

Seasonal Variation in Food Web Composition and Structure in a Temperate Tidal Estuary

S. AKIN† and K. O. WINEMILLER*

Section of Ecology, Evolutionary Biology and Systematics, Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, Texas 77843-2258

ABSTRACT: Seasonal variation in aquatic food web structure at Mad Island Marsh, Matagorda Bay, Texas, was examined using dietary information obtained from the analysis of gut contents from large samples of fish and crustacean specimens. Unique aspects of this study include the use of large samples of consumer gut contents ($n = 6,452$), long-term sampling (bimonthly surveys over 18 mo), and standard methods of data collection and analysis facilitating comparisons with other aquatic food webs. Dietary data were partitioned for analysis into warm (summer) and cold (winter) seasons. Most consumers fed low in the food web, with trophic levels ranging from about 2 to 3.5 during both summer and winter. Vegetative detritus was more important in macroconsumer diets than live algae and macrophytes. Low trophic levels of consumers reflected the important role of abundant detritivores (e.g., striped mullet *Mugil cephalus*, Gulf menhaden *Brevortia patronum*, and macroinvertebrates) in linking detritus to top predators via short food chains, a finding consistent with many other estuarine food web studies. Despite changes in community composition and population size structure of certain species, most food web properties revealed comparatively little seasonal variation. The summer food web had more nodes (86), more links (562), a higher density of links as indicated by connectance (0.08), and a slightly higher predator:prey ratio (0.51) compared to the winter food web (75 nodes, 394 links, connectance = 0.07, predator:prey ratio = 0.47). Proportions of top (0.06–0.07), intermediate (0.75–0.76), and basal (0.19) species did not vary significantly between seasons, but mean trophic level was higher during summer. Addition of feeding links based on information from the literature increased connectance to 0.13 during both seasons; other web parameters had values similar to those obtained for our directly estimated food webs. Seasonal variation in food web structure was influenced by changes in community composition (e.g., influxes of postlarval estuarine-dependent marine fishes during winter), availability of resources (e.g., more submerged macrophytes and amphipods during summer), and size structure and ontogenetic diet shifts of dominant consumer taxa. Our findings suggest that some basic properties of estuarine food web are resilient to seasonal changes in population and community structures and food web architecture.

Introduction

The concept of the food web, a summary of resource-consumer interactions in a community, enhances understanding of ecosystem structure and population dynamics (Pimm et al. 1991; Winemiller and Polis 1996; de Ruiter et al. 2005; Winemiller and Layman 2005). Motivated in part by May's theoretical research (1973) on the relationship between community diversity and stability (see also McCann 2000), a main theme of food web studies has been empirical descriptions of different ecosystems in pursuit of general patterns or rules (Schoener 1989; Cohen et al. 1993). Analysis of collections of published food webs (e.g., Cohen 1978; Pimm 1982; Briand 1983; Sugihara et al. 1989; Cohen et al. 1990) indicated that structure is nonrandom, possibly due to biological processes, such as predator-prey dynamics or energetic and morphological constraints. These food webs tend to

have short food chains (Pimm 1982; Cohen et al. 1986; Briand and Cohen 1987), constant fractions of top, intermediate, and basal species (Briand and Cohen 1984; Sugihara et al. 1989; Cohen et al. 1990), an inverse relationship between web connectance and number of species (Briand and Cohen 1984; Lawton 1989), infrequent omnivory (Pimm 1982; Pimm and Kitching 1987), and a constant predator : prey ratio (Briand and Cohen 1984; Jeffries and Lawton 1985).

These early food web studies stimulated new areas of research, but the data from which generalizations were derived have been strongly criticized (Paine 1988; Winemiller 1990; Polis 1991; Hall and Raffaelli 1993; Yodzis 1993). Many of these generalizations were artifacts due to taxonomic incompleteness, inappropriate or inconsistent scales of resolution, and other sources of bias. Recent years have seen greater efforts to obtain better food web descriptions based on data with higher resolution and encompassing temporal and spatial variations. Analyses of these higher quality food webs have rejected many of the generalizations derived from early food web compilations (Winemiller 1989; Hall

† Current address: Faculty of Agriculture, Department of Fisheries, Gaziosmanpasa University, 60240 Tokat, Turkey.

