Estuaries Vol. 25, No. 6A, p. 1143–1163 December 2002

Determining the Trophic Guilds of Fishes and Macroinvertebrates in a Seagrass Food Web

JOSEPH J. LUCZKOVICH[1,2,*], GARCY P. WARD[3], JEFFREY C. JOHNSON[1,4], ROBERT R. CHRISTIAN[2], DANIEL BAIRD[5], HILARY NECKLES[6], and WILLIAM M. RIZZO[7]

[1] *Institute for Coastal and Marine Resources, East Carolina University, Greenville, North Carolina 27858*
[2] *Department of Biology, East Carolina University, Greenville, North Carolina 27858*
[3] *North Carolina Department of Environment and Natural Resources, Division of Water Quality, 943 Washington Square Mall, Washington, North Carolina 27889*
[4] *Department of Sociology, East Carolina University, Greenville, North Carolina 27858*
[5] *Department of Zoology, University of Port Elizabeth, P.O. Box 1600, Port Elizabeth, South Africa*
[6] *United States Geological Survey, Patuxent Wildlife Research Center, 26 Ganneston Drive, Augusta, Maine 04330*
[7] *United States Geological Survey, Northern Prairie Wildlife Research Center, Missouri Field Station, University of Missouri—Columbia, 302 Gentry Hall, Columbia, Missouri 65211*

ABSTRACT: We established trophic guilds of macroinvertebrate and fish taxa using correspondence analysis and a hierarchical clustering strategy for a seagrass food web in winter in the northeastern Gulf of Mexico. To create the diet matrix, we characterized the trophic linkages of macroinvertebrate and fish taxa present in *Halodule wrightii* seagrass habitat areas within the St. Marks National Wildlife Refuge (Florida) using binary data, combining dietary links obtained from relevant literature for macroinvertebrates with stomach analysis of common fishes collected during January and February of 1994. Heirarchical average-linkage cluster analysis of the 73 taxa of fishes and macroinvertebrates in the diet matrix yielded 14 clusters with diet similarity $\geq$ 0.60. We then used correspondence analysis with three factors to jointly plot the coordinates of the consumers (identified by cluster membership) and of the 33 food sources. Correspondence analysis served as a visualization tool for assigning each taxon to one of eight trophic guilds: herbivores, detritivores, suspension feeders, omnivores, molluscivores, meiobenthos consumers, macrobenthos consumers, and piscivores. These trophic groups, cross-classified with major taxonomic groups, were further used to develop consumer compartments in a network analysis model of carbon flow in this seagrass ecosystem. The method presented here should greatly improve the development of future network models of food webs by providing an objective procedure for aggregating trophic groups.

Introduction

Trophic relationships comprise the framework upon which estuarine communities are organized. Increasingly, quantitative food-web models and carbon flow network analyses are being employed to study and describe the trophic structure in estuaries (Baird and Ulanowicz 1989; Baird et al. 1991, 1998; Monaco and Ulanowicz 1997; Christian and Luczkovich 1999). Such models are useful because the vast complexity of estuarine food web data from published studies can be summarized in a simplified model consisting of a network of compartments connected by trophic links or carbon flows.

It is often unclear what entities are to be included as the nodes or compartments in the network model. One approach would be to use species as nodes (or even ontogenetic stage within a species; Polis and Winemiller 1996). The species-level approach is often impractical, because it is difficult to identify and link quantitatively all species in the food web (especially the microbes) at the level of species (Cohen et al. 1993). Most published dietary studies on estuarine species do not identify prey to the level of species (Hicks and Coull 1983; Huh and Kitting 1985; Gaston et al. 1988, 1992; Livingston 1988; Motta et al. 1995). In network analysis packages such as ECOPATH (Christiansen and Pauly 1992, 1993; Heymans and Baird 2000) or NETWRK (Ulanowicz 1987), one must specify detailed input parameters for each designated compartment, including measurements of production, respiration, consumption, and biomass (Kay et al. 1989). These parameters may be unknown for all species present in the estuary. The typical solution for handling such missing data is to pool

* Corresponding author; e-mail: luczkovichj@mail.ecu.edu.

species into trophic groups and assume that all species in a group have similar diets and metabolic activity. Aggregation of species into trophically similar groups is a desirable goal for food web modelers (Yodzis 1996). Various notions have been suggested for aggregating taxa into trophic groups, including guilds, which include taxa that exploit similar prey resources (Root 1973) and trophospecies, which include taxa that have similar diets and similar predators (Briand and Cohen 1984; Yodzis 1989; Turner and Roff 1993; Yodzis and Winemiller 1999).

It is not clear how one should aggregate consumer taxa into trophic groups. While aggregation of taxa based on the diet relations is routinely done in network analysis, the past methods have been ad hoc or based on intuition alone. Current practice relies mostly on ad hoc methods of aggregation based on the modeler's perception of which groups of species have similar diets. Aggregation based solely on diet similarity, with groupings containing taxa that consume similar foods in a similar manner, is the basis for the trophic guild concept (Root 1973). In a guild analysis, diet similarity among taxa to be grouped can be measured through the use of niche overlap indices, clustering strategies, or ordination procedures (Sheridan 1979; Livingtson 1980, 1982; Grossman 1986; Motta et al. 1995). Similarity in both diet and predator relations could be jointly used to aggregate taxa, which is the trophospecies or trophic group concept proposed by Yodzis and Winemiller (1999). The trophic groups should reflect both the prey and predator relations (Turner and Roff 1993; Persson et al. 1996; Yodzis and Winemiller 1999; Johnson et al. 2001).

Problems arise for network modelers when attempting to use published dietary studies alone to specify both the predator and prey relations, because, as noted above, the prey and predator relations are not often specified at the level of species. An initial aggregation of taxa often has occurred during the publication of original diet analysis, and, even if a species' diet is known, its predators may not be well described. After the dietary data are compiled from the literature, they can be represented as a diet matrix with the various consumer taxa as rows and the aggregated foods consumed as columns, with fewer columns than rows. The resulting diet matrix will be rectangular. But network models require a square matrix for dietary data (i.e., all compartments must appear in both rows and columns and the cells represent the proportion of flow of material from each compartment to the others). A solution for this problem is to employ a dual-mode classification approach, which can be used on the rectangular matrix data to combine consumer taxa into a smaller number of groups with similar diets (trophospecies).

There are many multivariate approaches for analyzing such two-mode matrices, including such familiar ordination methods (factor analysis, PCA) or hierarchical clustering algorithms (Dillon and Goldstein 1984). These approaches show only the similarity among the rows or consumers based on similarity in diet, but not among the columns based on similarity among predators. An approach in which both relations can be discerned simultaneously is called dual-scaling analysis (Greenacre 1984; Gittins 1985). One such dual-scaling approach is correspondence analysis (or reciprocal averaging), which allows a simultaneous display of the similarity of consumer taxa in the same multivariate space as the aggregated prey categories (Gittins 1985). By using correspondence analysis, one can uncover similarity in both the diets of the consumers in the food web and in predator relations of the food or prey resources. Proximity of two consumers or food sources in a correspondence analysis factor score plot indicates a similar diet (for consumer taxa) or a similar suite of predators (for the food resources).

We demonstrate the use of cluster analysis and correspondence analysis to aggregate estuarine macroinvertebrates and fish into trophic groups based on measures of diet and predator similarity. This method is a type of guild analysis, in which predator relationships may also be discerned. We developed our trophic classifications using dietary data obtained during the construction of a carbon-flow network model of the St. Marks, Florida, *Halodule wrightii* seagrass ecosystem during the winter of 1994 (Baird et al. 1998; Christian and Luczkovich 1999). Cluster analysis was first used to group consumer taxa in to a small number of clusters, which could be coded for further analysis. A correspondence analysis was used to calculate factor scores of each of the food sources and the original list of consumers. A factor scores plot was visually examined to discern groups of consumer taxa (coded by cluster membership) and match them with their food sources. The resulting trophic groups were used in establishing the compartments in network models. We apply the method here, both to the fishes present in our study area, for which we collected some new dietary data, as well as the entire suite of macroinvertebrate and fish consumer taxa in the St. Marks Wildlife Refuge seagrass ecosystem.

Materials and Methods

Our study goal was to characterize the winter *H. wrightii* seagrass food web of the St. Marks National

Wildlife Refuge in St. Marks, Florida, ranging from the intertidal zone to 150 m offshore. Four study sites (each 200 m along the coast × 150 m offshore) were established in Apalachee Bay and Goose Creek Bay near the mouth of the St. Marks River. Two sites were chosen in Goose Creek Bay: Live Oak Island (30°4.5′N, 84°16.4′W) and Wakulla Beach (30°6.2′N, 84°15.6′W). These were sampled in January and February 1994. To assess sample adequacy and variability among sites, an additional site was established in Apalachee Bay each month: one site at Sprague Island (30°5.0′N, 84°12.2′W, in January) and another at the St. Marks Lighthouse (30°4.2′N, 84°11.0′W, in February). Water depth varied within this zone according to tides and winds, never exceeded 1.0 m during sampling, and averaged 0.75 m deep.

At each of these sites, we obtained replicate samples of the various zooplankton, benthic macroinvertebrate, and fish taxa along three 100-m transects perpendicular to the shore spaced 100 m apart. The minimal level of replication was three samples for each site (see individual sections below for details on replication).

Zooplankton

Zooplankton samples were obtained with a 29-cm diameter, 90-μm mesh plankton net towed over a 45.7-m distance (three replicate tows per site) along each transect. The net was pulled through the water with the aid of a small boat powered by an electric trolling motor, and the amount of water filtered in the samples was calculated to be 2.9 m^3. Zooplankton organisms (calanoid and harpacticoid copepods, nematodes, larval forms, and pycnogonids) were concentrated in a 1000-ml collection jar. The zooplankton samples were preserved with 5% formalin and rose bengal stain. Three replicate 2-ml subsamples were obtained with a calibrated pipette from each 1000-ml sample (after resuspension of the sample by repeated inversion and mixing of the sample in the jar) and the zooplankton taxa enumerated under low power magnification. The taxa were identified using Smith (1977). Zooplankton abundance data samples were used to get a species list of dominant taxa to be included as presence-absence data in the diet matrix as consumers.

Macrobenthos

The macrobenthos (which included the echinoderms, gastropods, bivalves, amphipods, decapods, isopods, cumacea, and polychaetes > 500 μm) within the study zone at each site were sampled using a 75-mm diameter PVC coring tube (Lewis and Stoner 1981). Ten macrobenthic cores samples (to 10 cm depth) were taken randomly along each of the three transects at a site. The transects were located along a very slight depth gradient (< 5 cm difference between ends of the transect), but all were contained within *Halodule* habitats at each site. All cores from a transect line were pooled, regardless of distance from shore, so that there were three groups of 10 pooled core samples from each site (thus 3 replicates per site). All core samples were sieved in the field and preserved in 10% formalin and stained with rose bengal for later sorting, identification, enumeration, and weighing in the laboratory. The amphipods, gastropods, bivalves, isopods, and decapods were all identified to the species level using identification guides in Schultz (1969), Gosner (1971), Bousfield (1973), Fox and Bynum (1975), Morris (1975), Myers (1981), Williams (1984), and Fox and Rupert (1985). The polychaetes were identified to the family level using Fauchauld (1977) and Uebelacker and Johnson (1984). Taxonomic names follow those given in Camp et al. (1998). Smaller benthic consumers (meiofauna, microfauna, and benthic bacteria) were sampled separately (see Baird et al. 1998; Christian and Luczkovich 1999) and were not included as consumer taxa in this analysis.

Fishes and Nekton

The fishes and large mobile invertebrate nekton were sampled using a barrier seine, which was developed for this study, and gill nets. Barrier nets (3.2-mm mesh seines, 1.22-m high by 11-m long on each side tied to PVC poles driven into the sediment) were placed approximately 10 m beyond the end of each transect line, forming two sides of a 60-m^2 triangular area. There were three barrier nets set up at each site. The barrier nets were deployed upon arriving at a site in the morning, and sampled about 2 h later, to allow nekton to recover. The barrier nets were sampled using a 15.2-m long by 1.8-m high collection seine (3.2-mm mesh) with a 3-m by 2-m collection bag sewn into the middle, which was stretched along the hypotenuse of the triangular sampling area while being held tightly to one of the corner poles. When the collection seine had been completely stretched along the hypotenuse, the net was pulled inside the barrier nets along the two remaining sides of the triangle, until reaching around to its other end, thus completely encircling the area to be sampled. This procedure swept the area clear of most fishes and mobile invertebrates. At this point the collection bag was pursed and lifted into a large plastic basin for examination and preservation of the catch. Mark and recapture studies indicated that an average of 45% of fin-clipped pinfish *Lagodon rhomboides* (~45 mm SL, n = 283 tagged fish) introduced within the enclosed 60-m^2 area were recovered on three rep-

TABLE 1. A list of the compartments included in the network models for January and February 1994. Consumer taxa are listed by identification code, common name or taxonomic group, and taxon name. The diet matrix linkages for consumers were obtained from the listed references.

