae	*Prionotus alatus* (Goode and Bean, 1896)	Ross, 1977*	PALA	47.8–156.5 mm SL		BPISC
Triglidae	*Prionotus martis* Ginsburg, 1950	Ross, 1977*	PMAR	50.1–168.0 mm SL		BCAR
Triglidae	*Prionotus ophryas* Jordan and Swain, 1885	Ross, 1977*	POPH	63.0–188.5 mm SL		BCAR
Triglidae	*Prionotus roseus* Jordan and Evermann, 1887	Ross, 1977*	PROS	67.4–183.0 mm SL		BCAR
Triglidae	*Prionotus rubio* (salmonicolor) Jordan, 1886	Ross, 1977*	PSAL	107.0–221.5 mm SL		BCAR
Triglidae	*Prionotus scitulus* Jordan and Gilbert, 1882	Ross, 1978*	PSCIE	21–140 mm SL	CBI	
Triglidae		Ross, 1977*	PSCIS	26.3–156.5 mm SL		BCAR
Triglidae	*Prionotus tribulus* Cuvier, 1829	Ross, 1977*	PTRI	57.5–211.0 mm SL		BCAR
Moronidae	*Morone saxatilis* (Walbaum, 1792)	Manooch, 1973*	MSAX	125–714 mm TL	BCAR	
Serranidae	*Centropristis philadelphica* (Linnaeus, 1758)	Ross et al., 1989*	CPHI	< 75 to 224 mm SL		SCAR
Serranidae	*Centropristis striata* (Linnaeus, 1758)	Steimle and Ogren, 1982*	CSTR	50 to > 250 mm SL		SCAR

Table 1. Continued.

					Trophic Guild	
Family	Species	Study of Origin	Predator Code	Size	Estuary	Shelf
Serranidae		Sedberry, 1988*				
Serranidae	*Epinephelus niveatus* (Valenciennes, 1828)	Dodrill et al., 1993*	ENIV	335–1,100 mm TL		SCAR
Serranidae	*Mycteroperca microlepis* (Goode and Bean, 1879)	Ross and Moser, 1995*†	MMIC	10–200 mm SL	SCAR	
Serranidae	*Serranus subligarius* (Cope, 1870)	Hastings and Bortone, 1980*	SSUB1	20–40 mm SL		SCAR
Serranidae			SSUB2	40–90 mm SL		SCAR
Malacanthidae	*Caulolatilus microps* Goode and Bean, 1878	Ross, 1982*	CMIC	400–780 mm TL		SCAR
Pomatomidae	*Pomatomus saltatrix* (Linnaeus, 1766)	Naughton and Saloman, 1984*†	PSLT	0–999 mm FL		PPISC
Rachycentridae	*Rachycentron canadum* (Linnaeus, 1766)	Arnedt et al., 2001*	RCANE	370–1,410 mm FL	SCAR	
Rachycentridae		Smith, 1985*	RCANS	390–1,420 mm FL		SCAR
Carangidae	*Decapterus punctatus* (Cuvier, 1829)	Donaldson and Clavijo, 1994*	DPUN	46–151 mm SL		SPISC
Carangidae	*Seriola dumerili* (Risso, 1810)	Manooch and Haimovici, 1983*	SDUM	397–1,386 mm TL		SPISC
Carangidae	*Seriola rivoliana* Valenciennes, 1833	Manooch and Haimovici, 1983*	SRIV	276–1,094 mm TL		SPISC
Coryphaenidae	*Coryphaena hippurus* Linnaeus, 1758	Rose and Hassler, 1974*	CHIP	250–1,530 mm		PPISC
Coryphaenidae		Manooch et al., 1983*				
Lutjanidae	*Lutjanus analis* (Cuvier, 1828)	Duarte and Garcia, 1999*	LANA	210–460 mm		SPISC
Lutjanidae	*Lutjanus griseus* (Linnaeus, 1758)	Franks and VanderKooy, 2000*	LGRI	71.2–151.1 mm SL	SCAR	
Lutjanidae	*Lutjanus synagris* (Linnaeus, 1758)	Franks and VanderKooy, 2000*	LSYN1	63.7–86.5 mm SL	SCAR	
Lutjanidae		Duarte and Garcia, 1999*	LSYN2	105–335 mm SL		SCAR
Lutjanidae	*Rhomboplites aurorubens* (Cuvier, 1829)	Sedberry and Cuellar, 1993*	RAUR	1 to > 175 mm SL		SPISC
Lutjanidae		Grimes, 1979*				
Gerreidae	*Eucinostomus gula* (Quoy and Gaimard, 1824)	Motta et al., 1995*	EGUL	64–89 mm SL	CBI	
Haemulidae	*Haemulon aurolineatum* Cuvier, 1830	Sedberry, 1985*†	HAUR	1–200 mm SL		SCAR
Sparidae	*Archosargus probatocephalus* (Walbaum, 1792)	Sedberry 1987*†	APRO	< 300 to > 410 mm SL		BROW

Table 1. Continued.

Family	Species	Study of Origin	Predator Code	Size	Trophic Guild	
					Estuary	Shelf
Sparidae	*Calamus leucosteus* Jordan and Gilbert, 1885	Sedberry, 1990*†	CLEU	< 125 to > 272 mm SL		BCAR
Sparidae	*Diplodus holbrooki* (Bean, 1878)	Pike and Lindquist, 1994*	DHOL	60–160 mm SL		BROW
Sparidae	*Lagodon rhomboides* (Linnaeus, 1766)	Stoner, 1980*†	LRHO1	11–15 mm SL	PLA	
Sparidae			LRHO2	16–35 mm SL	BSI	
Sparidae			LRHO3	36–80 mm SL	BSI	
Sparidae			LRHO4	> 80 mm SL	BSI	
Sparidae		Motta et al., 1995*	LRHO5	123–159 mm SL	BIN	
Sparidae	*Pagrus pagrus* (Linnaeus, 1758)	Manooch, 1977*	PPAG	46–625 mm TL		SCAR
Sciaenidae	*Cynoscion regalis* (Bloch and Schneider, 1801)	Merriner, 1975*	CREG	0–4 yrs: only age reported	BCAR	
Sciaenidae	*Larimus fasciatus* Holbrook, 1855	Ross, 1989*	LFAS	19–182 mm SL		BCAR
Sciaenidae	*Sciaenops ocellatus* (Linnaeus, 1766)	Bass and Avault, 1975*	SOCE1	0–9 mm SL	PLA	
Sciaenidae		Bass and Avault, 1975*	SOCE2	10–19 mm SL	SOCE2	
Sciaenidae		Bass and Avault, 1975*	SOCE3	20–29 mm SL	BCAR	
Sciaenidae		Boothby and Avault, 1971*				
Sciaenidae		Bass and Avault, 1975*	SOCE4	30–39 mm SL	BCAR	
Sciaenidae		Boothby and Avault, 1971*				
Sciaenidae		Bass and Avault, 1975*	SOCE5	40–49 mm SL	BCAR	
Sciaenidae		Boothby and Avault, 1971*				
Sciaenidae		Bass and Avault, 1975*	SOCE6	50–59 mm SL	BCAR	
Sciaenidae		Boothby and Avault, 1971*				
Sciaenidae		Bass and Avault, 1975*	SOCE7	60–69 mm SL	BCAR	
Sciaenidae		Boothby and Avault, 1971*				
Sciaenidae		Bass and Avault, 1975*	SOCE8	70–79 mm SL	BCAR	
Sciaenidae		Boothby and Avault, 1971*				
Sciaenidae		Bass and Avault, 1975*	SOCE9	80–89 mm SL	BCAR	
Sciaenidae		Boothby and Avault, 1971*				

Table 1. Continued.