* Corresponding author; tele: 979/862-4020; fax 979/845-4096; e-mail: k-winemiller@tamu.edu

and Raffaelli 1991; Martinez 1991; Closs et al. 1993; Thompson and Townsend 2005). Leaving aside other shortcomings (lack of standard methods to obtain abundance and diet data, aggregation of species), the early food webs did not take into account temporal and spatial variations in community structure and predator-prey interactions. Most ecological communities occur within fluctuating environments where primary production sources and the abundance, size structure, and trophic interactions of populations vary accordingly (Wine-miller 1990; Polis et al. 1996). Aquatic animals change their diets in association with ontogeny and seasonal dynamics of prey availability (Werner and Gilliam 1984). Many food web comparisons were based on snapshots of the community and failed to reveal variation over time and space.

A recent challenge in food web studies is to understand the effects of seasonal environmental change on food web properties. In temperate estuarine ecosystems, the composition and diversity of biota undergo strong interannual and seasonal changes due to behavioral and demographic responses to changes in temperature, salinity, and other environmental factors (Akin et al. 2003; Garcia et al. 2003). Seasonal influxes of estuarine-dependent marine fishes and shrimp alter community structure and the potential number of feeding interactions. Warmer temperatures during summer should increase metabolism and rates of feeding by ectotherms. These factors might be expected to increase the density of feeding interactions in the food web. The large detrital pool normally associated with estuarine systems could influence trophic dynamics and increase stability of food web components (DeAngelis 1992). To our knowledge, no estuarine study has directly investigated seasonal variation on food web structure and properties. Our study examines seasonal variation in feeding interactions estimated from gut content analyses of large samples from an estuarine fish and macroinvertebrate community on the Texas Gulf coast. Seasonal effects on the food web were determined by analyzing differences in web structure based on monthly data aggregated as two periods, winter and summer. A second objective was to determine major sources of primary production that support the food web during each season. A third objective was to compare characteristics of the Mad Island Marsh web with those of other webs reported in the literature.

Materials and Methods

STUDY AREA

The study was conducted on Mad Island Marsh Preserve (MIM) located on the northwestern coast

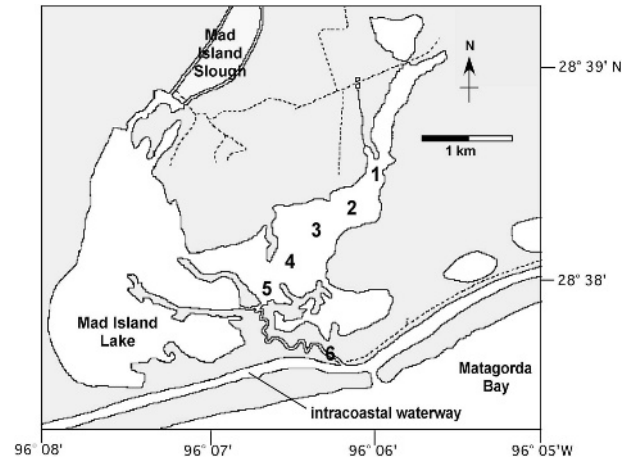


Fig. 1. Map of estuary at Mad Island Marsh Preserve on the Texas Gulf of Mexico coast showing locations of the survey sites.