	ID Code	Common Name or Taxonomic Group	Taxon Name	Diet References
1	ACATON	Calanoid copepod	*Acartia tonsa*	Turner 1984
2		Shrimp	*Alpheus normanni*	Leber 1983
3		Amphipods	*Ampelisca* sp.	Mills 1967
4		Amphipods	*Ampithoe longimana*	Duffy and Hay 1991
5	ANCMIT	Bay anchovy	*Anchoa mitchelli*	Sheridan 1978
6		Bay scallop	*Argopecten irradians*	Dame 1996
7		Polychaete	*Aricidea* sp.	Gaston 1987
8	ARIFEL	Hardhead catfish	*Arius felis*	Motta et al. 1995
9		Mussel	*Brachidontes exustus*	Dame 1996
10		Gastropod	*Busycoptypus spiratus*	Paine 1963
11	CALSAP	Blue crab	*Callinectes sapidus*	Leber 1983
12		Polychaete	Capitellidae	Fauchauld and Jumars 1979, Lopez and Levinton 1987, Gaston 1987, Gaston and Nasci 1988, Gaston et al. 1988
13		Amphipods	*Caprella penantis*	Venier 1997
14		Amphipods	*Cerapus* sp.	Gaston and Nasci 1988, Gaston et al. 1988
15		Gastropod	*Cerithium lutosum*	Kohn 1983
16	CHASAB	Florida blenny	*Chasmodes saburrae*	Reid 1954
17		Bivalve	*Chione cancellata*	Peterson 1982, Dame 1996
18		Polychaete	Cirratulidae	Fauchauld and Jumars 1979
19		Amphipods	*Corophium* sp.	Lopez and Levinton 1987, Gaston and Nasci 1988, Gaston et al. 1988
20		Gastropod	*Crepidula fornicata*	Kohn 1983, Hughes 1986
21		Amphipod	*Cymadusa compta*	Zimmerman 1978, Zimmerman et al. 1979
22	CYPVAR	Sheepshead minnow	*Cyprinodon variegatus*	Motta et al. 1995
23	DASSAB	Atlantic stingray	*Dasyatis sabina*	Snelson and Williams 1981, Gilliam and Sullivan 1993
24	EDOTRI	Isopod	*Edotia triloba*	Gaston and Nasci 1988, Gaston et al. 1988
25	FORAMS	Foraminifera		Turner and Roff 1993
26	FUNSIM	Longnose killifish	*Fundulus similis*	This study
27		Amphipods	*Gammarus mucronatus*	Zimmerman 1978, Zimmerman et al. 1979
28		Polychaete	Glyceridae	Fauchauld and Jumars 1979, Gaston 1987
29		Gastropod	*Haminoea* sp.	Chester 1993
30	HARPAC	Harpacticoid copepods		Hicks and Coull 1983, Seifreid and Durbaum 2000
31	HESION	Polychaete	Hesionidae	Fauchauld and Jumars 1979, Gaston 1987
32	HIPZOS	Dwarf seahorse	*Hippocampus zosterae*	Lourie et al. 1999
33		Shrimp	*Hippolyte zostericola*	Leber 1983
34	LAGRHO	Pinfish	*Lagodon rhomboides*	This study
35	LEIXAN	Spot	*Leiostomus xanthurus*	This study
36		Spider crab	*Libinia dubia*	Leber 1983
37	MALDAN	Polychaete	Maldanidae	Fauchauld and Jumars 1979
38		Amphipod	*Melita* sp.	Zimmerman 1978, Zimmerman et al. 1979
39	MENPEN	Tidewater silverside	*Menidia peninsulae*	This study
40	MICGUL	Clown goby	*Microgobius gulosus*	This study
41		Mysid	*Mysidopsis* sp.	Gaston and Nasci 1988, Gaston et al. 1988
42		Gastropod	*Natica* sp.	Hughes 1986
43		Copepod nauplii		Turner and Roff 1993
44		Mud crab	*Neopanope* sp.	Leber 1983
45		Polychaete	Nereididae	Fauchauld and Jumars 1979, Lopez and Levinton 1987, Gaston 1987, Gaston and Nasci 1988, Gaston et al. 1988
46		Brittle star	*Ophiderma brevispinum*	Thayer et al. 1978
47		Polychaete	Onuphidae	Fauchauld and Jumars 1979, Gaston 1987
48		Polychaete	Orbiniidae	Fauchauld and Jumars 1979
49		Ostracods	Ostracoda	Venier 1997
50	PAGMAC	Hermit crab	*Pagurus mclaughlinae*	Hazlett 1981
51	PAGSP	Hermit crab	*Pagurus* sp.	Hazlett 1981
52		Shrimp	*Palaemon floridanus*	Leber 1983
53	PARALBA	Gulf flounder (>80 mm)	*Paralichthys albigutta*	This study
54	PARALBJ	Gulf flounder (≤80 mm)	*Paralichthys albigutta*	This study
55		Polychaete	Paraonidae	Fauchauld and Jumars 1979, Gaston et al. 1992
56		Polychaete	Pectinariidae	Fauchauld and Jumars 1979

TABLE 1. Continued.

ID Code	Common Name or Taxonomic Group	Taxon Name	Diet References
57 FARDUO	Shrimp	*Farfantepenaeus duoarum*	Leber 1983
58 POLINICES	Gastropod	*Polinices* sp.	Paine 1963, Kohn 1983, Hughes 1986
59	Polychaete larvae		Turner and Roff 1993
60 PRIONOT	Searobins	*Prionotus* sp.	Richards et al. 1979
61	Shrimp	*Processa bermudensis*	Leber 1983
62 SABELL	Polychaetes	Sabellidae	Fauchauld and Jumars 1979
63 SCIACEJ	Red drum (juveniles)	*Sciaenops ocellatus*	Peters and McMichael 1987
64 SCIOCEA	Red drum (adults)	*Sciaenops ocellatus*	Peters and McMichael 1987
65	Polychaetes	Serpulidae	Fauchauld and Jumars 1979
66	Polychaetes	Spionidae	Fauchauld and Jumars 1979, Gaston and Nasci 1988, Gaston et al. 1988
67 STRMAR	Atlantic needlefish	*Strongylura marina*	This study
68	Polychaete	Syllidae	Fauchauld and Jumars 1979, Gaston 1987
69 SYMPLA	Blackcheek tonguefish	*Symphurus plagisua*	Topp and Hoff 1972
70 SYNSCO	Gulf pipefish	*Syngnathus scovelli*	Huh and Kitting 1985, Motta et al. 1995
71	Tanaeid	*Hargeria rapax*	Gaston and Nasci 1988, Gaston et al. 1988
72 UROFLO	Southern hake	*Urophycis floridana*	This study
73	gastropod	*Urosalpinx perrugata*	Kohn 1983, Hughes 1986

Food sources

ALGA	Macro-algae	FISH	Fishes	WCAL	Calanoid copepods
AMPH	Amphipods	FORA	Foraminifera	WCIL	Water-column ciliates
BACT	Bacteria	GAST	Gastropods	WDET	Suspended detritus
BIVA	Bivalves	HARP	Haracticoid copepods	WFOR	Water-column foraminiferans
CARRION	Carrion	ISOP	Isopods		
CILL	Cilliated protozoans	MALG	Microalgae and diatoms	WHAR	Water column harpacticoid copepods
CRAB	Crabs	MYSID	Mysids		
CUMA	Cumaceans	NEMA	Nematodes	WMIC	Water-column microalgae (phytoplankton)
DETR	Detritus	POLY	Polychaetes		
DOC	Dissolved organic carbon	SEAG	Seagrasses	WNEM	Water-column nematodes
ECHI	Echinoderms	SHRIMP	Shrimp	WPOL	Water-column polychaetes
EPIP	Epiphytic algae	WBAC	Water-column bacteria	WPYC	Water-column pycnogonids

licate net sweeps. Fishes and invertebrates were placed in 10% formalin for later sorting, identification, enumeration, weighing, and stomach content analysis. Adjacent to each barrier net, a monofilament gill net (45.7-m long by 1.2-m high, with 3.8-cm and 7.6-cm stretch mesh panels) was placed by tying it to 2-m PVC poles driven into the sediment. Three gill nets were set immediately upon arriving at a site and sampled at or before sunset in February, but were allowed to fish overnight in January because of low daytime tide levels. Fishes were identified using Robbins and Ray (1986).

Diet Analysis

In order to determine the structure of the diet matrix required for the network food web model, diets were summarized based on the existing literature (Table 1) or examined directly for some species of fishes (see Results). A diet matrix was constructed using the feeding relationships, which consisted of binary data (1 = food, 0 = not food) indicating the trophic links between the 73 consumer taxa and 33 possible food sources. The rows of this rectangular matrix were the consumer taxa and the columns were the food sources, and links were based on the published diet studies (Table 1) and our own data for some of the fishes. An additional 23 macroinvertebrate taxa were identified in benthic samples, but no dietary data were available for these taxa in the literature, so they were excluded from this analysis. We assumed that when detritus was indicated as a food source in the literature, benthic or planktonic bacteria were included as an additional food source (Lopez and Levinton 1987).

The trophic link data were obtained from the most common fish species in our collections following a modified sieve-fractionation stomach-content-analysis methodology (Carr and Adams 1972, 1973; Leber 1983; Luczkovich 1987; Luczkovich and Stellwag 1993). In this method, the stomach contents of individual fish (gulf flounder, *Paralichthys albigutta,* and Atlantic needlefish, *Strongylura marina*) or pooled stomach contents of up to 15 individuals (spot, *Leiostomus xanthurus,* pinfish, *L. rhomboides,* tidewater silversides, *Menidia peninsulae,* southern hake, *Urophycis floridana,* longnose killifish, *Fundulus similis,* and clown goby, *Microgobius gulosus*) were passed through a series of nested sieves (from 75–2,000 μm). Fish with empty stomachs were not included in any diet analyses. Pooling was done for the species indicated above when

more than a single fish within a species was obtained from a site. Because individuals of the same species obtained from a site are not likely to be statistically independent, we used pooled stomach content data from within a barrier net collection for trophic link accumulation analyses. Gulf flounder *P. albigutta* was rare in the barrier and gill net collections, so additional stomach contents were obtained from a National Marine Fisheries Service trawl survey conducted from March through August 1995 in northeastern Gulf of Mexico seagrass meadows (Koenig personal communication) and analyzed using our methods. After sieving, each prey item (or parts of prey) retained on each sieve was identified as belonging to one of the 33 possible food sources and enumerated. Prey categories were kept as specific as possible (families of polychaetes or genera of crustaceans), but in most cases were not identified to the species level. The sieve fraction was dried at 60°C for 48 h then weighed. The proportional contribution of each food source was estimated using the numerical counts within a sieve fraction and the proportions were multiplied by the mass of the sieve fraction to obtain a dry mass retained on each sieve for each food source category. Masses for each food source were summed from all sieve fractions to obtain the percentage dry mass for each food source within a fish species. This stomach content analysis method was chosen because it is the similar to the method used by Leber (1983), which provided dietary data on the invertebrates in this region.

Trophic link accumulation curves for fishes collected in barrier nets were constructed by determining the cumulative number of links to food sources for pooled diets from each of the barrier net samples (Grossman 1986; Goldwasser and Roughgarden 1997). These curves represent the number of trophic links that were observed upon repeated sampling within the study areas, and thus the adequacy of diet analyses for each fish species collected. If asymptotes for these curves were reached for a fish species, we judged the diet analysis to be adequate for the sampling area and time period sampled.

Statistical Analysis

A hierarchical clustering procedure with average linkage and the Pearson's distance measure (calculated as distance = 1 − r, where r is the Pearson correlation among consumer taxa's diets; Systat 10.0, SPSS, Inc.) was used to group consumer taxa (rows in the rectangular binary diet matrix) on the basis of their similarity in diets (columns in the matrix). Although proportional dietary information was used in the later network models, for this analysis only binary data were needed. Two separate diet matrices were analyzed: a subset of the diet matrix consisting of the 20 species of fishes and their 22 possible food sources and the entire diet matrix with 73 macro-consumer taxa and their 33 food sources. We used an agglomerative hierarchical clustering strategy, with each taxon considered in its own cluster initially, and taxa were joined using the average linkage method, which averages all distances among taxa within clusters to calculate which cluster or taxon will be linked next. Such a clustering method was determined to be the best widely available clustering method for this type of data set by Yodzis and Winemiller (1999). A correspondence analysis (CA) between the consumer taxa (rows) and food sources (columns) was then used to compute CA factor scores for each diet matrix. CA is an ordination procedure that is one of a subset of methods referred to as dual-scaling of variables (Gittings 1985) that displays the similarity of two-mode data (e.g., in a rectangular matrix of species by environmental variables) in a common factor space. The CA procedure can be used on categorical or continuous data and was implemented using the network statistics software package UCINET 5 (Borgatti et al. 1999). Our procedures here are similar to a procedure called TWINSPAN in the ecological community analysis literature (Gauch and Whittaker 1981), which uses CA in conjunction with divisive clustering strategy. Using CA, one can simultaneously visualize the relationships among row (in this case fish or macro-consumer taxa clusters) and column (in this case food sources in the environment) data in the same low-dimensional vector space (Greenacre 1984). In the subset of the diet matrix consisting of fishes, a two-factor CA was done with factor scores for the fish species and their food sources plotted in a scatterplot; species that did not exceed a threshold of 0.4 Pearson's distance in the hierarchical cluster analysis were considered a separate cluster and identified on the CA factor scores plot. A three-factor CA was done for the complete diet matrix and factor scores from the CA were plotted for each possible food source and consumer taxon (106 points). The CA factor score plots were visually inspected to find clusters of consumer taxa that were close in multivariate space to one of the 33 food sources in each plot. By visualizing the cluster membership and the closest food sources in the plots, we established trophic guild membership for each species.