Family	Species	Study of Origin	Predator Code	Size	Trophic Guild	
					Estuary	Shelf
Sciaenidae		Bass and Avault, 1975*	SOCE10	90–99 mm SL	BCAR	
Sciaenidae		Boothby and Avault, 1971*				
Sciaenidae		Bass and Avault, 1975*	SOCE11	100–109 mm SL	BCAR	
Sciaenidae		Boothby and Avault, 1971*				
Sciaenidae		Bass and Avault, 1975*	SOCE12	110–119 mm SL	BCAR	
Sciaenidae		Boothby and Avault, 1971*				
Sciaenidae		Bass and Avault, 1975*	SOCE13	120–129 mm SL	BCAR	
Sciaenidae		Boothby and Avault, 1971*				
Sciaenidae		Bass and Avault, 1975*	SOCE14	250–932 mm SL		BCAR
Mullidae	*Upeneus parvus* (Poey, 1852)	Campos-Davila et al., 2002*	UPAR	73–150 mm		BCAR
Ephippidae	*Chaetodipterus faber* (Broussonet, 1782)	Hayse, 1990*	CFAB	10–510 mm TL	CBI	BROW
Sphyraenidae	*Sphyraena barracuda* (Walbaum, 1792)	Schmidt, 1989*	SBAR	33–442 mm TL	PCAR	
Scombridae	*Euthynnus alletteratus* (Rafinesque, 1810)	Manooch et al., 1985*	EALL	172–885 mm FL		PPISC
Scombridae	*Katsuwonus pelamis* (Linnaeus, 1758)	Dragovich, 1970*	KPEL	220–810 mm FL		PPISC
Scombridae		Batts, 1972*				
Scombridae	*Scomberomorus cavalla* (Curier, 1829)	Finucane et al., 1990*†	SCAV1	2.9–730 mm FL		PPISC
Scombridae		Naughton and Saloman, 1981*	SCAV2	117–432 mm FL		PPISC
Scombridae		Saloman and Naughton, 1983a*†	SCAVEF	0–1,599 mm FL		PPISC
Scombridae			SCAVGA	0–1,599 mm FL		PPISC

Table 1. Continued.

Family	Species	Study of Origin	Predator Code	Size	Trophic Guild	
					Estuary	Shelf
Scombridae			SCAVNS	0–1,599 mm FL		PPISC
Scombridae	*Scomberomorus maculatus* (Mitchill, 1815)	Finucane et al., 1990*†	SMAC1	2.8–420 mm FL		PPISC
Scombridae		Naughton and Saloman, 1981*	SMAC2	103–309 mm FL		PPISC
Scombridae		Saloman and Naughton, 1983b*†	SMACEF	50–749 mm FL		PPISC
Scombridae			SMACNS	50–749 mm FL		PPISC
Scombridae	*Thunnus albacares* (Bonnaterre, 1788)	Dragovich, 1970*	TALB	400–1,550 mm FL		PPISC
Scombridae		Manooch and Mason, 1983*				
Scombridae	*Thunnus atlanticus* (Lesson, 1831)	Manooch and Mason, 1983*	TATL	< 500–1,100 mm FL		PPISC
Paralichthyidae	*Paralichthys dentatus* (Linnaeus, 1766)	Powell and Schwartz, 1979*	PDEN1	100–200 mm TL	BCAR	
Paralichthyidae		Poole, 1964*	PDEN2	200–700 mm TL	BCAR	
Paralichthyidae	*Paralichthys lethostigma* Jordan and Gilbert, 1884	Powell and Schwartz, 1979*	PLET1	100–200 mm TL	BCAR	
Paralichthyidae			PLET2	200–300 mm TL	BCAR	
Tetraodontidae	*Sphoeroides spengleri* (Bloch, 1785)	Targett, 1978*	SSPR	16–129 mm SL	BSI	
Tetraodontidae	*Sphoeroides testudineus* (Linnaeus, 1758)	Targett, 1978*	STES	72–208 mm SL	BSI	
Diodontidae	*Chilomycterus schoepfi* (Walbaum, 1792)	Motta et al., 1995*	CSCH	119–210 mm SL	BSI	

in the southeast U.S. and northern Gulf of Mexico. An attempt was made to limit the number of non-peer reviewed sources used in analyses (< 15%), but this desire was again balanced with the goal of maximizing the number of species included.

A variety of diet indices and measures are used in fish diet studies making comparison difficult (Hyslop, 1980; Cortes, 1997). At least 15 different measurements have been used for fishes of the southeast United States (Marancik and Hare, 2005), many of which indicate number of prey consumed (e.g., percent frequency of occurrence), but not the biomass of prey consumed (e.g., percent volume). This variety of measures precludes the conversion of all studies to a common measure. As a result, only those studies that measured diet as percent volume or percent weight were included in the present analysis. Volume and weight data have biases, namely that soft bodied and hard bodied prey digest at different rates, but these quantities measure consumption biomass, which is the measure frequently used in modeling trophic relationships (Hyslop, 1980; Cortes, 1997; Christensen and Walters, 2004). Percent volume and percent weight are not equal and differ by the density of prey items. Both, however, have successfully been used together in other examinations of trophic relationships (Swedberg and Walburg, 1970), and no effort was made to use a taxa-specific adjustor to standardize between percent volume and percent weight.

The prey categories analyzed (Table 2) represent a balance between including as many studies as possible, while retaining the ecological significance of the individual prey categories. While some studies report prey at the genus or species level, many others report prey at much higher taxonomic levels, such as phylum and class. In a few studies included here (~2%), some prey were identified at a level that combined several of the prey categories used for some taxa, while most prey were identified at a level compatible with the prey categories used in this study. In these instances, the percent weight or percent volume values were split equally among prey categories only if the prey category that was split constituted a minor component of the overall diet. The impact on the analyses was minimal, but the approach allowed these species to be included. For example, Ross and Moser (1995) identified some prey to the category amphipod (< 1%); this value was split equally among the three categories of amphipods used here (Gammaridea, Caprellidea, and Hyperiidea).

Data Analysis.—Data from the percent volume and percent weight matrix were subdivided into two habitat types based on where the study was conducted: estuarine habitat and shelf habitat. A predator vs prey matrix was created for each dataset with predators as columns and prey as rows (Appendix A, available as an Excel® file in the online version of this paper at www.rsmas.miami.edu/bms). The two habitat datasets incorporated percent volume and percent weight data from 50 studies and for 60 predator species and 77 prey taxa (Tables 2, 3). It is important to recognize that these data are not a random sampling of species from each habitat; rather they are based on the non-random selection of individual species for diet analysis by different researchers.

Predator and prey guilds were classified using hierarchical clustering and correspondence analysis (CA). CA is a multivariate ordination technique, which portrays large multidimensional datasets on a lower dimensional map. CA ordinations can be analyzed by proximity of points as well as by dimensionality. Distance between points on the low dimensional map represents similarity or dissimilarity; points close together are more similar than points farther apart. Points along an axis (or dimension) fall along an environmental gradient (in this case a prey gradient). In addition, CA can plot predator and prey data together in one space making direct links between predator guilds and prey groups possible.