of the Gulf of Mexico, in Matagorda Bay, Texas (Fig. 1). Samples for stomach contents analysis were taken from six sites located along a longitudinal estuarine gradient. Aquatic habitats in MIM span physiochemical gradients from freshwater in Mad Island Slough and diked wetlands, to an oligohaline-mesohaline lake and salt marsh, to a polyhaline tidal bayou. The area is managed by the Nature Conservancy of Texas, which has a restoration program that conducts controlled burns and augments freshwater inflow to restore and enhance marsh habitat. Dominant vegetation of the marsh includes saltwater cordgrass (*Spartina alterniflora*) and gulf cordgrass (*Spartina spartinae*). Submerged aquatic vegetation, such as widgeon grass (*Ruppia maritima*) and skunkweed (*Chara* sp.), occurs seasonally with widgeon grass especially dominant at upper estuarine sites. Percent coverage of aquatic vegetation ranged from 0% to 90% and is highest in upper estuarine reaches during late spring through early fall (Akin et al. 2003). Water depth in the estuary ranged from 0.14 to 0.74 m. In most of the estuary and fringing marsh, substrate consisted of a dense mud-sand mixture, covered by an approximately 5-cm layer of decomposing vegetation. Substrate near the intracoastal waterway consisted of mud, sand, and crushed oyster shell. Water temperature ranged annually from 16.5°C to 37.2°C, range of salinities was 3.5–29.4‰ with higher values generally recorded from locations closer to the bay, and dissolved oxygen concentration varied from 2.66 to 13.9 mg l⁻¹. The measurements were taken every other month for 18 mo from multiple locations at the site. Recorded environmental values were intended to reflect conditions during the period of sampling and reveal seasonal rather than diel variation (more

detailed descriptions of environmental conditions throughout the study period appear in Akin et al. 2003). Diurnal tidal flux at the site is low (0.1–0.25 m, with 0.5 m infrequently), and the largest variation in water depth is associated with local precipitation (Gelwick et al. 2001).

FIELD SAMPLING

Every 2 mo for 18 mo, a metal drop sampler was used to quantify the density of benthic macroinvertebrates, as well as the density of macrophytes enclosed within an area of 0.09 m². During each survey, two samples were taken at each of five sites spaced approximately evenly along the longitudinal gradient of the estuary. The sampler was 1.0 m high, had no bottom, and was dropped by hand over an undisturbed area. All material inside the sampler (organisms, vegetation, and sediment to a depth of 10 cm) was collected by sweeping the water column and surface of the substrate with a fine-mesh dip net. Samples were then placed into 50-l plastic bags and preserved with 10% formalin. Entire sediment samples were sieved through a 0.25-mm mesh in the laboratory. Macrophyte fragments were identified and weighed, and invertebrates were sorted, identified to higher taxonomic/functional groups (in most cases a coarse resolution was employed to match that which was feasible for specimens obtained during stomach contents analysis), and counted.

Samples of fish and macroinvertebrate were taken every 2 mo between March 1998 and August 1999 along the longitudinal estuarine gradient (Fig. 1). Fishes and macroinvertebrates were captured using a bag seine (6 × 1.2 m, 4.5 mm mesh, bag 1.2 × 1.2 m) and experimental gill nets (38 m, 5 panels consisted of 25, 38, 50, 64, and 76 mm mesh). Number of hauls and distances seined were recorded in order to estimate relative abundance as catch per unit effort of fish and macroinvertebrate taxa (additional details of collecting methods appear in Akin et al. 2003). The duration of each gill net set was recorded, and relative abundance was estimated as number of individuals captured per hour. Captured fish and invertebrates were anesthetized in MS-222 then fixed in a 10% formalin solution in the field. For each sample, fish were sorted, identified to species, measured (standard length to nearest 0.1 mm), weighed (to nearest 0.1 g), and counted in the laboratory.

Prior to seining each site, water depth was measured with a tape measure, and temperature, dissolved oxygen, and salinity were measured with a Hydrolab Datasonde or YSI 85. Aquatic macrophyte abundance was estimated visually at each site as the approximate percentage of a 100-m² area with macrophyte coverage (widgeon grass stands extend-

ing near or to the surface) when viewed from above the water surface.