Results

Diet Analysis of Fishes

The diets of the fishes collected in the barrier and gill nets showed that most fishes consumed

TABLE 2. Fish stomach contents (% dry mass) pooled from barrier seine collections at all sites (1, 2, 3, and 4) in January and February 1994. Additional samples of gulf flounder were analyzed in 1995 from nearby sites to increase the sample size.

Prey Item	Pinfish	Spot	Tidewater Silverside	Gulf Flounder <80 mm SL	Gulf Flounder >80 mm SL	Atlantic Needlefish	Southern Hake	Clown Goby	Hardhead Catfish	Longnose Killifish	Sheepshead Minnow
Amphipods	0.09	0.03	0.34	0.07	0.00	0.00	0.04	0.11	0.00	0.21	0.00
Calanoid copepods	0.03	0.01	0.00	0.01	0.00	0.04	0.00	0.00	0.00	0.00	0.00
Crabs	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.36	0.01	0.00
Crustacean remains	0.00	0.08	0.04	0.25	0.01	0.00	0.21	0.47	0.00	0.19	0.03
Cumacea	0.00	0.01	0.00	0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cladoceran	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Diatoms	0.23	0.24	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07
Eggs	0.05	0.00	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Fish remains	0.00	0.00	0.11	0.14	0.18	0.36	0.12	0.00	0.02	0.04	0.01
Fish scales	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.00
Fishes	0.00	0.00	0.13	0.04	0.73	0.59	0.30	0.00	0.04	0.00	0.00
Gastropods	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.00	0.00	0.00
Harpacticoid copepods	0.28	0.38	0.00	0.00	0.00	0.00	0.00	0.31	0.00	0.00	0.01
Insects	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Isopods	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00
Macroalgae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.27	0.81
Mussels	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.05	0.00
Mysids	0.00	0.00	0.00	0.24	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Nematodes	0.02	0.01	0.00	0.00	0.01	0.00	0.00	0.02	0.00	0.03	0.00
Ophuroids	0.00	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ostracods	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Polychaetes	0.03	0.23	0.08	0.00	0.00	0.00	0.00	0.00	0.27	0.10	0.00
Pycnogonids	0.08	0.01	0.01	0.00	0.00	0.00	0.01	0.02	0.00	0.00	0.01
Shrimps	0.00	0.00	0.12	0.10	0.07	0.00	0.26	0.00	0.06	0.00	0.00
Tanaeidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vascular plant	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.09	0.08	0.07
Total	1.00	1.00	0.98	1.00	1.00	1.00	1.00	0.99	1.00	1.00	1.00
Average SL (mm)	15.0	13.0	77.7	52.0	134.4	377.5	83.3	28.9	335.0	62.9	46.0
Sample size (n)	45	94	7	11	20	2	9	20	1	12	23

benthic prey (Table 2). Tidewater silversides *M. peninsulae* ($\bar{x}$ SL = 77.7 mm) preyed heavily on macrobenthic prey such as amphipods and polychaetes, which was unexpected for this pelagic species. Even more surpisingly, in addition to benthic prey, tidewater silversides also fed on small fishes, primarily juvenile spot of the same size as in our samples, which composed 13% of their diet. Other smaller fishes (clown goby *M. gulosus* $\bar{x}$ SL = 28.9 mm, pinfish *L. rhomboides* $\bar{x}$ SL = 15.0 mm, and spot *L. xanthurus* $\bar{x}$ SL = 13.0 mm) fed heavily on meiofauna (harpacticoid copepods). Other large fishes (gulf flounder *P. albigutta* > 80 mm, $\bar{x}$ SL = 134.4 mm, Atlantic needlefish *S. marina* $\bar{x}$ SL = 377.5 mm, and southern hake *U. floridana* $\bar{x}$ SL = 83.3 mm) were piscivores, with the proportion of fishes in the diet varying from 30% in southern hake to 73% in gulf flounder ≥ 80 mm SL. Because some of the gulf flounder were obtained from a National Marine Fisheries Service trawl study conducted over a wider region of the northeastern Gulf of Mexico during the winter, spring, and summer following this study (Koenig personal communication), ontogenetic classes were used for this species (Fig. 1). For further analyses, gulf flounder > 80 mm SL were pooled into a single ontogenetic class that was largely piscivorous; small gulf flounder ≤ 80 mm SL ($\bar{x}$ SL = 52.0 mm) were kept as a separate ontogenetic class, which consumed various crustaceans (25% of diet were unidentifiable crustacean remains), mysids (24% of the diet), cumacea (15%), and a small amount of

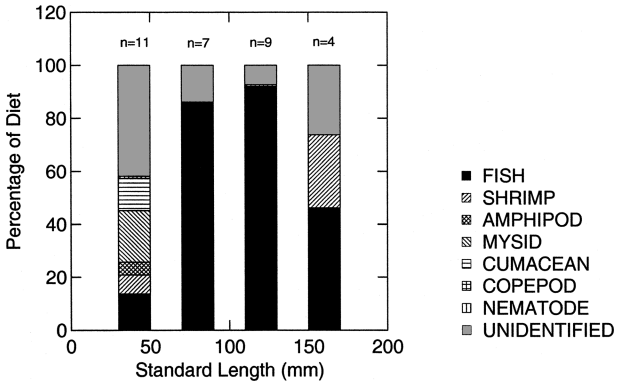

Fig. 1. A bar graph showing ontogenetic changes of gulf flounder, *Paralichthys albigutta,* diets collected in the St. Marks study areas and in a National Marine Fisheries Service trawl survey of northeastern Gulf of Mexico seagrass beds. The percentage of diet is based on dry mass of fish stomach contents. Fish with empty stomachs have been excluded.

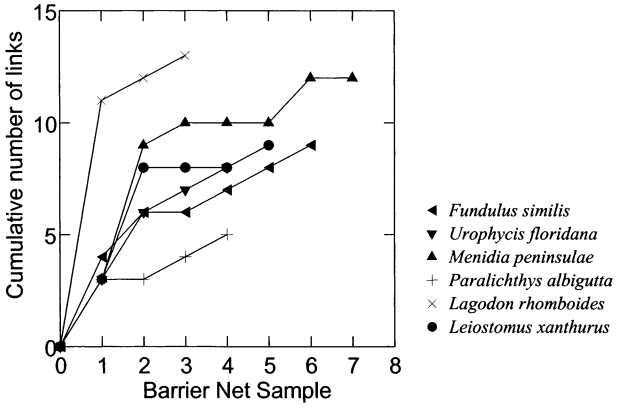

Fig. 2. Trophic linkage accumulation curves for longnose killifish, *Fundulus similis,* southern hake, *Urophycis floridana,* Gulf flounder, *Paralichthys albigutta,* tidewater silverside, *Menidia peninsulae,* pinfish, *Lagodon rhomboides,* and spot, *Leiostomus xanthurus,* showing the cumulative number of prey categories identified within the stomachs of each species of fish examined at each site.

fishes and fish remains (18%; Fig. 1). Longnose killifish *F. similis* $\bar{x}$ SL = 62.9 mm, hardhead catfish *Arius felis* (a single individual had food in the stomach, SL = 335.0 mm), and sheepshead minnows (*Cyprinodon variegatus* $\bar{x}$ SL = 28.9 mm) were omnivorous, consuming macroalgae, diatoms, and vascular plants, as well as amphipods, polychaetes, crabs, crustacean remains, harpacticoid copepods, and fish remains. Few fish were strictly zooplanktivorous, although pinfish and Atlantic needlefish consumed some calanoid copepods (< 3% of the diet). Ontogenetic classes were not used here for any species other than gulf flounder because of the uniformity of sizes of individuals captured during the 2 mo of sampling. Fish predators played a diversity of trophic roles, including zooplanktivores, benthic invertebrate consumers, and piscivores, although there was a great deal of overlap among species. Because of this overlap, a multivariate approach is required to assign species to trophic classes, which we will address in the next section.

Dietary analyses for the various transect locations were first judged for sampling adequacy using trophic link accumulation curves. The cumulative number of trophic links (where L = number of prey categories) within fish diets when plotted as a function of the number of barrier net replicates showed that the trophic link accumulation curves for spot (L = 8) and tidewater silversides (L = 12) appeared to reach an asymptote after 3 net samples, but then increased again after the 5th and 6th net sample (Fig. 2). The cumulative number of links did not reach an asymptote for pinfish (L = 13), longnose killifish (L = 9), southern hake (L = 8), or gulf flounder ≤ 80 mm SL (L = 5; only gulf flounder caught in our barrier net sampling at St. Marks are included in this trophic link analysis). For some fish species (e.g., Atlantic needlefish, *S. marina,* hardhead catfish, *A. felis,* and clown goby, *M. gulosus,* each of which occurred in < 2 net sets, although 20 clown goby stomachs contained food), the sample size was too low to conclude anything about accumulation of dietary links. In terms of estimating the presence of rare prey in the diet, these trophic link accumulation curves indicated that the diet analysis for fishes captured in the St. Marks area was inadequate. Since our goal was to document the presence of dominant food sources in the stomachs of these species during the months of sampling, these diet data were the best available for the locations and seasons being modeled. They were included in the diet matrix analyzed below, in addition to published dietary data available from other areas on the same species.

Trophic Guilds of Fishes and Macroinvertebrates

The trophic guilds were established in two steps from the diet matrix (Table 3). First, a hierarchical clustering strategy was used to initially group the consumer taxa; second, a CA was then used to simultaneously display the factor scores of the consumers (coded for cluster group membership) and the food resources in the same multivariate space. In the resulting scatter plots, the proximity of points (factor scores) for each taxon indicates the similarity of that consumer with respect to other consumer taxa and their food sources; proximity of food sources in the plot indicates similarity of their consumers. These associations were then used to develop the trophic guilds reported here.

In order to demonstrate our method on a simple example, we chose a subset of the total food web, examining the 20 species of fishes and their 22 food sources. There were five clusters of the fish species with distances ≤ 0.40 (Fig. 3): Cluster 1 comprised dwarf seahorse *Hippocampus zosterae* (HIPZOS) and blackcheek tonguefish *Symphurus plagiusa* (SYMPLA); Cluster 2 comprised gulf pipefish *Syngnathus scovelli* (SYGSCO) and southern hake *U. floridana* (UROFLO); Cluster 3 comprised searobins *Prionotus* sp. (PRIONOT) and gulf flounder *P. albigutta* ≤ 80 mm SL (PARALBJ); Cluster 4 comprised red drum *Sciaenops ocellatus* adults (SCIOCEA), gulf flounder *Paralichthys albigutta* > 80 mm SL (PARALBA), and Atlantic needlefish *S. marina* (STRMAR); and Cluster 5 comprised Florida blenny *Chasmodes saburrae* (CHASAB) and hardhead catfish *A. felis* (ARIFEL). Although some of these cluster groupings were unexpected (e.g.,

TABLE 3. The diet matrix (1 = food item for that taxa, 0 = not a food item for that taxa) of the 33 possible food sources (columns) and the 73 fish and invertebrate taxa (rows) entered into the cluster and correspondence analyses. See Table 1 for names associated with macroconsumers and food source identification codes.