Predator guilds were defined based on similarity of prey found in their guts. To reduce the subjective nature of grouping predators and prey based on proximity, a group average hierarchical cluster analysis using the Bray-Curtis similarity index was employed to objectively define predator guilds (Luczkovich et al., 2002). Objective classification was based on the bootstrapping technique described by Jaksic and Medel (1990). All quantities of prey were randomly re-assigned within each predator; 100 random datasets were created. The distances at which 95% of random linkages occurred were used to define guilds for each of the three da-

Table 2. Prey taxa used in analyses. Prey codes used in correspondence analyses also are shown. Prey separating each trophic guild are labeled: benthic/demersal, pelagic, and structure-associated carnivores (CAR); benthic invertebrate consumers (BIN); cnidarian and benthic invertebrate consumers (CBI); benthic and epibenthic seagrass invertebrate consumers (BSI); planktivores (PLA); transitional *Sciaenops ocellatus* guild (SOCE2); benthic/demersal, pelagic, and structure-associated piscivores (PISC); browsers (BROW).

		Trophic Guild	
Prey Taxa	Prey Code	Estuary	Shelf
Foramineferia	FOR	CAR	CAR
Dinoflagellates	DIN		PISC/CAR
Algae	ALG	BIN/CBI	BROW
Porifera	POR	CBI	BROW
Hydrozoa	HYD	CBI	BROW
Cubozoa	CUB	CBI	BROW
Anthozoa	ANT	CBI	BROW
Ctenophore	CTE	CBI	CAR
Platyhelminthes	PLA	BSI	CAR
Nemertea (Rhynchocoela)	NEM		CAR
Nematoda	NET	CAR/SOCE2	PISC/CAR
Amphineura	AMP		CAR
Gastropoda (excluding Pteropods)	GAS	BSI	CAR
Pteropods	PTE	CAR	CAR
Nudibranch	NUD	BIN	PISC
Bivalvia/Pelecypoda	BIV	BSI	CAR
Bivalvia/Pelecypoda veliger	BIVEL		CAR
Scaphopoda	SCA	BSI	
Cephalopoda	CEP	CAR	PISC
Polychaeta	POL	BIN/CBI	CAR
Echiura	ECHIR	BSI	
Sipuncula	SIP	BIN/CBI	CAR
crustacea	CRU	CBI	CAR
Ostracoda	OST	BSI	CAR
Leptostraca	LEP	CBI	CAR
Stomatopoda	STO	CAR	CAR
Stomatopoda larvae	STOLAR		PISC
Euphausiacea	EUP		PISC/CAR
Decapod Larvae	DECL	BSI	CAR
Sergestoidea	SER	CAR	CAR
Panaeidea	PAN	CAR	CAR
Anomura	ANO	CAR	CAR
Anomura larvae	ANOLAR	BSI	PISC/CAR
Brachyura	BRAC	CAR	CAR
Caridea	CAR	CAR	CAR
Lobster	LOB	CAR	PISC/CAR
Lobster larvae	LOBLAR		PISC
Thalassinoidea	THAL	CAR	CAR

Table 2. Continued.

		Trophic Guild	
Prey Taxa	Prey Code	Estuary	Shelf
Caprellidea	CAP	BSI	CAR
Gammaridea	GAM	BSI	CAR
Hyperiidea	HYP	BSI	PISC/CAR
Cumacea	CUM	BIN	CAR
Isopoda	ISO	BSI	CAR
Mysida	MYS	CAR/SOCE2	CAR
Tanaidacea	TAN	CAR	BROW
Calanoida	CAL	PLA	CAR
Cyclopoida	CYC	PLA	CAR
Harpacticoida	HAR	PLA	CAR
Poecilostomatoida	POE		CAR
Cirripedia	CIR	BSI	CAR
Cyprid larvae	CYP	BSI	PISC/CAR
Branchiopoda	BRAN	BSI	BROW
Chelicerata	CHE	BIN	PISC/CAR
Insecta	INS	CAR	PISC
Ectoprocta (Bryozoa)	BRY	BSI	BROW
Brachiopoda	BRAP	CBI	CAR
Chaetognatha	CHA		CAR
Echinoidea	ECHI		CAR
Asteroidea	AST		CAR
Holothuroidea	HOL	CAR	CAR
Ophiuroidea	OPH	BSI	CAR
Hemichordata	HEM	CBI	
invertebrate eggs	INV	PLA	
Appendicularia	APP	BIN	BROW
Ascidiacea	ASC	BIN	CAR
Thaliacea	THA	BIN	PISC/CAR
Cephalochordata	CEPH	CBI	CAR
Chondrichthys	CHO	CAR	CAR
Osteichthys	OSTE	CAR	PISC
Organic matter	ORG	CAR	CAR
Amorphous matter	AMO	BSI	CAR
Inorganic matter	INO	CAR	CAR
Plantae	PLAN	BSI	PISC/CAR

tasets examined here: shelf (16.35 similarity), estuary (18.19 similarity), and shelf and estuary combined (16.51 similarity). Guilds that formed at similarity values higher than those defined by the bootstrapping technique were unlikely to occur by chance. Hierarchical clusters were created using the PRIMER statistical software (Clarke and Warwick, 2001). Only taxa which grouped together in both the cluster diagrams (at varying levels of similarity) and the CA ordinations were considered trophic guilds and described further.

Conversely, prey groups were defined based on co-occurrence in fish guts. These prey guilds were examined primarily to assist in defining the predator guilds. Predator and prey groups were defined first for each habitat individually. Then, by analyzing data from both habitats together, similarities between estuarine and shelf predator guilds were described, providing a comparison of trophic structures between habitats.

Table 3. Eigenvalues for each correspondence analyses (CA) axis by each habitat and all data combined. A sharp drop in the eigenvalue marks the axes that explain most of the data.

	CA Axis			
Habitat	Axis 1	Axis 2	Axis 3	Axis 4
Shelf Eigenvalue	0.718	0.609	0.572	0.484
Estuary Eigenvalue	0.719	0.693	0.626	0.609
All Eigenvalues	0.69	0.619	0.536	0.518

Results

Shelf-Habitat.—Four significant branches were defined by the cluster diagram (similarity = 16.35; α = 0.05). Three species (*Chaetodipterus faber, A. probatocephalus,* and *Diplodus holbrooki*) occurred as individual branches (Fig. 2A), but consumed similar diets and grouped together in the CA (Fig. 2B, C). These three species were considered one trophic guild. The fourth and largest of the branches contained almost 95% of the shelf taxa. This one branch appeared as two groups in the CA (Fig. 2B, C), which separated along the dimension that described most of the variability (Table 3). This dimension was related to the percentage of fish in the diet and thus approximates the degree of piscivory (Fig. 3). Therefore to increase guild resolution, the large branch from the cluster analysis was divided at the next major division (α = 0.025; Jaksic and Medel, 1990). Thus, three trophic guilds were identified: benthic- and structure-browsers, piscivores, and carnivores.

The benthic- and structure-browsing guild was formed at 10% similarity in the cluster analysis (Fig. 2A), but was well defined in the CA ordination (Fig. 2B,C; BROW). This browser guild included *C. faber*, *Diplodus holbrooki*, and *A. probatocephalus* (Fig. 2; Table 1). Browsers primarily fed on (~60%) bryozoans, algae, poriferans, hydrozoans, and anthozoans, but also included branchiopods, cubozoans, and appendicularians (Figs. 2C, 4).