STOMACH CONTENTS ANALYSIS

Stomach contents analysis was performed to document food web structure at MIM using methods described in Winemiller (1990). Whenever possible at least 30 specimens of each fish species and 3–5 specimens of each macroinvertebrate species (e.g., shrimp and crabs) from each site during each month were dissected for analysis. When a sample contained >30 specimens, individuals were selected for dissection so that size classes were represented in proportions approximating those in the field sample. All available specimens of piscivores were dissected for stomach contents. All food items were removed from the anterior half of the gut and examined under a dissecting microscope or compound microscope depending on the size of the prey.

Most food items recovered from stomachs were recorded as fairly broad functional and taxonomic categories (Akin and Winemiller unpublished data), and this was largely due to limited capabilities to identify fragmented or partially digested items with finer taxonomic resolution. Taxonomic aggregation of invertebrate prey and plants (algae) reduced estimates of species richness and feeding links within lower levels of the food web. The level of scale and resolution for these food web components are quite similar to those employed by previous studies with which results are compared. Small invertebrate prey, such as microcrustacea and insects, were classified to taxonomic order. Fishes and macrocrustacea, such as grass shrimp (*Palaemonetes pugio*), brown shrimp (*Farfantepenaeus aztecus*), white shrimp (*Litopenaeus setiferus*), blue crab (*Callinectes sapidus*) and mud crabs (*Neopenope sayi* and *Eurypanopeus debressus*), were classified to species. Some categories (Akin and Winemiller unpublished data) (e.g., fish parts, unidentified fish) were deleted from the food web analyses that involved taxonomic nodes. For larger prey items (>0.1 ml), the entire prey item was blotted dry and its volume was measured by water displacement in a graduated cylinder. For volumes <0.1 ml, items were placed on a glass slide and visually estimated by comparing its size with a water droplet of known volume extracted from a graduated pipette.

Detritivores and algivores were handled differently. The entire gut was removed and a small sample of its contents from the foregut was placed on a glass slide for examination under a compound microscope. The volume of the entire gut and its contents was measured by water displacement. The relative proportion (by area) of each identifiable item on the slide was estimated, then multiplied by the

volume of the guts plus contents to yield percent of total gut volume.

FOOD WEB MATRICES

Because some species were abundant only at some of the collection sites, we were not able to examine spatial variation in food web structure. Monthly consumer-resource matrices were constructed by pooling dietary data of each species from all six sites. Seasonal variation in fish and macroinvertebrate assemblage structure is much greater than spatial variation within our study reach (Akin et al. 2003). Based on the seasonal pattern of water temperatures at MIM, we divided the year into the warmer summer (April–September; monthly mean water temperature $>29^{\circ}\text{C}$) and colder winter (October–March; monthly mean temperature $<29^{\circ}\text{C}$) periods. In addition to these two seasonal food webs, an annual food web was created by pooling dietary data from both seasons into a cumulative resource matrix. Only those species with sample sizes having at least 6 specimens with stomachs containing food were included in resource matrices, so these food webs represent interactions among common food web elements. For each consumer species, the reliability of diet estimates was evaluated using yield-effort curves plotted as the cumulative percentage of feeding links in relation to the cumulative number of specimens examined (Cohen et al. 1993). Yield-effort curves for all common species ($n > 100$) and most of the uncommon consumers ($5 < n < 100$) attained or approached an asymptote, indicating that our samples had revealed most of the feeding links.

Four of the fish species included as consumers in our matrix were not documented as prey within any stomachs analyzed during this study, yet they have been reported by other studies to be prey of certain species included in the MIM food web. Instead of considering these potential prey species as top predators (species having no predators), we assigned trophic links (having the minimum observed volumetric proportion for the consumer taxon) based on literature accounts. Information on predators of gizzard shad (*Dorosoma cepedianum*), gulf pipefish (*Syngnathus scovelli*), bluntnose jack (*Hemicaranx amblyrhynchus*), and bay whiff (*Citharichthys spilopterus*) was obtained from Patillo et al. (1997). The seasonal and annual food webs comprised of field-estimated trophic links leading to fish and macroinvertebrate consumers are referred to here as original food webs.