Numeric Code	DETR	CARRION	BACT	SEAG	ALGA	MALG	EPIP	CILL	FORA	NEMA	HARP	GAST	BIVA	AMPH	MYSID	CUMA	ISOP	CRAB	SHRIMP	POLY	ECHI	FISH	WDET	WBAC	WMIC	WCIL	WFOR	WNEM	WHAR	WCAL	WPOL	WPYC	DOC
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
2	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0
6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0
7	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0
10	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
12	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
13	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0
15	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0
18	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0
20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0
21	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22	1	0	0	1	1	1	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
24	1	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
26	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
27	1	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
29	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	1	1	1	0	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	1	0	0	0	0	0
31	1	0	1	0	1	1	0	0	1	0	1	1	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0
32	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
33	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
34	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	0
35	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	1	1	1	0	0	0
36	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
37	1	0	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
38	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
39	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	1	1	1	0
40	0	0	0	1	0	0	0	0	0	1	1	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
41	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
42	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
43	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0
44	1	0	1	1	1	1	1	0	0	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
45	1	0	1	0	1	1	0	0	1	1	1	0	0	1	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	1
46	1	0	1	1	1	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0
47	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
48	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
49	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
50	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
51	0	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0
52	1	0	1	0	0	1	1	0	0	0	0	0	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
53	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
54	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0
55	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
56	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
57	1	0	1	0	0	1	1	0	1	1	1	1	1	1	0	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0
58	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
59	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0
60	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	1	0	0	0
61	1	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
62	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0
63	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
64	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
65	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0
66	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0
67	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
68	1	0	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
69	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
70	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0
71	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0
72	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	1	0	1	0
73	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Florida blennies and hardhead catfish were grouped because they consume similar prey when aggregated prey categories from the published diet data were used, even though they may eat quite different prey species), most make sense intuitively and suggest some potential trophic groupings based on diet similarity alone.

The CA factor scores of the fish consumers, which explained 23% of the variation in these data, coded by the cluster memberships identified

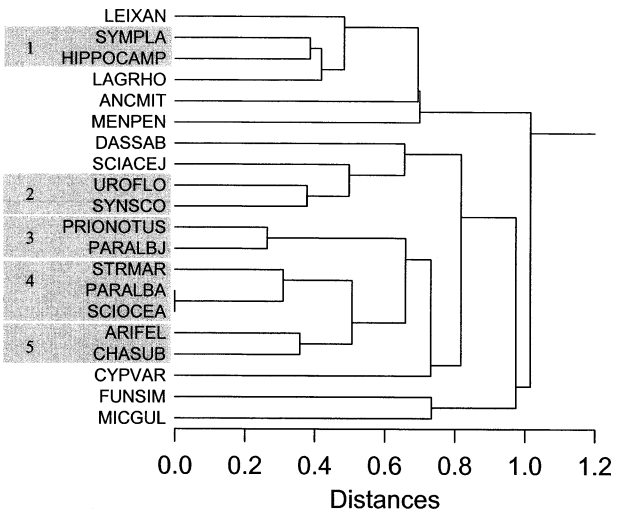

Fig. 3. Average linakge cluster tree diagram showing the similarity in diets among 20 fish taxa using the distance measure 1 − r, where r is the Pearson correlation coefficient among the taxa. The fish taxa are labeled using the text codes given in Table 1. Taxa were considered members of the same cluster (indicated by numbers in gray boxes) if the distance measure ≤ 0.40.

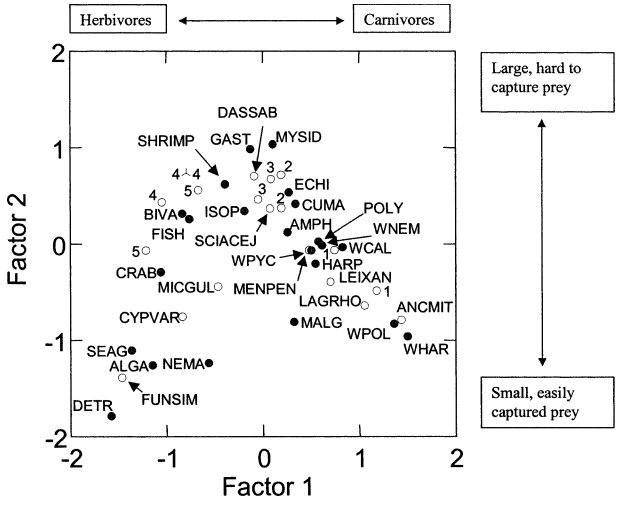

Fig. 4. A plot of the factor scores on factors 1 and 2 from the correspondence analysis of the 20 fish taxa (open circles) and the 22 food source categories (closed circles). The fish taxa and food sources are labeled using the text codes given in Table 1 or by cluster numbers (gray boxes in Fig. 3). A ⅄ in the upper left is used to indicate three overlapping points in cluster 4.

above, were plotted along with the factor scores of the food sources (Fig. 4). Fish consumers with scores that were high on factor 1 tend to reflect planktonic and meiobenthic food sources, such as calanoid (WCAL) and harpacticoid (HARP, WHAR) copepods, polychaetes (WPOL), and nematodes (WNEM) food sources (Fig. 4). These taxa were the zooplanktivorous and meiobenthos-consuming fishes. Those fishes with low scores on factor 1 were omnivorous, plotting near plants and algae as well as animal food sources. Factor 1 seems to represent an axis of plant food at one end and animal foods at the other. Fish consumers with high factor scores on factor 2 seem to plot closest to large prey with either hard shells or with well-developed predator avoidance behaviors, including benthic mollusks, nektonic shrimp, and fishes. Fish consumers with low scores on factor 2 were associated with small prey that posess poor escape ability. Factor 2 thus appears to represent an axis of prey size and difficulty of capture.

The individual fishes that are members of the five clusters identified in the cluster analysis above are in close proximity to one another in the CA plot, suggesting that the cluster analysis and the CA give similar results. Other species of fish consumers, not included in the cluster groups, can be observed in the same regions of this plot, suggesting that they have similar food sources and could be included in these same trophic groups. If we examine which food sources are associated with each of the clusters, we can label the trophic groups and include additional species.

An obvious trophic group in the factor scores plot comprised the zooplanktivores and meiobenthos consumers, which had high scores on factor 1 and low scores on factor 2 (Fig. 4). The fishes in cluster 1 (dwarf seahorse and blackcheek tonguefish) were in this trophic group and have factor scores similar to the bay anchovy (ANCMIT), small pinfish (LAGRHO), small spot (LEIXAN), and tidewater silversides (MENPEN); indeed, some of these latter species fell between the cluster members on the factor scores plot. Tidewater silversides were unlike other members of this group because they consumed large prey as well, including macrobenthos and fish (Table 2); the factor scores for silversides are lower on factor 1 and higher on factor 2, placing this species close to the macrobenthos consumer and piscivore consumer groups (see below).

The next trophic group visible in Fig. 4 comprised macrobenthos-consuming fishes, which had scores that were intermediate on factor 1 and high on factor 2. Consumers in Cluster 2 (gulf pipefish and southern hake) and Cluster 3 (searobins and juvenile gulf flounder (≤ 80 mm SL) were in this trophic group and had factor scores that were similar to juvenile red drum (SCIOCEJ) and Atlantic stingray (DASSAB). All of these consumers had factor scores that reflected similar food sources of amphipods (AMPH), polychaetes (POLY), cumaceans (CUMA), echinoderms (ECHI), isopods (ISOP),

gastropods (GAST), and mysids (MYSID). The similar factor scores for fishes in clusters 2 and 3 suggest that all of these fishes could be grouped together along with juvenile red drum as a macrobenthos-consuming trophic group, even though they did not cluster together closely. The inclusion of gulf pipefish in this group may seem unusual, because they mostly consume zooplankton; however, this group assignment reflected that gulf pipefish are reported to consumed gastropods, amphipods, isopods, and mysids, as well as calanoid copepods (Huh and Kitting 1985; Motta et al. 1995).

A clear trophic group comprised the piscivores in Cluster 4 (gulf flounder > 80 mm SL, Atlantic needlefish, and adult red drum), which had factors scores associated with the fish (FISH) food source. Some species in this piscivore trophic group also consumed shrimp, placing them near the shrimp (SHRIMP) food source in the CA space. Fishes in cluster 5 (Florida blenny and hardhead catfish) had factor scores that were not only near the fish and shrimp food sources, but were also associated with isopods (ISOP), mysids (MYSID), bivalves (BIVA), and gastropods (GAST) food sources, all of which they have been reported to consume (Reid 1954; Motta et al. 1995). Hardhead catfish were lower on both factors 1 and 2 than the others in this group, reflecting that they consumed fishes (juvenile spot was 23% of the diet) as well as macrobenthic prey such as crabs, polychaetes, shrimp, and even some seagrass (Table 2). It is convenient to group all fishes in Clusters 4 and 5 into a piscivore trophic group, although members of Cluster 4 did not consume any mollusks, whereas Cluster 5 members consumed fish as well as mollusks and benthic macroinvertebrates.

The remaining fishes were not grouped at a distance of ≤ 0.4 in the cluster analysis, including sheepshead minnow (CYPVAR), clown goby (MICGUL), and longnose killifish (FUNSIM), which were grouped into an additional trophic group, based on their similar positions in the plot. All these fishes consumed plant or algae producers to some degree (Table 2), and thus this trophic group is best characterized as omnivores. Longnose killifish were the most herbivorous of all of these (Table 2), and had the lowest factor scores on both factor 1 and factor 2. Food sources in the factor scores plot confirm this omnivore trophic grouping, as these fishes were associated with detritus (DETR), seagrass (SEAG), macroalgae (ALGA), diatoms and microalgae (MALG) as well as crabs (CRAB) and nematodes (NEMA).

The various food sources associated with the fish consumers and cluster analysis groups are easily visualized using a CA factor scores plot. Using such a plot, each fish consumer can be assigned to a unique trophic group, even those fishes that did not exceed the arbitrary threshold we established in the cluster analysis.

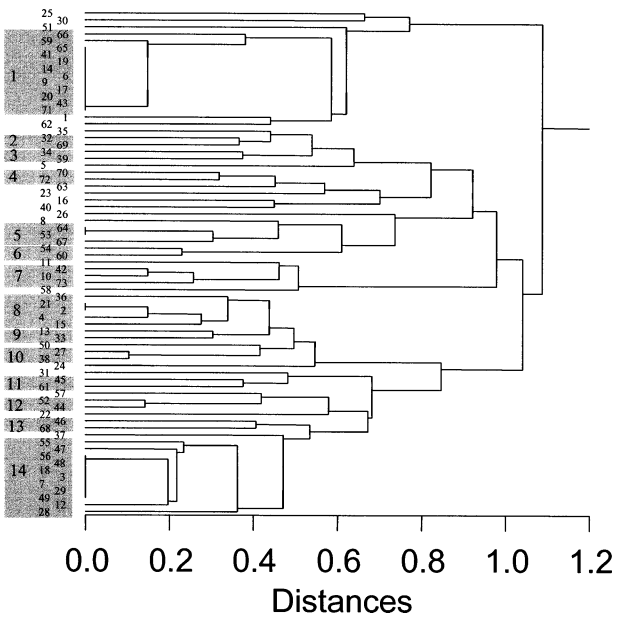

Fig. 5. Average linkage cluster tree diagram showing similarity in diets among the 73 macroinvertebrate and fish taxa (numeric codes listed in Table 1) using 1 − r as a distance measure. Taxa were considered members of the same cluster (as indicated by cluster number shown in the gray boxes) if the distance measure ≤ 0.40.

Next we use the approach outlined above to consider the complete diet matrix for all zooplankton, macrobenthos, and fish consumers and their food sources simultaneously using the clustering strategy and a three-factor CA. Fourteen cluster groups were identified with diet similarity > 0.60 (or Pearson distances ≤ 0.40) in the hierarchical cluster analysis of consumer taxa (Fig. 5). The first three CA factors explained 23% of the variation in the diets and predators of the food sources. In general, CA factor 1 separated the benthic- and suspension-feeding trophic groups (Fig. 6). Low scores on factor 1 were associated with suspension feeding consumer taxa, microalgae, and bacteria food sources in the water column and suspended detrital food sources. High scores on CA factor 1 were associated with fishes and benthic macroinvertebrates such as consumers, benthic invertebrates, producers, carrion, and detritus as food sources. Some exceptions to this interpretation were the water column food sources with high scores on CA factor 1 (WCAL = calanoid copepods, WPOL = polychaete larvae, WPYC = pycnogonids, WHAR = harpacticoid copepods, and MYSID = mysids). These planktonic foods' placement on CA factor 1

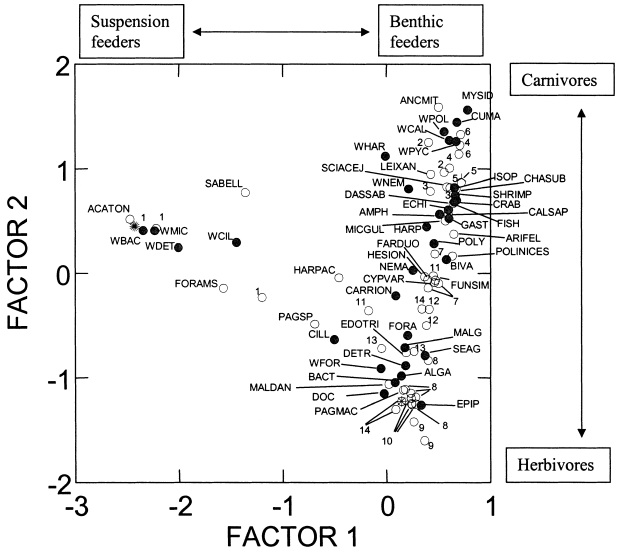

Fig. 6. A plot of the factor scores on factors 1 and 2 from the correspondence analysis. The 73 macroinvertebrate and fish taxa (open circles) are identified using cluster number (from gray boxes in Fig. 5) or text codes for taxa not included in the cluster groups (Table 1). The 33 food source categories are shown as closed circles (text codes in Table 1). Sunflower symbols (stars) indicate overlapping points (i.e., the numbers of arms on each symbol is equal to the number of overlapping points).