Piscivores had the most similar diet of the three shelf guilds based on both the close proximity of the guild's predatory species and prey taxa in the CA ordination (Fig. 2B,C; PISC), and the relatively high percent similarity (40%) in the cluster diagram. This guild included 15 predator species, mostly migratory pelagics such as *S. cavalla*, *S. maculatus*, *C. hippurus*, and *Pomatomus saltatrix,* but also some reef associated snapper and eels (Table 1). Fish were the dominant prey in this guild (almost 80% composition by volume; Fig. 3) with all other prey taxa making up considerably less of the percent volume and weight (20% composition combined; Fig. 4).

Because of the difficulty identifying soft-bodied prey from gut samples, fish were lumped together in a collective fish category. In 91 studies describing fish as prey, 35% identified all fish prey as one group (labeled as osteichthys, fish, teleostei, or fish parts), 59% identified fish species, but a substantial amount were still left at the generic fish level, and only 5.5% were able to identify all fish prey to the family, genus, or species level. The resultant piscivore group was large and may not provide enough detail to adequately classify a system, so adult habitat (vertical distribution in the water column because, overall, vertical distribution of prey was one of the underlying factors in our groupings) was used to further divide the piscivores into: benthic/demersal piscivores (*Prionotus alatus*), pelagic piscivores (*P. saltatrix, C. hippurus, Euthynnus alletteratus, Katsuwonus pelamis, S. cavalla, S. maculatus, Thunnus alb-*

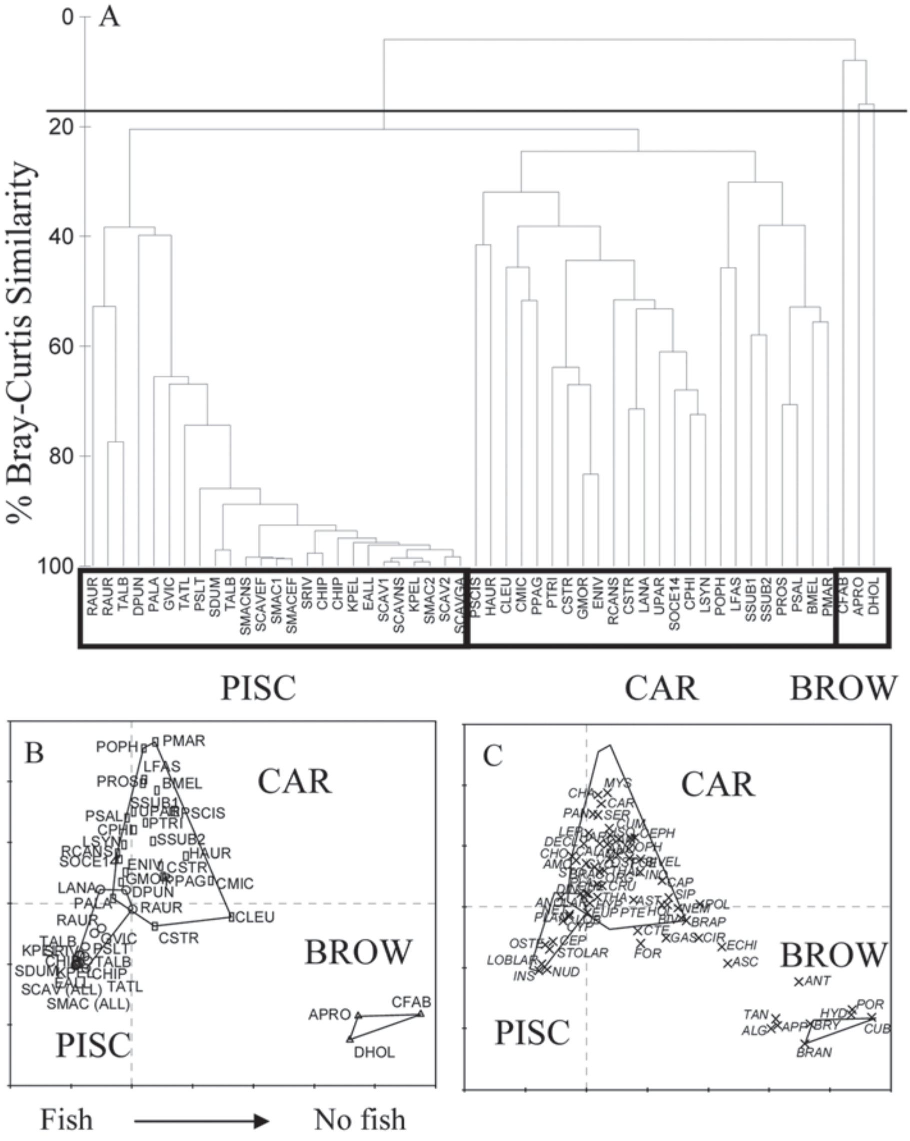

Figure 2. The trophic guilds of the shelf habitat defined by (A) cluster diagram of predators based on similarity in prey taxa, (B) correspondence analysis (CA) ordination of predators, and (C) CA ordination of prey with the predator trophic guild polygons. The dashed lines intersect at the origin of each ordination. Definitions of predator and prey codes are in Table 1. Boxes surround members of each guild in the cluster diagram defined at roughly 21% similarity (α = 0.025). The predator guilds are labeled in the ordinations: BROW is the browser guild; PISC includes the benthic/demersal, pelagic, and structure-associated piscivore guilds, and CAR includes the benthic/demersal and structure-associated carnivore guilds.

acares, and *Thunnus atlanticus*), and structure-associated piscivores (*Gymnothorax vicinus, Decapterus punctatus, Seriola dumerili, S. rivoliana, Lutjanus analis,* and *Rhomboplites aurorubens*).

Rhomboplites aurorubens grouped with the piscivores in the cluster diagram, but were associated with the carnivores in the CA ordination (Fig. 2). On inspection of

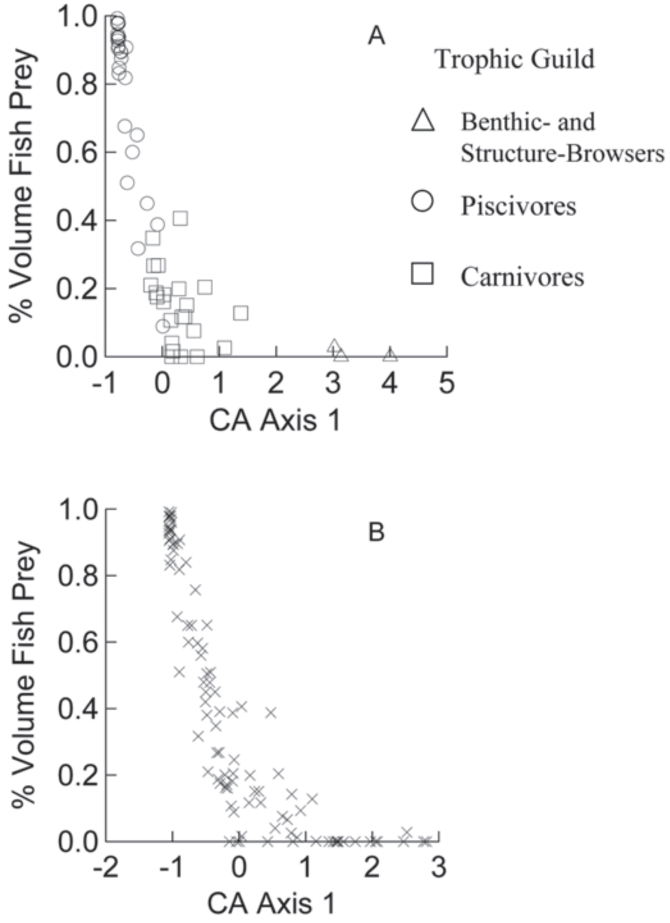

Figure 3. Percent volume of fish prey eaten vs the correspondence analysis (CA) score for axis one showing that (A) shelf and (B) combined shelf and estuary predators with low CA scores (the far left of the ordinations in Figs. 2 and 8) consumed a higher percentage of fish prey. Piscivores include the benthic/demersal piscivore, pelagic piscivores, and structure-associated piscivores. Carnivores include the benthic/demersal carnivores and structure-associated carnivores.

the raw data, *R. aurorubens* consumed considerably more cephalopods than fish, though fish were consumed. Since most piscivores also ate other prey, it is important to recognize that there is a transition area between piscivores (> 80% fish) and carnivores (< 20% fish) (see Fig. 3) into which some species fell (*Prionotus salmonicolor* (*rubio*), *Gymnothorax moringa*, *Sciaenops ocellatus* (250–930 mm), *Centropristis striata*, *R. aurorubens*, *D. punctatus*, *L. analis*, *T. albacares*, *G. vicinus*, *P. alatus*, and *T. atlanticus*).