To facilitate comparisons of our results with recently published food webs, we compiled a second version of each of the three food webs that included our dietary data for fishes and macroinvertebrates

(original webs) plus feeding links for the common small invertebrates, such as worms and amphipods, inferred from literature reports (Pennak 1978; Merrit and Cummins 1996). These webs containing crude approximations for diets of small invertebrates are referred to as composite webs. The literature-based feeding links contained within composite webs were kept consistent between seasons.

ANALYSIS OF TROPHIC DATA

Since our aim was to look at the relative amounts of various categories consumed by the entire community each season and annually, we standardized dietary data relative to sampling effort. Fishes and macroinvertebrates were collected using seine and gill nets. Since seine samples yielded more individuals than gill net samples, each species' dietary data were standardized in relation to sampling effort using the following procedure. Since striped mullet (*Mugil cephalus*) were collected effectively by both sampling gears, this species' biomass data were used to derive a crude conversion factor for seine and gill net efforts. These calculations revealed that 100 m of seining effort approximated 0.2 h of gill netting for mullet. For each species, we estimated its overall relative abundance (A_j) based on both seine and gill net captures. Although admittedly crude, this method permits the combination abundance data for both capture methods, each of which has its own bias in terms of vulnerability to capture of certain taxa. The conversion factor only applied to species that were captured by both methods.

The average volume of each prey item consumed by a given predator species (V_{ij}) was calculated by dividing its total volume taken from stomachs (V_{Tij}) by the number of specimens dissected (N_j) then multiplying this ratio by the predator's standardized abundance (A_j) as defined above. In order to determine proportional volumetric consumption of individual food items (p_{ij}), the total volume of each prey category consumed by a given species (V_{Tij}) was divided by the total volume of food consumed by that species (V_{Tj}).

Food resource diversity (Simpson 1949) within the entire food web was calculated using Simpson's diversity index formula:

$$D = \frac{1}{\sum p_i^2}$$

where p_i is the proportion of prey item i consumed by the entire community of fishes and macrocrustacea in a season. Levin's standardized index was used to calculate diet breadth of individual consumer species (Krebs 1999).

Dietary overlap (similarity) was calculated using Pianka's (1973) symmetrical measure of niche overlap:

$$\theta_{jk} = \frac{\sum_{i=1}^n P_{ij}P_{ik}}{\sqrt{\sum_{i=1}^n P_{ij}^2 \sum_{i=1}^n P_{ik}^2}}$$

where θ_{jk} measures niche overlap between species j and k , p_{ij} is the volumetric proportion of resource i used by species j , p_{ik} is the volumetric proportion of resource i used by species k , and n is the total number of resource states. Dietary overlap was calculated based on seasonal matrices from which unidentified prey items and terrestrial insects were removed. Calculations were performed for those samples that had at least 6 stomachs with food. Dietary overlap also was calculated for conspecifics during two different seasons as means to assess seasonal diet shifts of individual species.

Trophic levels of fishes and macrocrustacea were calculated for each season using the formula presented in Adams et al. (1983):

$$T_i = 1.0 + \sum_{j=1}^n T_j(p_{ij})$$

where T_j is the trophic level of prey species j , and p_{ij} is the fraction of the consumed food (volume) of species i consisting of prey species j . Because primary producers were coded as $T_j = 1$, primary consumers (feeding on only plant material) were $T_j = 2.0$, and a consumer eating exactly half plant and half herbivore tissue was $T_j = 2.5$. T_j values for herbivorous species range from 2 to 2.5, those for omnivores ranged from 2.5 to 3.0, those for primary carnivores ranged from 3 to 3.5, and tertiary carnivores had $T_j > 3.5$ (Winemiller 1990; Hall and Raffaelli 1993).