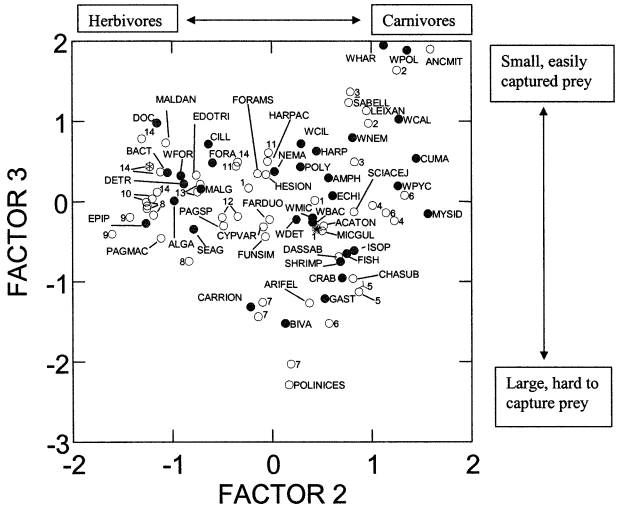

Fig. 7. A plot of the factor scores on factors 2 and 3 from the correspondence analysis. The 73 macroinvertebrate and fish taxa (open circles) are are identified using cluster group codes (Fig. 4) or text codes for taxa not included in the cluster groups (Table 1). The 33 food source categories are shown as closed circles (text codes in Table 1). Sunflower symbols (stars) indicate overlapping points (i.e., the numbers of arms on each symbol is equal to the number of overlapping points).

reflected the position of their fish consumers, which ate zooplankton as well as benthic prey. Benthic producer food sources, such as epiphytic algae, algae, microalgae, benthic bacteria, and dissolved organic carbon scored low on CA factor 2; fish and benthic invertebrate food sources scored high on this factor (Fig. 6). CA factor 2 appears to be directly related to the trophic position of the consumers and food sources. Gastropod and bivalve food sources had intermediate scores on CA factor 2, along with crustacean benthic invertebrate food sources (Fig. 6). CA factor 3 further separated the consumer taxa on the basis of their ability to capture small prey (Fig. 7). Fish consumer taxa showed the best separation on factor 3, grouping into piscivores and mollusk feeders (low scores), macrobenthos-consuming fishes (intermediate scores), and meiofauna feeders (high scores; Fig. 7).

In the sections that follow, we interpret the cluster groups (Fig. 5) as trophic guilds by comparing consumer taxa and food source factor scores (Figs. 6 and 7), and adding consumer taxa to the guilds based on similarity in factor scores. Then, using three-dimensional plots of factors 1, 2, and 3, we visualized the position of each of the guilds in relation to their food sources by plotting average CA factor scores within cluster groups (Fig. 8). Each trophic group position within the CA three-factor space represents their feeding habitat in the water (factor 1), their trophic position (factor 2), and the degree to which they depend upon small, easy-to-capture prey (factor 3). At the same time, proximity of points within this plot indicated the asso-

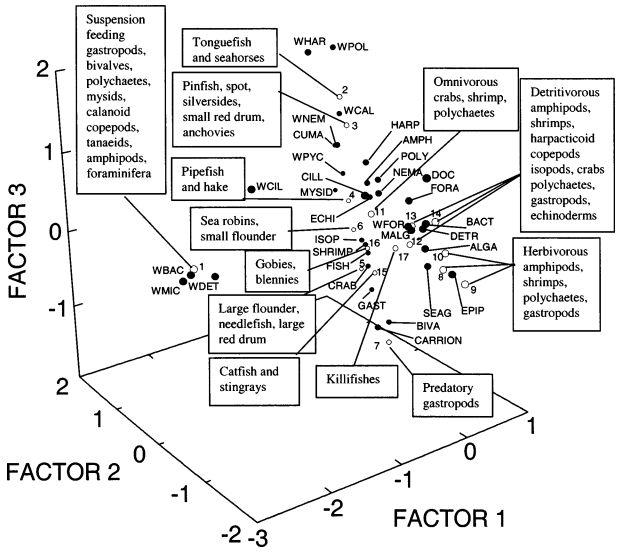

Fig. 8. A three-dimensional plot of the correspondence analysis factor scores of the trophic groups of consumers and the food sources. Open circles indicate the average factor scores of the trophic groups, closed circles indicate the factor scores of the food sources. See Fig. 5 and the text for taxa included in each trophic group number identification code. The identification codes for food sources are given in Table 1.

ciation of each trophic group and their food sources. In the description of each trophic group that follows, we present these food source associations and the taxa composing each trophic group.

The consumer taxa in Group 1 were all suspension feeders. Group 1 was composed of spionid (66) and serpulid (65) polychaetes, mysids *Mysidopsis* sp. (41), amphipods *Corophium* sp. (19) and *Cerapus* sp. (14), the tanaeid *Hargeria rapax* (71), copepod nauplii (43), polychaete larvae (59), the bay scallop *Argopecten irradians* (6), the mussel *Brachidontes exustus* (9), the clam *Chione cancellata* (17), and the gastropod *Crepidula fornacata* (20) (Fig. 5). Members of this cluster had CA factor scores that were low on factor 1 and intermediate on factor 2 (Fig. 6), as did some other taxa not included in this cluster, including the copepod *Acartia tonsa* (ACATON), foraminifera (FORAMS), and polychaetes in the Sabellidae (SABELL). All of these taxa were assigned to the suspension-feeding trophic group (Fig. 8), as these taxa had factor scores most similar to the food sources in the water column, which included bacteria in the water column (WBAC), phytoplankton (WMIC), and suspended detritus (WDET).

The next few trophic groups (2–6) were composed of fishes; these groups (Fig. 5) were similar to the ones discussed in the previous analysis (Fig. 3). All of these groups have factor scores that are intermediate to high on factor 1 and high on factor 2 (Fig. 6). Group 2 was a meiofauna-feeding group, consisting of the dwarf seahorse (32) and blackcheek tonguefish (69; Figs. 5 and 8). Group 3 comprised pinfish (34) and tidewater silversides (39; Fig. 5); these fish were similar in that they both consumed zooplankton, meiobenthos, and macrobenthos (Table 2). These small pinfish ($<$ 40 mm SL) had not yet begun to consume plant materials and algae, as has been reported for large pinfish (Luczkovich et al. 1995). Based on similar factor scores, we also included spot (LEIXAN), bay anchovy (ANCMIT), and juvenile red drum (SCIOCEJ) in this trophic group (Fig. 8). Group 4 was composed of gulf pipefish (70) and southern hake (72), which is another feeding group that takes small animal prey (macrobenthos and zooplankton). Group 5 was a piscivore and shrimp-feeding cluster, consisting of gulf flounder $>$ 80 mm SL (53), adult red drum (64), and Atlantic needlefish (67), all of which had factors scores that were similar to the shrimp and fish food sources on factors 1 and 2 (Figs. 6 and 8). Group 6 consisted of gulf flounder $\leq$ 80 mm SL (54) and searobins (60), both of which are shrimp and macroinvertebrate consumers. Some fish taxa did not exceed the $>$ 0.60 Pearson coefficient threshold for inclusion in the cluster groups, but nonetheless were assigned to a trophic group for our network model. We assigned the mollusk, fish, and crustacean consuming hardhead catfish, *A. felis,* and Atlantic stingray, *Dasyatis sabina,* to a new trophic group (Group 15) for network modeling, because they had a large body size and intermediate scores along factors 2 and 3 (Fig. 8). This placed them between the fish, decapod, isopod, gastropod, and bivalve food sources in the factor scores plot (Figs. 6 and 7). In addition the Florida blenny (CHASAB) and the clown goby *M. gulosus* (MICGUL) were combined into a single trophic group (Group 16) based on their small body size (a network modeler will normally include species with similar body size in a trophic grouping) and similar scores on factors 2 and 3 (Fig. 8). The sheepshead minnow *C. variegatus* (CYPVAR) and longnose killifish (FUNSIM) clearly belonged to an omnivore killifish group (Group 17) based on their intermediate scores on factor 2 (Fig. 8). These killifishes, which consumed a significant amount of algae (Table 2), plotted close to the invertebrate herbivore and detritivore trophic groups, with intermediate factor scores on factors 2 and 3 (Fig. 7). Members of these fish trophic groups plotted in the upper right corner of Fig. 6, which indicated that they were carnivores that took benthic prey. When the CA scores for these groups were plotted on factor 3 (Fig. 7), they are arranged inversely with prey size. High factor scores were associated with small prey (meiofauna) consumers (Group 2 and 3), intermediate scores were associated with large prey (macrofauna) feeders (Group 4 and 6), and the low scores were associated with piscivores (Group 5). When we plotted the average factor scores for these fish trophic groups on all three factors, groups 2, 3, 4, 5, 6, 15, and 16 were all within the benthic carnivore region of the multivariate space (high on factors 1 and 2), but were arranged inversely along a prey-size axis (factor 3), such that fishes taking the smallest prey were at the top of the plot (Fig. 8).

Another cluster defined a predator-scavenger invertebrate trophic group. Group 7 was composed of predatory gastropods *Busycoptypus spiratus* (10), *Natica* sp. (42), and *Urosalpinx perrugata* (73); these taxa had factor scores that were high on factor 1 (i.e., benthic feeders) and intermediate on factor 2 (i.e., omnivores), and reflected the factor scores of the food sources bivalves (BIVA) and carrion (CARRION; Fig. 6). These taxa also had scores that were lowest on factor 3 (i.e., large, difficult to capture prey), an axis that separated mollusks and carrion-feeding gastropods from other taxa (Fig. 7). The gastropod *Polinices* sp. (POLINICES) had factor scores that were similar to Group 7 consumer taxa and the bivalve (BIVA) food source; it was placed in the predatory gastropod trophic group.

The consumers included in this trophic group had a very distinct position near the bivalve, carrion, and gastropod food sources when visualized within CA three-factor space (Fig. 8).

A series of trophic groups (Groups 8, 9, and 10) were largely herbivorous (Fig. 8). Group 8 was a group of epiphyte-grazing invertebrates, including the shrimp *Alpheus normani* (2), amphipods *Ampithoe longimana* (4) and *Cymadusa compta* (21), gastropod *Cerithium lutosum* (15), and the spider crab *Libinia dubia* (36; Fig. 5). These taxa had CA factor scores that were high on factor 1, low on factor 2, and that corresponded closely with the epiphytic algae food source (EPIP) in the factor scores plot (Figs. 6 and 8). Group 9 is also an epiphyte-grazing trophic group, consisting of the amphipod *Caprella penantis* (13) and the shrimp *H. zostericola* (33; Fig. 5). These taxa had factors scores that were lowest on factor 2, corresponding to both to Group 8 taxa and to the EPIP food source (Figs. 6 and 8). Group 10 consisted of amphipods *Gammarus mucronatus* (27) and *Melita* sp. (38; Fig. 5). These consumers were epiphyte-grazing and detritus-feeding taxa, had factor scores high on factor 1 and low on factor 2, and were associated with the scores of the epiphyte (EPIP), dissolved organic carbon (DOC), detritus (DETR), bacteria (BACT), and macroalgae (ALGA) food sources (Figs. 6 and 8). Trophic groups 8, 9, and 10 are all members of the herbivorous amphipod, shrimp, polychaetes, and gastropod trophic group (Fig. 8).

The invertebrates of Group 11 were plant and animal consumers, so this was the omnivore trophic group (Fig. 8). Group 11 was composed of the polychaetes in the Nereidae (45) and the shrimp *Processa bermudensis* (61; Fig. 5). These taxa were predatory and detritivorous consumers, and had factors scores that were high on factor 1 and intermediate on factor 2 (Fig. 6). These consumer taxa had factor scores that corresponded with the scores for the food sources carrion, detritus, and nematodes (NEMA; Fig. 6). Hermit crabs (PAGSP and PAGMAC) also had factor scores near these consumers, as well as detritus and algal food sources, and were included in either the detritivore (*Pagurus mclaughlini* in Group 14) or omnivore (*Pagurus* sp. in Group 11) trophic group. The shrimp *Farfantepenaeus duoarum* (FARDUO) had high scores on factor 1 and intermediate scores on factor 2 and 3, and so it was included in this omnivorous trophic group.