The last shelf guild comprised the carnivores (CAR; Fig. 2). The largest numbers of predator species (22 species) and prey taxa (50 taxa) were included in this guild, which formed at 25% similarity in the cluster diagram. Sea robins (Triglidae), sea basses (Serranidae), and grunts (Haemulidae) fed on a variety of prey ranging from benthic to pelagic prey with varying degrees of mobility (Tables 2, 4). The dominant prey types for this guild, however, were fish, crabs, and shrimp (Fig. 4). Again, because of the difficulty identifying fish from stomach content samples, the carnivore

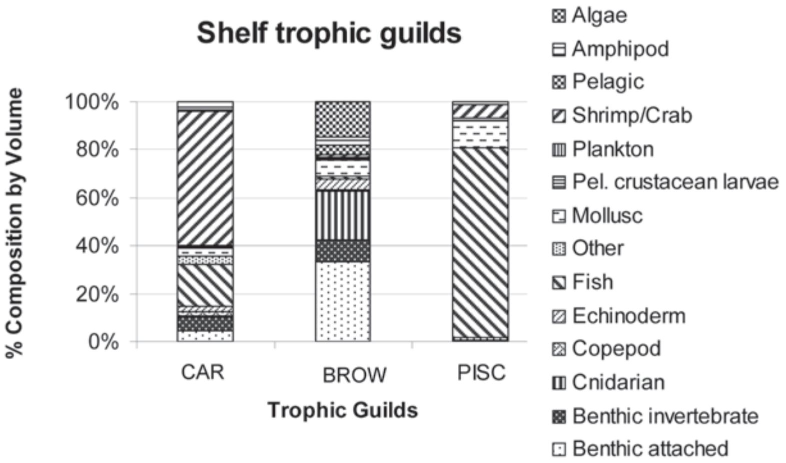

Figure 4. Percent composition by volume of the three shelf guilds. CAR is the benthic/demersal and structure-associated carnivore guilds; BROW is the shelf browsers; PISC is the shelf benthic/demersal, pelagic, and structure-associated piscivores.

group was subdivided into benthic/demersal carnivores (*Bellator militaris, Prionotus martis, Prionotus ophryas, Prionotus roseus, Prionotus rubio, Prionotus scitulus, Prionotus tribulus, Calamus leucosteus, Larimus fasciatus, S. ocellatus,* and *Upeneus parvus*) and structure-associated carnivores (*G. moringa, C. philadelphica, C. striata, Epinephelus niveatus, Serranus subligarius, Caulolatilus microps, Rachycentron canadum, Lutjanus synagris, Haemulon aurolineatum,* and *P. pagrus*).

Estuarine Habitat.—The estuarine habitat trophic guilds were not as clearly delineated by the cluster analysis and CA as the shelf habitat trophic guilds. Six significant branches were observed in the cluster diagram ($\alpha = 0.05$; similarity = 18.19). Two CA dimensions described most of the variance (Table 3) and three gradients along these two dimensions distinguished the six branches identified in the cluster analysis (Fig. 5). One gradient, which generally followed CA axis 2, was from primarily pelagic to benthic prey. A second gradient from the bottom right to the middle left of the CA ordination was from small pelagic prey to prey inhabiting seagrass to large prey from non-seagrass habitats. A third gradient from the top right of the ordination to the middle left split the predators that consume cnidarians from those that eat invertebrates of other groups. Thus, six guilds were defined: a planktivore guild, a benthic and epibenthic seagrass invertebrate consumer guild, a carnivore guild, a transitional guild, a benthic invertebrate consumer guild, and a cnidarian and benthic invertebrate consumer guild.

The planktivore guild (PLA; Fig. 5B,C) included small *L. rhomboides* and small *S. ocellatus* and primarily consumed invertebrate eggs and calanoid copepods (95% composition, Fig. 6). Only five other prey taxa were consumed by the fish of this guild, and all were small crustaceans. The planktivore guild formed at 40% similarity in the cluster diagram (Fig. 5A).

The benthic and epibenthic seagrass invertebrate consumer guild (BSI; Fig. 5B) included fish with small mouths (e.g., *L. rhomboides, Sphoeroides springleri, S. testudineus, Harengula jaguana*, and *Anchoa hepsetus*) that were collected in seagrass habitats. These fish formed a guild at 20% similarity in the cluster diagram (Fig. 5A).