In order to evaluate the importance of prey items and primary production sources for summer and winter communities, two separate seasonal principal components analyses (PCA) were performed on dietary data, from which sand and unidentified items were removed (independent variables), that were summarized for each species (observations). The matrices for PCA were manipulated according to the method reported by de Crespin de Billy et al. (2000).

Seasonal variation in diet breadth and trophic level were tested using analysis of variance. Prior to analysis, all variables were tested for normality (Kolmogorov-Smirnov) and equality of variances (Cochran's test). All variables satisfied both criteria. Statistical tests, including tests of bivariate relation-

ships (Pearson's correlation) and PCA, were performed using MINITAB version 13.1.

FOOD WEB STATISTICS

The number of species in the web (S) was the number of taxonomic species (fishes and macroinvertebrates) plus aggregated trophospecies, such as diatoms and calanoid copepods, that were prey of consumers in original webs. The number of predator-prey interactions (L) was the number of non-zero elements in the community resource matrix. Connectance, a measure of system complexity or the degree to which species interact in the web, was calculated in three ways. Trophic connectance (Warren 1989) is the number of links divided by the number of possible links, defined as $C_T = L/(S(S - 1))$. Lower connectance (Pimm et al. 1991) was defined as $C_L = 2L/(S(S - 1))$. This formula takes into account the fact that $S(S - 1)$ is the correct estimate of possible links only when cannibalism is excluded. Directed connectance (Martinez 1991) was calculated as $C_D = L/S^2$, and takes into account both cannibalism and mutual predation between species.

The number of basal species (autotrophs), intermediate species (taxa that eat other species and are themselves preyed upon), and top species (consumer taxa not fed upon by any of the other species included in the web) were determined and converted to proportions of the total species in the web. The ratio of the number of predator taxa divided by the number of prey taxa (Jefferies and Lawton 1985) was calculated for each web. The incidence of omnivory was estimated as the fraction species with trophic levels between 2.5 and 3.0.

Results

SPECIES ABUNDANCE AND COMPOSITION

A total of 36,773 fishes from 40 species and 19 families was collected with the seine during summer (Akin and Winemiller unpublished data). The two most abundant species, comprising 85% of the total seine samples, were Gulf menhaden (*Brevortia patronus*) (40.7%) and bay anchovy (*Anchoa mitchilli*) (44.2%). Other common species, in order of abundance, were pinfish (*Lagodon rhomboides*), tide-water silverside (*Menidia peninsulae*), striped mullet, and inland silverside (*Menidia beryllina*). A marked decline in the abundance of young Atlantic croaker (*Micropogonias undulatus*) and spot (*Leiostomus xanthurus*), species that recruit into the estuary as postlarvae during late winter, was apparent over the summer months. A total of 32,637 macroinvertebrates representing 8 species was collected with the seine during summer (Akin and Winemiller unpublished data). Of these species, grass shrimp was

the most abundant (85.2%), followed by brown shrimp (11.2%). A total of 12,762 fishes representing 27 species and 14 families was collected in the seine during winter (Akin and Winemiller unpublished data). Gulf menhaden, Atlantic croaker, bay anchovy, and spot comprised 91.4% of individuals in the seine. Seine samples yielded a total of 22,592 macroinvertebrates from 8 species during winter. Grass shrimp and white shrimp comprised more than 98.5% of individuals in seine samples.

A total of 581 individual fishes from 17 species and 10 families was captured in gill nets during summer (Akin and Winemiller unpublished data). An increase in the relative abundance of striped mullet (38.2%) and hardhead catfish (*Arius felis*; 11.2%) and a pronounced decline in the relative abundance of gizzard shad (from 35.8% to 19.45%) were the major differences in summer gill net capture data compared to winter. Winter gill net samples yielded a total of 463 individual fishes from 18 species and 10 families (Akin and Winemiller unpublished data). Striped mullet, gizzard shad, and red drum (*Sciaenops ocellatus*) were the most abundant species during winter. Hardhead catfish, black drum (*Pogonias cromis*), and alligator gar (*Atractosteus spatula*) also were common in winter gill net samples.