A final series of trophic groups (Groups 12, 13, and 14) contained all detritivores to varying degrees (Fig. 8). These detritivores, and in some cases consumers of benthic invertebrates, all had negative scores on factor 2 (Fig. 6). Group 12 consisted of the shrimp *Paleomon floridanus* (44) and the mud crab *Neopanope* sp. (52; Fig. 5). Group 13 contained brittle star *Ophiderma brevispinum* (46) and polychaetes in the family Syllidae (68; Fig. 5). The largest cluster was Group 14, which contained the amphipod *Ampelisca* sp. (3), ostracods (49), the gastropod *Haminoea succinea* (29), and various polychaetes in the families Paraonidae (7 and 55), Onuphidae (47), Orbiniidae (48), Cirratulidae (18), Capitellidae (12), Glyceridae (28), and Pectanariidae (56; Fig. 5). This is a deposit-feeding trophic group, because all of these taxa had factor scores that corresponded to the food sources dissolved organic carbon (DOC), bacteria (BACT), macroalgae (ALGA), detritus (DETR), and epiphytic algae (EPIP; Figs. 6 and 8). Polychaetes in the families Maldanidae (MALDAN) and Hesionidae (HESION) also were grouped with these deposit feeders because they had factor scores near the DETR and BACT food sources (Fig. 6). Trophic groups 12, 13, and 14 were positioned close to the detritus (DETR) and benthic bacteria (BACT) food sources and had factor scores high on factor 1 (benthic feeders) and in the intermediate regions of factors 2 and 3, suggesting that that should be assigned to a benthic-detritivore trophic group (Fig. 8).

Discussion

The methods we report here to identify trophic guild structure illustrate that, even though there was a wide diversity of fish and invertebrate consumer taxa in the seagrass meadows near the St. Marks National Wildlife Refuge, cluster analysis and CA could be used together to identify major trophic guilds in the food web. Using these methods, we established the final compartments in a series of carbon exchange network models (Baird et al. 1998; Christian and Luczkovich 1999). The approach outlined here should prove useful to future network modelers who want to visualize and create trophically similar compartments in their models.

Fishes in this seagrass ecosystem showed the greatest trophic diversity and exhibited the least amount of similarity among the clusters and correspondence analyses of all consumers taxa examined. This may be due to the fact that fish diets in the published literature and in our study here are well characterized. We sampled fish stomach contents directly at the study areas to obtain food web linkages that were appropriate for the exact location and times being modeled. This allowed our diet matrix to reflect the food web configuration for this ecosystem as accurately as possible. For example, we identified small spot (~20 mm SL) as prey of tidewater silversides, which is a result that was not expected based on diet information avail-

able in the literature when we started the analysis (although we later discovered an unpublished report that detailed a similar trophic link; Levine unpublished report). Without direct diet estimates, we would have not obtained the species-specific link to spot from tidewater silversides that was included in our published network models.

The trophic diversity of these fishes may even be greater than we have shown. Because some of the fish species examined for stomach contents did not appear to reach an asymptote in the trophic link accumulation curves, it is fair to conclude that more than nine barrier net samples should have been used to adequately characterize the trophic diversity of these fishes. Our method to correct for this inadequacy was to supplement the diet matrix with dietary data collected elsewhere, for species in which our sample size was small. Nevertheless, we did collect and analyze the stomach contents of more than 20 individuals for pinfish, spot, gulf flounder, clown goby, and sheepshead minnow, a sample size that was more than adequate based on previous studies (Livingston 1980, 1982, 1984, 1988; Stoner 1980). Our approach here differed from previous studies in that we used net samples, not individual fish, as replicates for the trophic accumulation curves. The lack of asymptotic curves indicated that as we sampled in new areas, new, rare trophic links were being added to the food web, even though dominant prey links may have been well characterized. Such monotonically increasing, rather than asymptotic, trophic link accumulation curves were also detected in the terrestrial tropical food-web sampling simulation study of Goldwasser and Roughgarden (1997), who concluded that many trophic links would not be detected at sampling intensities routinely used in field work. Although further sampling may have allowed the asymptotes to be reached in our study at St. Marks, Goldwasser and Roughgarden's (1997) simulation study suggested that the sampling effort required to reach such an endpoint would exceed the resources and budgets of most ecological investigations. This is a problem that will plague all future food web modeling efforts, and stems from the fact that all ecosystems are open and rare species will come and go. It was our intention to define a boundary for the St. Marks ecosystem in time and space, and present the data we collected so that others could see its limitations. The inadequacy of our fish diet data as judged by trophic link accumulation curves is a limitation, but our data best represent the food web present in the study area at the time of sampling.

In contrast to the fishes, the dietary data of the invertebrates was drawn solely from the literature, and shows less trophic diversity, as can be observed in the high similarity among consumer taxa ultimately grouped into suspension-feeding and deposit-feeding trophic groups. This result is most likely due to the poor taxonomic resolution of the published diet data for such consumers, which often included highly aggregated food source categories, such as detritus, bacteria, and phytoplankton. This aggregation of food sources is a continuing problem when using dietary studies as a basis for the construction of food webs. Such pre-aggregation is especially common in taxa that are small (copepods) or in low trophic positions in the food web (amphipods; Cohen et al. 1993). Aggregation of species into prey categories in published diet studies can present a problem for developing trophic groups using our method. Such trophic grouping occurs routinely in published diet studies, and should be avoided in the future if such data are to be included in food webs meant to reflect the reality of trophic interactions. Alternatively, species-level dietary data could be deposited in on-line archives or made available to authors wishing to construct food web models with a high degree of taxonomic resolution. We acknowledge that high taxonomic resolution is difficult to achieve, but it should remain a desirable goal. Another problem is that stomach contents data may be biased towards prey that resist digestion and the digestion process often prevents identification to the species level (Scholz et al. 1991). These methodological problems will preclude for the present time the construction of a true topological food web (food web showing binary links among individual species), because food sources are often more aggregated than is desired (e.g., the food source categories of amphipod, fish, or polychaete used in this paper). It would be preferable to have species-level data, because it would have allowed the creation of a square diet matrix, with all taxa represented as both predators and prey. Other analytic approaches based on graph theory and trophic role structure could then be used to group taxa based on similarities of their links to both predators and prey (Johnson et al. 2001; Luczkovich et al. in press). In general, it is best for ecologists to keep prey taxa ungrouped as much as possible, so that aggregation can be accomplished objectively during the trophic model construction.

In spite of having limited dietary data and not having a square diet matrix for the St. Marks seagrass ecosystem, we were able to use CA to identify clear trophic groups. The CA did an excellent job at allowing us to visualize the food sources and prey consumed by the various fish and invertebrate consumers. Moreover, the factors could be interpreted in an ecologically meaningful way, with factors representing feeding position in the water col-

umn (suspension feeding versus benthic feeding), the approximate trophic position of consumer taxa, and the difficulty of capture associated with prey of various sizes and escape mechanisms. There was, however, a generally low percentage of variance explained by the CAs. The reason for such low percentages is that there were a great many variables to be explained in a complex estuarine food web; we had 33 food sources and 73 consumers. The CA explained 100% of the variance with 32 factors (one less than the number of food sources), but using this many factors would be counterproductive. The first several factors explained the greatest amount of the variance in both cases, and we were primarily interested in visualizing the feeding guild relationships using these factors. The CA was useful, in spite of the low percentage of variance explained, because it helped us visualize the trophic guilds present in the food web. It was more useful than a cluster dendrogram alone, because it simultaneously reflected why consumer taxa were grouped together (i.e., they were linked to food sources that had similar factor scores).

Care should be used when interpreting the factor score plots. In some cases food sources that plotted near a consumer in the factor scores plot were, in fact, not consumed by that consumer (e.g., Group 5 taxa were largely fish consumers, and although they had similar factor scores to the bivalve food source, they did not consume bivalves). By carefully comparing the relative positions of the consumer taxa and food sources in the factor score plots, we easily identified the food sources for each cluster and further grouped all the macro-consumers into eight broad trophic guilds: suspension-feeders, herbivores on algae and seagrass, bacterial and detritus consumers, omnivores, benthic-meiofauna consumers, benthic-macrofauna consumers, molluscivores, and piscivores.

Any aggregation process is a balance of the perceptions and desires of the observer with the nature of the observed system (Ahl and Allen 1996). We could have chosen a less rigorous cut-off to establish cluster membership, which would have created a few large clusters, or a more rigorous one, which would have established many more clusters, each with fewer members. This aspect of aggregation is thus left up to each investigator to decide. One method for determining such thresholds, detailed in Luczkovich et al. (in press), involves examination of the within-cluster to between-cluster variance ratios and an associated R^2 estimate for cluster partitions of various sizes. It is important to note that no matter which cut-off we selected in the cluster analysis, the factor scores of the macroinvertebrate and fish consumer taxa and the food sources in the correspondence analysis would not have changed, simply the cluster identifiers. This is our rationale for including consumer taxa in the final trophic groups that were above the similarity cut-off used in the cluster analysis: these taxa were similar in CA factor scores, and had similar food sources. We could have used the correspondence analysis alone to assign individual macroinvertebrate and fish taxa to trophic groups using the similarity of scores. Such factor score plots would be difficult to interpret without first applying a cluster analysis. Cluster analysis was useful in uncovering underlying trophic groups at an arbitrary level of aggregation, but CA was useful in determining the sources of food that caused the clusters to be formed and then adding taxa with similar factor scores to the trophic groups. No matter what cluster membership criterion is selected, the use of CA allows one to further reduce the number of taxa into a small number of trophic groups for food web models.

Application to Network Analyses

We used these broad trophic groupings to guide our other research using ecological network analysis of carbon flow, but we recognized the need to subdivide further these groupings on a taxonomic or body size basis. In the network models constructed from these data (Baird et al. 1998; Christian and Luczkovich 1999), once the compartments were defined, we estimated carbon flow among compartments using published data on consumption, respiration, egestion, and assimilation rates for various taxa. Because published data on metabolic rates and predator relations are reported by taxonomic groups, we elected to keep consumers separated by taxonomic as well as trophic classifications in the network models. We elected to assign some invertebrate taxonomic groups (amphipods, polychaetes, crabs, etc.) to separate compartments in the final network models, although we always subdivided them into trophic groups within a taxonomic group (e.g., detritivorous amphipods and herbivorous amphipods were in separate compartments). Separate network model compartments were maintained when metabolic rates and body sizes of the taxa differered greatly, even if they fell within the same CA-based trophic groupings. For this reason, we did not aggregate amphipods and spider crabs, even though they were both considered seagrass and algae-consuming herbivores.

The fishes were largely retained at the species level, because we had direct dietary information from our site on those taxa, but also because they varied greatly in trophic diversity and body sizes among species. We did group certain taxa on the basis of taxonomic group membership, body size,

and trophic guilds identified in the current analysis: clown gobies and Florida blennies, hardhead catfish and Atlantic stingrays, tidewater silversides and bay anchovies, gulf pipefish and dwarf seahorses. When appropriate, we kept ontogenetic stages within species separate (e.g., gulf flounder and red drum). In network models, flounder ≥ 80 mm SL were grouped with Atlantic needlefish, based largely on the diet information from the analyses reported here. For similar reasons, we placed adult and juveniles stages of red drum in separate consumer taxa here and in separate compartments in the network models, based on diet analyses from the literature (Peters and McMichael 1987). We did not collect enough individual red drum to include dietary data from the St. Marks sites without resorting to the literature.

This aggregation of fish and invertebrate consumer taxa into taxonomically subdivided trophic guilds reduced by approximately one half the number of compartments being modeled from 73 taxa to 42 compartments. With the inclusion of the bird consumers, producers (*H. wrightii,* phytoplankton, benthic algae and diatoms, and epiphytic algae), and particulate and dissolved organic carbon (detritus), we settled on 51 compartments to be estimated for biomass in one network model (Baird et al. 1998) and 48 compartments in the other (Christian and Luczkovich 1999).

In order to create reliable and quantitative food web models, ecologists need to be explicit about the way such models are constructed (Cohen et al. 1993). Our approach was to use a multivariate statistical procedure to derive network model compartments in an objective way. However, experienced scientists should review such classifications prior to establishing trophic guilds for metabolism-based carbon flow network models. The approach we present employs common multivariate tools that are available for network modelers in constructing their models.

Trophic Organization of Seagrass Ecosystems

The macroconsumer taxa comprising these guilds in the *H. wrightii* seagrass meadow included various species of crustaceans (amphipods, cumaceans, tanaeids, shrimps, crabs), polychaetes, gastropods, bivalves, echinoderms, and fishes. These trophic guilds encompass most of the common aquatic consumer taxa encountered in seagrass ecosystems, although we excluded from our trophic guild analysis microbes, meiofauna, macrofauna with unknown diets, and birds (although these groups were all included in our network models). Subsets of these same macroinvertebrate and fish consumer taxa have been grouped previously based on diet similarity (Livingston 1982, 1984; Leber 1983), but never such a large set of taxa. Below, we contrast our findings with those presented previously for seagrass ecosystems in the northeastern Gulf of Mexico.