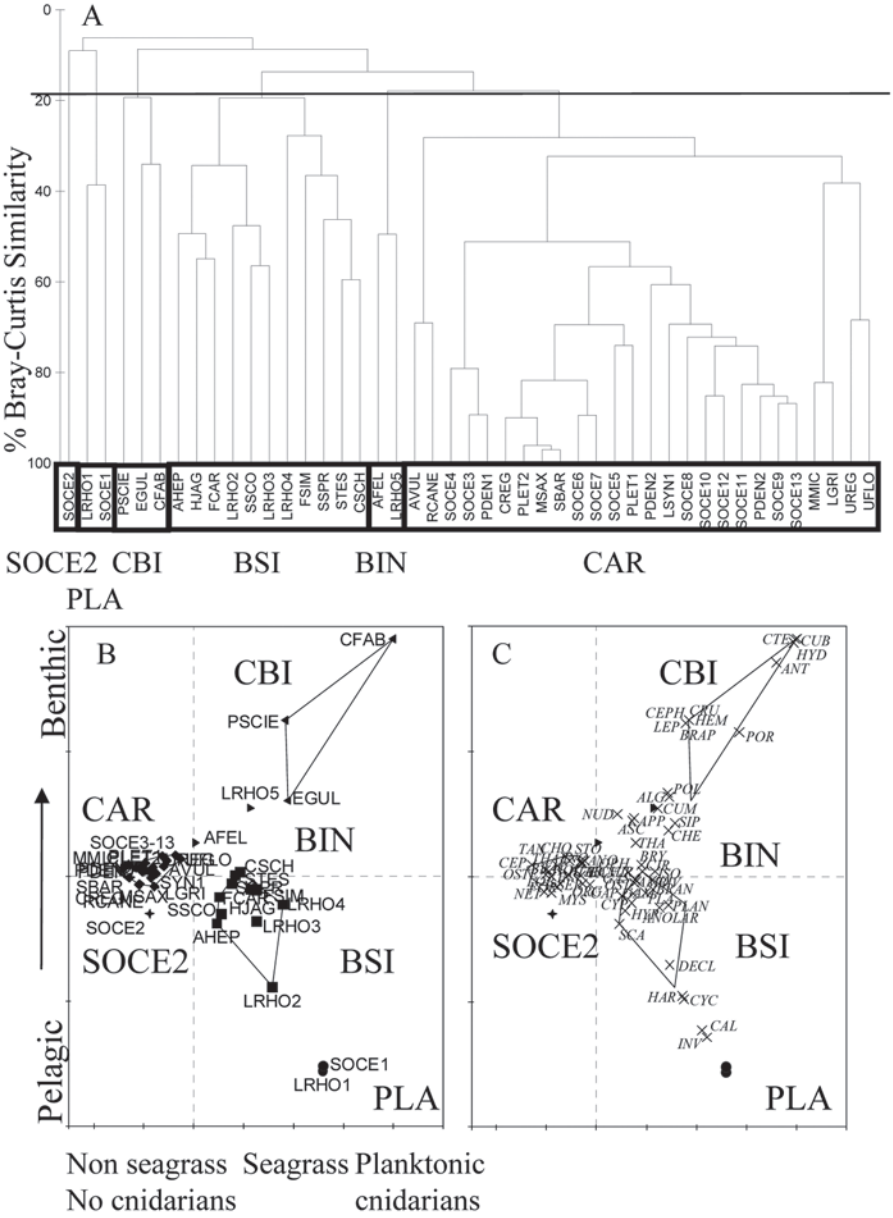

Figure 5. The trophic guilds of the estuarine habitat defined by (A) cluster diagram of predators, (B) correspondence analysis (CA) ordination of predators, and (C) CA ordination of prey with the predator polygons. The dashed lines intersect at the origin of each ordination. Definition of predator and prey codes can be found in Table 1. Boxes surround members of each guild in the cluster diagram defined at 18.19 ($\alpha = 0.05$) similarity. The predator guilds are labeled in the ordinations: CBI is the cnidarian and benthic invertebrate consumer guild; BIN is the benthic invertebrate consumer guild; CAR is the benthic/demersal, pelagic, and structure-associated carnivore guilds; SOCE2 is the transitional *Sciaenops ocellatus* guild; BSI is the benthic and epibenthic seagrass invertebrate consumer guild, and PLA is the planktivore guild.

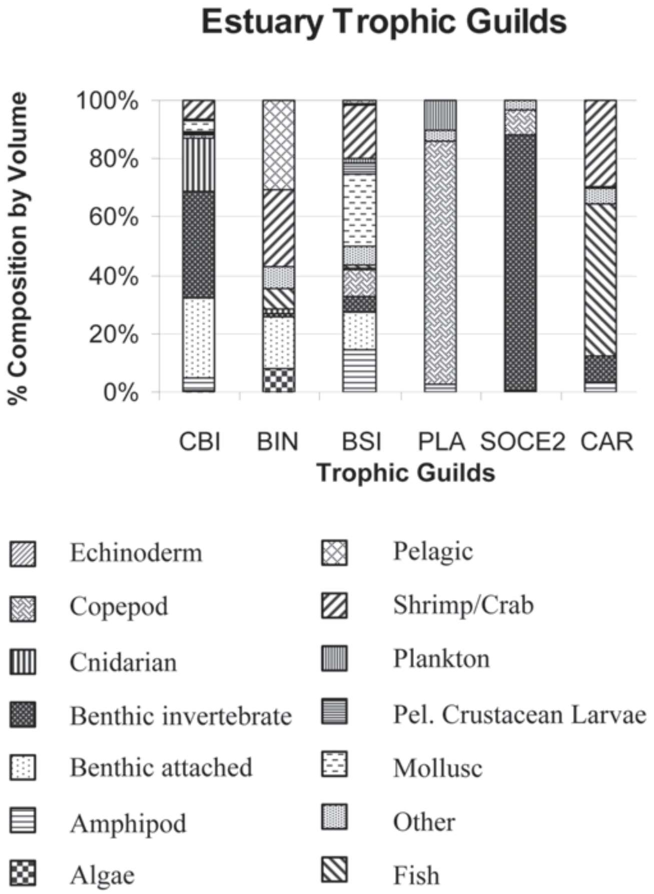

Figure 6. Percent composition of the six estuarine trophic guilds. CBI is the estuarine cnidarian and benthic invertebrate consumers; BIN is the benthic invertebrate consumers; BSI is the benthic and epibenthic seagrass invertebrate consumers; PLA is the planktivores; SOCE2 is the transitional *Sciaenops ocellatus* guild, and CAR is the benthic/demersal, pelagic, and structure-associated carnivore guilds.

Their prey consisted of mollusks, small crustaceans (e.g., isopods and larvae), and echinoderms (Figs. 5C, 6).

A carnivore guild (CAR) contained a large number of predators that consumed mostly fish and crustaceans (75% composition by volume; Figs. 5C, 6). The predators included drum (Sciaenidae), snapper (Lutjanidae), flounders (Paralichthyidae), cobia (*R. canadum*), hakes (*Urophycis floridanus* and *Urophycis regia*), and great barracuda (*Sphyraena barracuda*) (Table 1). These fish were mostly collected from non-seagrass habitats and formed a guild at 35% similarity in the cluster analysis (Fig. 5A). Each species consumed a variety of prey taxa (2–23 taxa), but diets were dominated by crustaceans (brachyuran crabs, caridean shrimps, mysids, and anomuran crabs) and fish (osteichthys). Again, because of difficulty identifying soft-bodied prey from gut samples, fish were lumped together in a collective fish category. Therefore, the carnivore group was subdivided by location of adult habitat into: benthic/demersal carnivores (*Albula vulpes, U. floridanus, U. regia, Morone saxatilis, Cynoscion regalis, S. ocellatus, Paralichthys dentatus,* and *Paralichthys lethostigma*), pelagic carnivores

(*S. barracuda*), and structure-associated carnivores (*M. microlepis, R. canadum, Lutjanus griseus,* and *Lutjanus synagris*).

Sciaenops ocellatus (10–19 mm SL; SOCE2) appeared unrelated to the carnivores in the cluster diagram, but occurred in close proximity to this guild in the CA ordinations (Fig. 5). Taxa consumed by this size class of *S. ocellatus* included small frequently benthic oriented crustaceans (87% mysids) and lacked fish and planktonic prey (Figs. 5C, 6). This size class also corresponds to the stage at which *S. ocellatus* settles to the bottom. Thus, 10–19 mm *S. ocellatus* was an intermediate size class between pelagic larvae and demersal juveniles and between the small planktivorous stage (< 10 mm) and the larger carnivorous stages (> 19 mm).

A guild of two species that mostly ate benthic invertebrates (BIN) included *Arius felis* and *L. rhomboides* (123–159 mm SL, LRHO5) and grouped together at 50% similarity in the cluster diagram (Fig. 5; Table 1). These benthic invertebrate consumers predominantly ate anomurans, brachyurans, algae, appendicularians, ascidacians, and thaliaceans (Fig. 5C).

Another guild that consumed benthic invertebrates was distinguished by the inclusion of cnidarians in their diet (CBI). This guild was composed of *Chaetodipterus faber, Eucinostomus gula,* and *Prionotus scitulus* and formed a guild at 20% similarity in the cluster diagram. In addition to the cnidarians, the predators of this guild ate mostly benthic sessile prey. Unlike the shelf browser guild, which ate hydrozoan and anthozoan cnidarians, this estuarine guild incorporated cubozoans (pelagic box jellyfish) into their diet. The cnidarian and benthic invertebrate consumer guild consumed a fairly high number of prey taxa (26–32); however, hydrozoans, polychaetes, and cephalochordates made up 50%–60% of the diet volume (Figs. 5C, 6).