A summary of benthic fauna and infauna in sediment core samples appears in Table 1.

Total abundance of benthic organisms varied seasonally, with the summer total almost twice that of winter. Annelid worms, gastropods, chironomid larvae, and mysid shrimp made up more than 85% of the total benthic sample during winter, but during summer amphipods and annelid worms alone made up over 80% of the total sample. Abundances of chironomid larvae and mysid shrimp declined to just 1% and 4% during summer, respectively. Annually, the most abundant benthic taxa were amphipods, annelid worms, and chironomid larvae.

TROPHIC DATA

We dissected a total of 5,865 fish and 587 macroinvertebrate specimens for stomach contents analysis (3,658 fish and 349 invertebrates for summer; 2,207 fish and 238 macroinvertebrates for winter). Based on diets standardized relative to sampling effort for these macroconsumers (seine, gill net), the total volume of food recovered from consumer stomachs during summer was 127 ml compared to only 27 ml during winter. Resource diversity was higher during summer (6.04) than winter (5.77). According to volumetric percentage, detritus was the most important food category (>50% by volume) for macroconsumers during both seasons, with more detritus consumed during

TABLE 1. Estimates of benthic organism densities from core samples.

Species	Summer (# m ²)	Summer (%)	Winter (# m ²)	Winter (%)
Spider	0.00	0.00	0.93	0.08
Mayfly	0.00	0.00	0.93	0.08
Amphipoda	1,051.85	49.89	38.89	3.37
Mysid shrimp	28.70	1.36	150.00	13.02
Bivalvia	21.30	1.01	0.93	0.08
Chironomid larvae	77.78	3.69	201.39	17.48
Other Diptera larvae	2.78	0.13	0.00	0.00
Diptera adult	0.00	0.00	5.56	0.48
Gastropoda	55.56	2.64	293.52	25.47
Isopoda	0.00	0.00	1.39	0.12
Other annelid worm	616.67	29.25	355.56	30.86
Polychaete worm	90.74	4.30	42.59	3.70
<i>Myrophis punctatus</i>	1.85	0.09	0.00	0.00
<i>Eurypanopeus debressus</i>	0.93	0.04	9.26	0.80
<i>Palaemonetes pugio</i>	123.15	5.84	35.19	3.05
<i>Farfantepenaeus aztecus</i>	0.93	0.04	0.00	0.00
<i>Litopenaeus setiferus</i>	0.00	0.00	1.39	0.12
<i>Callinectes sapidus</i>	8.33	0.40	4.63	0.40
<i>Callinectes similis</i>	1.85	0.09	0.00	0.00
<i>Anchoa mitchilli</i>	0.00	0.00	0.93	0.08
<i>Citharichthys spilopterus</i>	0.00	0.00	1.85	0.16
<i>Cyprinodon variegatus</i>	8.33	0.40	0.00	0.00
<i>Gobionellus boleosoma</i>	0.00	0.00	1.39	0.12
<i>Gobiosoma bosc</i>	0.93	0.04	0.93	0.08
<i>Gobiosoma robustum</i>	0.00	0.00	0.93	0.08
Other Gobiidae	1.85	0.09	0.00	0.00
<i>Lagodon rhomboides</i>	1.85	0.09	0.00	0.00
<i>Lucania parva</i>	4.63	0.22	0.00	0.00
<i>Microgobius gulosus</i>	0.00	0.00	0.93	0.08
<i>Paralichthys lethostigma</i>	0.00	0.00	0.93	0.08
Unidentified Sciaenidae	0.00	0.00	0.46	0.04
Unidentified fish	8.33	0.40	1.85	0.16
Total	2,108.33	100.00	1,152.32	100.00
# m ²	488.04		355.65	