Based on eight years of multi-season trophic data, Livingston (1982) used a hierarchical clustering strategy to group 43 trophic units (or ontogenetic stages) of the seagrass-associated fishes in Apalachee Bay. He identified three major trophic groups: plankton-, harpacticoid-, and polychaete-consuming fishes (Group I); benthic omnivores and carnivores (Group II); and crustacean feeders (Group III). We grouped the fishes at the St. Marks *H. wrightii* ecosystem into four trophic guilds (Fig. 4): the benthic-meiofauna feeders (trophic group 1 in our analysis of the subset of fish consumers), the benthic-macroinvertebrate consumers (trophic groups 2 and 3), omnivorous fishes, and fish consumers (trophic groups 4 and 5). Our trophic group 1 included the zooplankton-feeding bay anchovy and meiofauna-consuming stages of spot, pinfish, blackcheek tonguefish, and tidewater silversides. This group appears to correspond to Livingston's Group I, which included small stages of pinfish (< 25 mm SL), spot, and bay anchovy (Livingston 1982). Bay anchovies were the most dissimilar of the fishes in our trophic group 1, having factor scores similar to the zooplankton food sources (WCAL) and plotting in the small prey size region of the scatterplot (low on factor 2). Large stages of pinfish (> 26 mm SL) were included in Livingston's Group II, but these stages of pinfish were not collected in our samples. Early life stages of pinfish collected in winter do not consume as much plant material as the older stages that occur in the summer (Stoner 1980; Luczkovich et al. 1995). Our trophic group 1 and Livingston's Group I are similar in that they include species that feed on small prey, whether they are in the zooplankton or part of the benthic meiofauna. Our trophic groups 2 and 3 (benthic macroinvertebrate consumers) included gulf pipefish, southern hake, searobins, and small gulf flounder. This group may be analogous to Livingston's crustacean feeders (Group III), which also included gulf pipefish. Our trophic group 4 (the piscivores) included gulf flounder, Atlantic needlefish, and large red drum. There was no piscivore group in Livingston's analyses, although he did report collecting southern flounder (*Paralichthys lethostigma*), he did not examine their diet. Our trophic group 5 included hardhead catfish, which consumed seagrasses, benthic invertebrates, and fishes; these omnivores had factor scores that were similar to the picivores in our analysis. Livingston's benthic omnivores and carnivores (Group II) included hardhead catfish. Our omnivorous fish trophic group included long-

nose killifish and sheepshead minnows, which were not collected by Livingston (1982).

In general, our trophic groupings bear some resemblence to those reported in Livingston (1982), but many of fish species do not occur in both analyses. Livingston's groups were developed using dietary data for an entire year, whereas ours was based solely on data obtained during the winter. Such seasonal differences may account for the varying species and trophic groupings observed in both studies.

Based on these trophic groupings and on a long-term database of fish, benthos, and zooplankton abundances, Livingston (1984) presented a conceptual model of the seasonally varying trophic structure of the Apalachee Bay seagrass ecosystem in the northeastern Gulf of Mexico. Although Livingston (1984) did not use a statistical method to develop trophic groupings for the invertebrates, he did list detritus-consuming amphipods and polychaetes as being abundant in winter (January and February). Our analysis, which was developed for that season, showed that the detritus-consuming amphipods and polychaetes were the dominant trophic guild as well. This detritus-based pathway of carbon flow from amphipods and polychaetes to higher trophic levels appears to be quantitatively important during the winter (Baird et al. 1998; Christian and Luczkovich 1999), which confirms Livingston's (1984) conceptual model. Benthic algae-consumers (herbivorous gastropods, herbivorous crustaceans, omnivorous fishes, omnivorous crabs, and detritivorous polychaetes) also form a prominent guild within the St. Marks seagrass ecosystem during winter (Christian and Luczkovich 1999). Their importance in the carbon flow is not as large as detritivores in the winter months, but may be greater in the summer months, when direct seagrass herbivory is a common occurrence (Leber 1983; Greenway 1995). Although suspension-feeding copepods and zooplankton were included in Livingston's model (1984) as an important food source for some fish species during winter, we did not observe high carbon flow through this pathway (Christian and Luczkovich 1999). Bivalves and gastropods were not included in Livingston's (1984) model, but our guild analysis and network models included such molluscan predators and prey; they derived significant amounts of carbon from detritus and carrion.

Our quantitative network models and the trophic guilds reported here represent the most complete description of the food web interactions for producers and consumers in a *H. wrightii* ecosystem, but is limited in scope to the winter months. Our models do not fully represent the food web interactions described by Livingston (1984) for the fishes in seagrass habitats during other seasons, and network models of the spring, summer, and autumn should be done in the future.

Conclusions

We have addressed the common questions that arise when developing a food web network model: Should aggregation of taxa be attempted or held at the level of species; If aggregation is desired, what methods should be used to aggregate taxa; and How does one address the problem of aggregation of taxa already published in the literature? Although the choice of entities to use as nodes in a network model is left open to each investigator, for the foreseeable future, most models will use trophic guilds as network nodes, particularly when high taxonomic resolution within the web is not possible. As dietary and physiological databases become more developed, network models with nodes at the level of species (or ontogenetic stage within species) can be developed. The method we presented for establishing trophic guilds used cluster analysis of a rectangular diet matrix to group consumer taxa on the basis of diet similarity; followed by correspondence analysis to visualize the trophic groups identified in the cluster analysis to obtain trophic guilds. Such dual-mode ordination methods are demanded because of the rectangular (unequal number of rows and columns) matrix of feeding relations, which is caused by the pre-aggregation of prey taxa in most published dietary studies. The degree to which taxa should be grouped in the guilds will depend on the goals of the investigators. Some users of network models (coastal, fishery, and wildlife managers) will desire species-specific output for higher consumers (red drum and gulf flounder), requiring that those taxa can be kept ungrouped. Other taxa are less frequently the focus of such trophic models (polychaetes), and can be usefully assigned to trophic guilds by the methods described here.

The methods we used in modeling this food web included direct diet determination for highly variable taxa such as the commonly occurring fishes, literature-derived trophic links for less common fishes and the benthic invertebrates, and a combination of cluster analysis and correspondence analysis for developing the trophic guild structure. We aggregated the community of interacting species using a descriptive statistical approach into a manageable number of trophically similar ecosystem compartments for modeling. Because the binary diet matrix was established both from the published literature and direct sampling of diets, the resultant general, steady-state, multi-compartment carbon-flow models (Baird et al. 1998, Christian and Luczkovich 1999) should be applicable to

other *H. wrightii* seagrass ecosystems during winter. Caution should be used when applying our trophic guild structure and network models without verification to other seagrass ecosystems in other locations and in other seasons. The general approach we have outlined, with new trophic link data collected specific to the area and time of interest, should be widely applicable.

Acknowledgments

This research was supported by the U.S. Department of the Interior, Fish and Wildlife Service Contract Number 14-48-0009-93-972 and the Department of Biology at East Carolina University. We especially acknowledge the contribution of Bob Ulanowicz of the Chesapeake Biological Laboratory, who was invaluable as a source of ideas and suggestions for improvement of the manuscript. We gratefully acknowledge the help of the following students and colleagues who have helped in various aspects of field sampling and laboratory analysis of the data: Lori Beavers, Patrick Bishop, Giuseppe Castadelli, David Christian, Susan Dailey, Deborah Daniel, Karl Faser, Matt Ferguson, Andrew Fletcher, Karen Halliday, Brian Harris, Jennifer Holmes, Stephen Johnson, Martha Jones, Kris Lewis, Ed Moss, and Chris Pullinger.

Literature Cited

Ahl, A. H. L. and T. F. H. Allen. 1996. Hierarchy Theory. Columbia University Press, New York.

Baird, D., J. J. Luczkovich, and R. R. Christian. 1998. Assessment of spatial and temporal variability in ecosystem attributes of the St. Marks National Wildlife Refuge, Apalachee Bay, Florida. *Estuarine, Coastal and Shelf Science* 47:329–349.

Baird, D., J. M. McGlade, and R. E. Ulanowicz. 1991. The comparative ecology of six marine ecosystems. *Philosophical Transactions of the Royal Society of London B* 333:15–29.

Baird, D. and R. E. Ulanowicz. 1989. The seasonal dynamics of the Chesapeake Bay ecosystem. *Ecolological Monographs* 59: 329–364.

Borgatti, S. P., M. G. Everett, and L. C. Freeman. 1999. UCINET 5 for Windows: Software for Social Network Analysis. Analytic Technologies, Natick, Massachusetts.

Bousefield, E. L. 1973. Shallow-water Gammaridean Amphipoda of New England. Comstock Publishing Associates, Cornell University Press, Ithaca, New York.

Briand, F. and J. E. Cohen. 1984. Community food webs have scale-invariant structure. *Nature* 307:264–266.

Camp, D. K., W. G. Lyons, and T. H. Perkins. 1998. Checklist of selected shallow-water marine invertebrates of Florida. Florida Marine Research Institute Technical Report TR-3. Florida Department of Environmental Protection, St. Petersburg, Florida.

Carr, W. E. S. and C. A. Adams. 1972. Food habits of juvenile marine fishes: Evidence of cleaning habit in the leatherjacket, *Oligoplites saurus* and the spottail pinfish, *Diplodus holbrooki. Fishery Bulletin, U.S.* 70:1111–1120.

Carr, W. E. S. and C. A. Adams. 1973. Food habits of juvenile marine fishes occupying seagrass beds in the estuarine zone near Crystal River, Florida. *Transactions of the American Fisheries Society* 102:511–540.

Chester, C. M. 1993. Comparative feeding biology of *Acteocina canniculata* and *Haminoea solitaria* (Say, 1822) (Opistobranchia: Cephalaspidea). *American Malacological Bulletin* 10:93–101.

Christensen, V. and D. Pauly. 1992. ECOPATH II—A software for balancing steady-state ecosystem models and calculating network characteristics. *Ecological Modelling* 61:169–185.

Christensen, V. and D. Pauly (eds.). 1993. Trophic models of aquatic ecosystems. International Center for Living Aquatic Resources Management, Conference Proceedings Number 26. Manilla, Philipines.

Christian, R. R. and J. J. Luczkovich. 1999. Organizing and understanding a winter's seagrass foodweb network through effective trophic levels. *Ecological Modelling* 17:99–124.

Cohen, J. E., R. Beaver, S. Cousins, D. DeAngelis, L. Goldwasser, K. Heong, R. Holt, A. Kohn, J. Lawton, N. Martinez, R. O'Malley, L. Page, B. Patten, S. Pimm, G. Polis, M. Rejmanek, T. Schoener, K. Schoenly, W. G. Sprules, J. Teal, R. Ulanowicz, P. Warren, H. Wilbur, and P. Yodzis. 1993. Improving food webs. *Ecology* 74:252–258.

Dame, R. F. 1996. Ecology of Marine Bivalves: An Ecosystem Approach. CRC Press, Boca Raton, Florida.

Dillon, W. R. and M. Goldstein. 1984. Multivariate Analysis: Methods and Applications. John Wiley and Sons, New York.

Duffy, J. E. and M. E. Hay. 1991. Food and shelter as determinants of food choice by an herbivorous marine amphipod. *Ecology* 72:1286–1298.

Fauchauld, K. 1977. The polychaete worms: Definitions and keys to orders, families and genera. *Natural History Museum of Los Angeles County, Science Series* 28:1–190.

Fauchauld, K. and P. A. Jumars. 1979. The diet of worms. A study of polychaete feeding guilds. *Oceanography and Marine Biology Annual Review* 17:193–284.

Fox, R. S. and K. H. Bynum. 1975. The amphipod crustaceans of North Carolina estuarine waters. *Chesapeake Science* 16:223–237.

Fox, R. S. and E. E. Rupert. 1985. Shallow-water marine benthic macroinvertebrates of South Carolina. University of South Carolina Press, Columbia, South Carolina.

Gaston, G. R. 1987. Benthic polychaeta of the Middle Atlantic Bight: Feeding and distribution. *Marine Ecology Progress Series* 36:251–262.

Gaston, G. R., D. L. Lee, and J. C. Nasci. 1988. Estuarine macrobenthos in Calcasieu Lake, Louisiana: Community and trophic structure. *Estuaries* 11:192–200.

Gaston, G. R., J. A. Mclelland, and R. W. Heard. 1992. Feeding biology, distribution, and ecology of two species of benthic polychaetes: *Paraonis fulgens* and *Paraonis pygoenigmatica* (Polychaeta: Paraonidae). *Gulf Research Reports* 8:395–399.

Gaston, G. R. and J. C. Nasci. 1988. Trophic structure of macrobenthic communities in the Calcasieu estuary, Lousiana. *Estuaries* 11:201–211.