Between Shelf and Estuary Trophic Structure Comparisons.—Data from both habitats were combined and analyzed with clustering and CA to put the trophic guilds described for each habitat into a broader context and to describe similarities between habitats. Six guilds formed at a significant similarity level ($\alpha = 0.05$; similarity = 16.51; Fig. 7). The pattern depicted by these branches was more complicated than the patterns described for the individual habitats. As in the estuarine habitat analyses, the diet of *S. ocellatus* (10–19 mm; SOCE2), the transitional stage between planktivorous larvae and carnivorous juveniles and adults, was separated from all other trophic guilds. The carnivore guilds (shelf and estuarine; CAR) and the shelf piscivore guilds (PISC) clustered together at about 25% similarity, likely due to the high percent volume of fish in all these diets. The remaining four guilds were not as easily explained. The browsers (BROW) and benthic invertebrate consumers (BIN) clustered together. The seagrass invertebrate consumer guild (BSI) and the cnidarian and benthic invertebrate consumers (CBI) each were split between two branches; half intermingled with carnivores and the planktivores (PLA), and half stood alone.

The CA ordinations show a similar, though slightly simpler, pattern (Fig. 8). Two gradients align with the two dimensions examined in the ordination (Table 3). The first dimension follows a fish to non-fish gradient. Predators along the left side consumed mostly fish, predators along the right side consumed no fish, and predators in the middle consumed some fish (Fig. 3B). Along the second dimension is a gradient from benthic to pelagic prey. In this scheme, the three trophic guilds that incorporated fish were in the left center of the ordination. The shelf browsers were in the bottom right corner. Above them, in the middle right of the ordination, were the benthic and epibenthic seagrass invertebrate consumer guild, the estuarine benthic inverte-

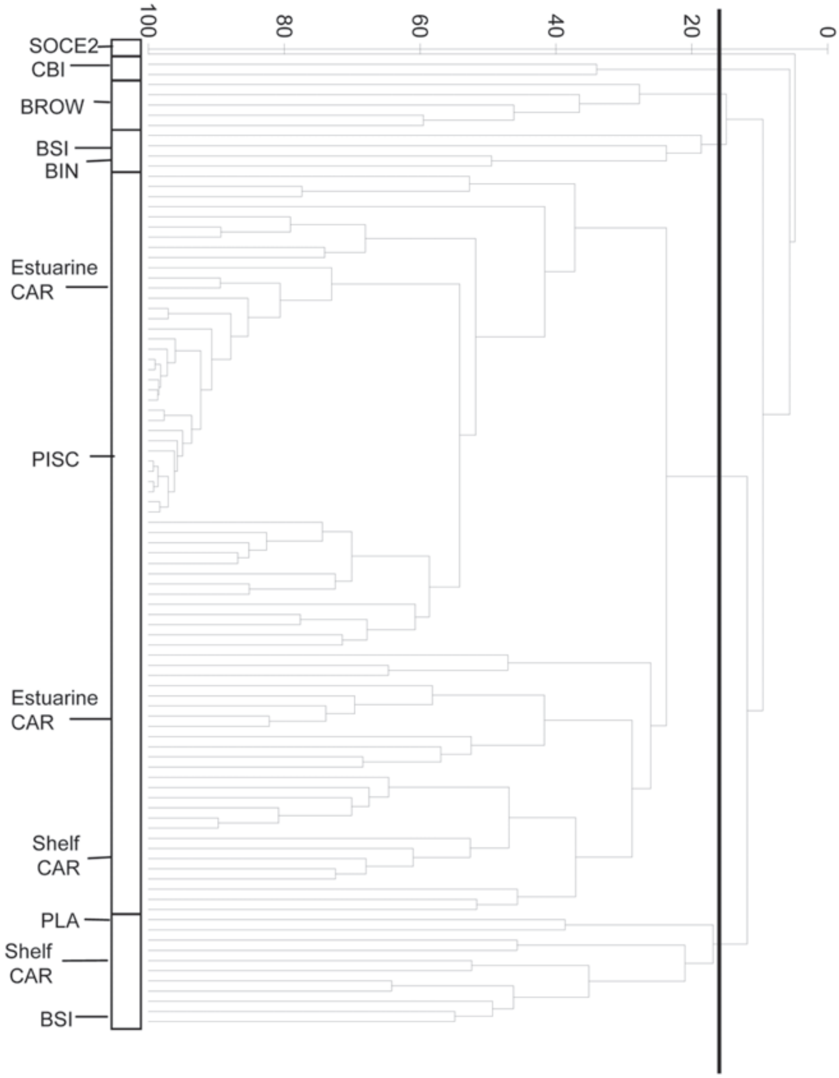

Figure 7. The trophic guilds of the estuarine and shelf habitats combined defined by cluster diagram of predators. The trophic guilds defined for each habitat separately are labeled and boxes are drawn around the predator guilds defined at 16.51 (α = 0.05) similarity in the cluster diagram.

brate consumer guild, and the cnidarian and benthic invertebrate consumer guild. In the upper right corner were the planktivores. Once again, the transitional *S. ocellatus* guild (SOCE2) was located intermediate between the carnivore and planktivore guilds, implying that it is a transition stage between larval and juvenile/settlement staged red drum. Also, the carnivore, seagrass invertebrate consumer, cnidarian and benthic invertebrate consumer, and benthic invertebrate consumer guilds were located closest to the origin of the ordination, implying that these guilds incorporate most of the possible prey into their diets, with slight specializations. The piscivore, planktivore, and browser guilds had less inclusive diets, specializing on specific prey taxa or small groups of prey taxa and occurred on the periphery.

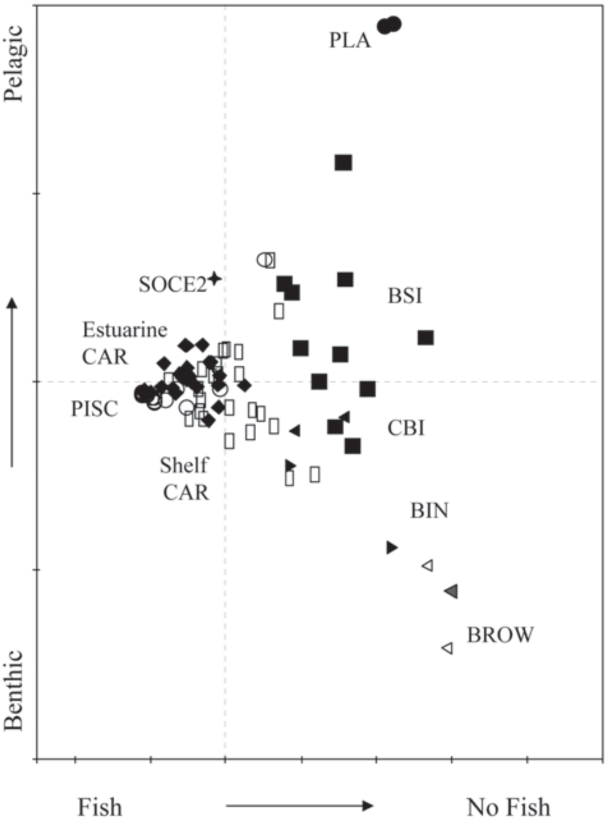

Figure 8. The trophic guilds of the estuarine and shelf habitats combined defined by correspondence analysis (CA) ordination of predators. The dashed lines intersect at the origin of each ordination. Definition of predator and prey codes can be found in Table 1. The trophic guilds defined for each habitat separately are labeled in the ordination. Filled symbols denote estuarine guilds, and open symbols denote shelf guilds.

The estuarine trophic guilds were more generalized than the shelf guilds. Guilds were defined at low percent similarity in the cluster analysis implying that the diets among predators in a guild were not that similar. In the CA, most of the data were scattered around the origin of the ordination implying that most fish ate a wide range of prey, with only a few fringe guilds specializing on specific prey types. Therefore, diet differences among trophic guilds may be subtle.

Trophic data for five species of fish predators were analyzed for both habitats: *C. faber, L. synagris, P. scitulus, R. canadum*, and *S. ocellatus*. Of these, three fell into the same guild in both habitats (Table 1). *Chaetodipterus faber* and *P. scitulus* were both cnidarian and benthic invertebrate eaters in the estuarine habitats, but on the shelf, *C. faber* was a browser, while *P. scitulus* was a benthic/demersal carnivore.

DISCUSSION

For management and modeling purposes, it is convenient to group fish together to lessen the potentially overwhelming complexity of an ecosystem, especially systems as diverse as the southeast United States continental shelf and estuaries. However, consideration must be given to the actual complexity in diet, while striving to provide a more realistic base for ecosystem approaches to fisheries management. For example, trophic guilds used in many biomass-based models may not accurately reflect the trophic structure of an ecosystem. Most models (e.g., Ecopath with Ecosim) depict the ecosystem as a set of guilds: each group of predators is treated as though their diet is discrete from those of other groups. Our results and the results of species-specific diet studies show that diet is more complex. Each species considered in this study specialized on a few taxa, but consumed an average of 15 prey taxa. Even the highly similar piscivores ate a wide variety of non-fish prey. It is important to recognize that some species consume an intermediate volume (or weight) of fishes, indicating a gradual transition rather than a definitive break between piscivore and non-piscivore guilds. The remaining predatory guilds defined in this study were opportunistic whose members ate mostly benthic invertebrates, but also ventured into the pelagic environment consuming jellyfish or plankton. Thus, two main gradients in consumption, rather than guilds, define trophic structure: degree of piscivory and location of prey in the water column (pelagic or benthic) (this study; northeast United States: Garrison, 2000; Garrison and Link, 2000a; southeastern Australia: Bulman et al., 2001). A less rigid scheme involving gradients rather than guilds may more accurately describe the intricacies of fish diet, while still reducing the complexity of the system.

Many problems arise when attempting to develop a large-scale trophic model based on gut content data. The state of digestion affects the ability to identify prey taxa, with higher taxonomic categories used for more digested prey. A result of this general taxonomic grouping in this study was that the same higher order prey taxa (or functional groups) were used for both estuarine and shelf habitats, yet the actual prey species within these categories likely differed between estuarine and shelf habitats (see Engle and Summers, 1999). Higher resolution prey data would enable more accurate divisions of trophic structure, but are not easily obtained from digested material. Molecular advances in prey identification may be an answer to this problem in the future. Taylor (2004), for example, used species-specific immunological assays to identify winter flounder eggs and juveniles several hours after being ingested by shrimp (10–16 hrs for eggs, 8–9 for juveniles). Additionally, prey types digest at different rates; therefore, stomach content studies may overestimate the importance of hard-bodied prey (e.g., crabs) due to longer residence time in the gut (Jackson et al., 1987). A better source of diet data or a way around the issues with stomach content data is needed.

The data obtained from diet studies are not entirely sufficient to develop a large-scale model of the southeast U.S.: the diets of too few species of fish have been studied, the measures of consumption are too diverse, and the data are too general. To optimize the number of predators analyzed in this study, diet information was taken from studies of the southeast U.S., the Gulf of Mexico, and one study from the northeast U.S. Several studies have shown that there are differences in diet between fish collected from the southeast U.S. and the Gulf of Mexico (Overstreet and Heard, 1978; Saloman and Naughton, 1983a,b; Naughton and Saloman, 1984; Finucane et al., 1990). Generally, these studies show that the taxa consumed are similar between regions, but dominance shifts by location due to differences in availability. The broad taxonomic level used here for prey reduces the effects of these regional differences. A trade-off was required between the number of species included and the number of species for which specific data were available for the southeast U.S. shelf, and we chose the former. Roughly 1200 species of fish occur in the region, but only 60 species were included in this study. These 60 species were not chosen randomly; rather they were chosen because diet studies had been conducted in such a way that allowed the combined analysis presented here. Thus, our view of the large-scale trophic structure is driven by the objectives of individual diet studies and not by a holistic need for understanding the trophodynamics in the system.

The amount of data combined for use here was also limited by the wide variety of gut contents measures used in the literature and the varying level of identification of gut content studies. Diet studies should use one or several common units of measure (e.g., volume) for future consolidation of data, in conjunction with the measures needed for the specific study. In addition, more accurate identification of prey will allow a finer resolution of guild structure, which is currently not possible.

Examination of multiple species using the same methods (e.g., Luczkovich et al., 2002) or individual studies that use the same detailed identification and quantification of prey (Sedberry 1985, 1987, 1990) would improve the number of species for which data could be combined for large scale analyses. A food studies program could be initiated in the southeast similar to that conducted in the northeast (Garrison and Link, 2000a) based on fishery independent (SEAMAP trap and trawl survey; SEAMAP-SA, 2000) and fishery-dependent catches (headboat survey; Parker and Dixon, 1998). Only through coordinated efforts will our view of the trophodynamics on the southeast U.S. shelf be advanced beyond the compilation presented here.

This study took a very broad view of the trophodynamics of the southeast United States, using only fish predators, broad prey taxa categories, and broad habitat definitions (estuarine or shelf). Though not ideal, diet data retained at broad levels made dietary differences among geographic regions a minor concern. Consequently, the results of this study have a broader application. For example, Luczkovich et al. (2002) described four fish trophic guilds in a seagrass bed in west Florida using clustering and CA: benthic-meiofauna feeders (group 1), benthic-macroinvertebrate consumers (groups 2 and 3), carnivorous fishes (group 6), and fish consumers (groups 4 and 5). Each of these guilds roughly corresponds to each of the six trophic guilds we defined for fishes of southeast U.S. estuaries (Fig. 5, Table 1). The prey categories between the two studies were slightly different, but the functional groups were similar. Thus, our results and those of Luczkovich et al. (2002) indicate that guild structure may be similar in other estuaries in warm-temperate ecosystems and more generally, that the guild structure presented here may be applicable at both large and small scales within the southeast United States, in the Gulf of Mexico, and on the southwestern Florida shelf.

Many studies attempting to create large-scale (region-wide) trophic models have run into problems based on a lack of comprehensive data. Many fish species have not been studied at all. Some have been studied, but not in enough detail to incorporate into these large-scale efforts. As a result, many trophic models are based on little actual data and fill in blanks with educated guesses. Though better than nothing, these subjective classifications can lead to biased conclusions influencing management. With this study, we have attempted to create a framework based on an objective grouping of species data collected from the literature. Rather than trophic guilds, we recommend incorporating gradients, namely degree of piscivory and location of prey in the water column. Our hope is that this framework will serve to improve models of the trophodynamics of the system. Because of the broad nature of our groups, this framework could also be used in the Gulf of Mexico and the southwestern Florida shelf, and is adaptable to smaller systems (e.g., Luczkovich et al., 2002). If nothing else, we hope that this compilation, which was based on combining data from disparate studies, will result in an integrated program using the same measures and taxonomic resolution across a broad range of species.

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