Gauch, H. G. and R. H.Whittaker. 1981. Heirarchical classification of community data. *Journal of Ecology* 69:537–557.

Gilliam, D. and K. M. Sullivan. 1993. Diet and feeding habits of the southern stingray *Dasyatis americana* in the central Bahamas. *Bulletin of Marine Science* 52:1007–1013.

Gittins, R. 1985. Canonical Analysis: A Review with Applications in Ecology. Springer-Verlag, Berlin, Germany.

Goldwasser, L. and J. Roughgarden. 1997. Sampling effects and the estimation of food web properties. *Ecology* 78:41–54.

Gosner, K. L. 1971. Guide to Identification of Marine and Estuarine Invertebrates. Wiley-Interscience, New York.

Greenacre, M. J. 1984. Theory and Applications of Correspondence Analysis. Academic Press, London, U.K.

Greenway, M. 1995. Trophic relationships of macrofauna within a Jamaican seagrass meadow and the role of the echinoid *Lytechinus variegatus* (Lamarck). *Bulletin of Marine Science* 56: 719–736.

Grossman, G. D. 1986. Food resource partitioning in a rocky intertidal fish assemblage. *Journal of Zoology, London (B)* 1:317–355.

Hazlett, B. A. 1981. The behavioral ecology of hermit crabs. *Annual Review of Ecology and Sytematics* 12:1–22.

Heymans, J. J. and D. Baird. 2000. Network analysis of the

Northern Benguela ecosystem by means of NETWRK and ECOPATH. *Ecological Modelling* 131:97–119.

Hicks, G. R. F. and B. C. Coull. 1983. The ecology of marine meiobenthic harpacticoid copepods. *Oceanography and Marine Biology: An Annual Review* 21:67–175.

Hughes, R. N. 1986. A Functional Biology of Marine Gastropods. The Johns Hopkins University Press, Baltimore, Maryland.

Huh, S.-H. and C. L. Kitting. 1985. Trophic relationships among concentrated populations of small fishes in seagrass meadows. *Journal of Experimental Marine Biology and Ecology* 92: 29–43.

Johnson, J. C., S. P. Borgatti, J. J. Luczkovich, and M. G. Everett. 2001. Network role analysis in the study of food webs: An application of regular role coloration. *Journal of Social Structure* Volume 2, May 8, 2001. This journal is published on-line only at: http://www.heinz.cmu.edu/project/INSNA/joss/index1.html.

Kay, J. J., L. A. Graham, and R. E. Ulanowicz. 1989. A detailed guide to network analysis, p. 15–61. *In* F. Wulff, J. G. Field, and K. H. Mann (eds.). Network Analysis in Marine Ecology: Methods and Applications, Coastal and Estuarine Studies. Springer-Verlag, Berlin, Germany.

Kohn, A. J. 1983. Feeding biology of gastropods, p. 1–63. *In* A. S. M. Saleuddin and K. M. Wilbur (eds.). The Mollusca, Volume 5, Physiology, Part 2. Academic Press, New York.

Leber, K. M. 1983. Feeding ecology of decapod crustaceans and the influence of vegetation on foraging success in a subtropical seagrass meadow. Ph.D. dissertation, Florida State University, Tallahassee, Florida.

Lewis, F. G. and A. W. Stoner. 1981. An examination of methods for sampling macrobenthos in seagrass meadows. *Bulletin of Marine Science* 31:116–124.

Livingston, R. J. 1980. Ontogenetic trophic relationships and stress in a coastal seagrass system in Florida, p. 423–435. *In* V. S. Kennedy (ed.). Estuarine Perspectives. Academic Press, New York.

Livingston, R. J. 1982. Trophic organization of fishes in a coastal seagrass system. *Marine Ecology Progress Series* 7:1–12.

Livingston, R. J. 1984. Trophic response of fishes to habitat variability in coastal seagrass systems. *Ecology* 65:1258–1275.

Livingston, R. J. 1988. Inadequacy of species-level designations for ecological studies of coastal migratory fishes. *Environmental Biology of Fishes* 22:225–234.

Lopez, G. R. and J. S. Levinton. 1987. Ecology of deposit-feeding animals in marine sediments. *Quarterly Review of Biology* 62:235–260.

Lourie, S. A., A. C. J. Vincent, and H. J. Hall. 1999. Seahorses: An Identification Guide to the World's Species and their Conservation. Project Seahorse, London, U.K.

Luczkovich, J. J. 1987. The patterns and mechanisms of selective feeding on seagrass-meadow epifauna by juvenile pinfish, *Lagodon rhomboides* (Linnaeus). Ph.D. Dissertation, Florida State University, Tallahassee, Florida.

Luczkovich, J. J., S. P. Borgatti, J. C. Johnson, and M. G. Everett. In press. Defining and measuring trophic role similarity in food webs using regular equivalence. *Journal of Theoretical Biology.*

Luczkovich, J. J., S. F. Norton, and R. G. Gilmore, Jr. 1995. The influence of oral anatomy on prey selection during the ontogeny of two percoid fishes, *Lagodon rhomboides* and *Centropomus undecimalis. Environmental Biology of Fishes* 44:79–95.

Luczkovich, J. J. and E. J. Stellwag. 1993. Isolation of cellulolytic microbes from the intestinal tract of the pinfish, *Lagodon rhomboides*: Size-related changes in diet and microbial abundance. *Marine Biology* 116:381–388.

Meyers, A. A. 1981. Amphipod crustacea; I. Familly Aoridae, p. 1–75. *In* Memoirs of the Hourglass Cruises, Volume V, part V. Florida Department of Natural Resources, Marine Research Laboratory, St. Petersburg, Florida.

Mills, E. L. 1967. The biology of an ampeliscid amphipod crustacean sibling species pair. *Journal of the Fisheries Research Board of Canada* 24:305–355.

Monaco, M. E. and R. E. Ulanowicz. 1997. Comparative ecosystem trophic structure of three U.S. mid-Atlantic estuaries. *Marine Ecology Progress Series* 161:239–254.

Morris, P. A. 1975. A field Guide to Shells Atlantic and Gulf Coasts and the West Indies. Houghton Mifflin Company, Boston, Massachusetts.

Motta, P. J., K. B. Clifton, P. Hernandez, B. T. Eggold, S. D. Giordano, and R. Wilcox. 1995. Feeding relationships among nine species of seagrass fishes of Tampa bay, Florida. *Bulletin of Marine Science* 56:185–200.

Paine, R. T. 1963. Trophic relationships of 8 sympatric predatory gastropods. *Ecology* 44:63–73.

Persson, L., J. Bengtsson, B. A. Menge, and M. E. Power. 1996. Productivity and consumer regulation—Concepts, patterns, and mechanisms, p. 396–434. *In* G. A. Polis and K. O. Winemiller (eds.). Food Webs: Integration of Pattern and Dynamics. Chapman and Hall, New York.

Peters, K. M. and R. H. McMichael. 1987. Early life history of the red drum, *Sciaenops ocellatus* (Pisces: Sciaenidae), in Tampa Bay, Florida. *Estuaries* 10:92–107.

Peterson, C. H. 1982. The importance of predation and intra- and interspecific competition in the population biology of two infaunal suspension-feeding bivalves, *Protothaca staminea* and *Chione undatella. Ecological Monographs* 52:437–475.

Polis, G. A. and K. O. Winemiller (eds.). 1996. Food Webs: Integration of Pattern and Dynamics. Chapman and Hall, New York.

Reid, G. K. 1954. An ecological study of the Gulf of Mexico fishes in the vicinity of Cedar Key, Florida. *Bulletin of Marine Science* 4:1–94.

Richards, S. W., J. M. Mann, and J. A. Walker. 1979. Comparison of spawning seasons, age, growth rates, and food of two sympatric species of searobins, *Prionotus carolinus* and *Prionotus evolans,* from Long Island Sound. *Estuaries* 2:255–268.

Robbins, C. R. and G. C. Ray. 1986. A Field Guide to Atlantic Coast Fishes. Houghton Mifflin Company, Boston, Massachusetts.

Root, R. B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: The fauna of collards (*Brassica oleracea*). *Ecological Monographs* 43:95–124.

Scholz, D. S., L. L. Matthews, and R. J. Feller. 1991. Detecting selective digestion of meiobenthic prey by juvenile spot *Leiostomus xanthurus* (Pisces) using immunoassays. *Marine Ecology Progress Series* 72:59–67.

Schultz, G. A. 1969. How to Know the Marine Isopod Crustaceans. William C. Brown Co., Dubuque, Iowa.

Seifried, S. and J. Durbaum. 2000. First clear case of carnivory in marine Copepoda Harpacticoida. *Journal of Natural History* 34:1595–1618.

Sheridan, P. F. 1978. Food habits of the bay anchovy, *Anchoa mitchelli,* in Apalachicola Bay, Florida. *Northeast Gulf Science* 2: 126–132.

Sheridan, P. F. 1979. Trophic resource utilization by three species of sciaenid fishes in a northwest Florida estuary. *Northeast Gulf Science* 3:1–15.

Smith, D. L. 1977. A Guide to Marine Coastal Plankton and Marine Invertebrate Larvae. Kendall/Hunt Publishing Company, Dubuque, Iowa.

Snelson, Jr., F. F. and S. E. Williams. 1981. Notes on the occurrence, distribution, and biology of elasmobranch fishes in the Indian River Lagoon system, Florida. *Estuaries* 4:110–120.

Stoner, A. W. 1980. Feeding ecology of *Lagodon rhomboides* (Pisces: Sparidae): Variation and functional responses. *Fishery Bulletin* 78:337–353.

THAYER, G. W., P. L. PARKER, M. W. LACROIX, AND B. FRY. 1978. The stable isotope ratio of the components of an eelgrass, *Zostera marina,* bed. *Oecologia* 35:1–12.

TOPP, R. W. AND F. H. HOFF, JR. 1972. Flatfishes (Pleuronectiformes). *Memoirs of the Hourglass Cruises* Volume 4, Part II. Marine Research Laboratory, Florida Department of Natural Resources, St. Petersburg, Florida.

TURNER, J. T. 1984. Zooplankton feeding ecology: Contents of fecal pellets of the copepods *Acartia tonsa* and *Labidocera aestiva* from continental shelf waters near the mouth of the Mississippi River. *PSZNI: Marine Ecology* 5:265–282.

TURNER, J. T. AND J. C. ROFF. 1993. Trophic levels and trophospecies in marine plankton: Lessons from the microbial food web. *Marine Microbial Food Webs* 7:225–248.

UBELACKER, J. M. AND P. G. JOHNSON (EDS.). 1984. Taxonomic guide to the polychaetes of the Northern Gulf of Mexico. Final Report to the Minerals Managment Service, contract 14-12-001-29091. Barry A. Vittor and Associates, Inc., Mobile, Alabama.

ULANOWICZ, R. E. 1987. NETWRK 4: A package of computer algorithms to analyze ecological flow networks. University of Maryland Chesapeake Biological Laboratory, Solomons, Maryland.

VENIER, J. M. 1997. Seasonal ecosystem models of the Looe Key NMS, FL. Masters Thesis, University of British Columbia, Vancouver, Canada.

WILLIAMS, A. B. 1984. Shrimps, lobsters, and crabs of the Atlantic Coast of the Eastern United States, Maine to Florida. Smithsonian Institution Press, Washington, D.C.

YODZIS, P. 1989. Introduction to Theoretical Ecology. Harper and Row, New York.

YODZIS, P. 1996. Food webs and perturbation experiments: Theory and practice, p. 192–200. *In* G. A. Polis and K. O. Winemiller (eds.). Food Webs: Integration of Pattern and Dynamics. Chapman and Hall, New York.

YODZIS, P. AND K. O. WINEMILLER. 1999. In search of operational trophospecies in a tropical aquatic food web. *Oikos* 87:327–340.

ZIMMERMAN, R. 1978. The feeding habits and trophic position of dominant gammaridean amphipods in a Caribbean seagrass community. Ph.D. Dissertation, University of Puerto Rico, Mayaguez.

ZIMMERMAN, R., R. GIBSON, AND J. HARRINGTON. 1979. Herbivory and detritivory among gammaridean amphipods from a Florida seagrass community. *Marine Biology* 54:41–47.

SOURCES OF UNPUBLISHED MATERIALS

KOENIG, C. Personal Communication. National Marine Fisheries Service Laboratory, Panama City Laboratory, 3500 Delwood Beach Road, Panama City, Florida 32408.

LEVINE, S. J. 1980. Gut contents of forty-four Lake Ponchartrain, Louisiana, fish species, p. 899–1030. *In* J. H. Stone (ed.). Environmental Analysis of Lake Ponchartrain, Louisiana, Its Surrounding Wetlands, and Selected Land Uses. Volume II. Center for Wetland Resources, Louisiana State University, Baton Rouge, Louisiana.

Received for consideration, February 10, 2000
Accepted for publication, May 21, 2002