summer (Fig. 2). Based on the estimated total volume of material consumed from standardized community samples, consumption of the detritus was almost six times higher during summer than winter. Algae, collectively, were the second most important food resource at MIM, with a greater percentage consumed by the community of macroconsumers during winter (Fig. 2) but a slightly higher absolute volume consumed during summer. The total volume of fishes consumed by the community was almost three times higher during summer than winter. The high volume of consumed fish prey was largely due to fact that several piscivores, such as red drum, alligator gar, southern flounder (*Paralichthys lethostigma*), and spotted sea trout (*Cynoscion nebulosus*), that were more abundant during summer (Akin and Winemiller unpublished data). Spotted sea trout fed heavily on striped mullet during summer (81% of diet by volume) and consume mostly Gulf menhaden (35%) and grass shrimp (27.5%) during winter. Hardhead catfish fed mostly on mollusks

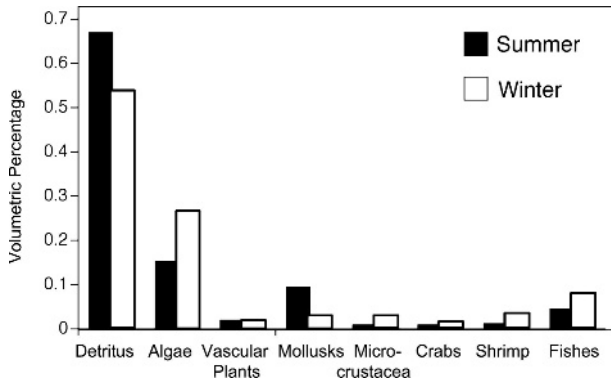


Fig. 2. Percentages of the total standardized volumes of the 8 most important food resources used by the assemblage of consumer taxa at Mad Island Marsh during summer and winter.

(42%) and blue crabs (37%) during summer, and pinfish (42.5%), white shrimp (41.5%), mud crabs (*N. sayi*, 17.5%), and blue crabs (16%) during winter.

Seasonal distributions of diet breadth values are presented in Table 2. Mean diet breadth of both summer (0.12) and winter (0.15) consumers did not differ significantly ($F_{1,31} = 0.91$, $p = 0.35$). Diet breadths of some species revealed strong seasonal variation. Bay anchovy had greater diet breadth in summer than winter. Mean trophic level was not significantly associated with diet breadth during summer ($r = 0.25$, $p = 0.24$) but was marginally significant for winter ($r = 0.38$, $p = 0.049$). Although the mean trophic level for summer (2.76) was higher than winter (2.64), this difference was not statistically significant ($F_{1,31} = 0.95$, $p = 0.33$). Associations between diet breadth and consumer body length (standard length) during both seasons were negative; associations were not significantly different for summer ($r = -0.133$, $p = 0.45$) or winter ($r = -0.099$, $p = 0.62$). In general, diet breadths of juvenile fishes and invertebrates were broader than those of large fishes. Diet breadth of large predatory species (e.g., red drum

TABLE 2. Total number of stomachs examined, diet breadth (B), proportional frequency of occurrence of detritus (Dfreq), and trophic level (TL) of Mad Island Marsh macroconsumers during summer and winter.

	Summer				Winter			
	N Stomachs	B	Dfreq	TL	N Stomachs	B	Dfreq	TL
<i>Adinia xenica</i>	53	0.11	0.32	2.02	—	—	—	—
<i>Anchoa mitchilli</i>	523	0.29	0.16	3.31	387	0.06	0.28	3.03
<i>Arius felis</i>	62	0.20	0.03	3.35	16	0.47	0.00	3.20
<i>Atractosteus spatula</i>	20	0.07	0.00	3.28	10	0.10	0.00	3.07
<i>Bairdiella chrysoura</i>	189	0.13	0.00	3.21	9	0.16	0.00	3.10
<i>Brevoortia patronus</i>	210	0.03	0.83	2.01	314	0.07	0.64	2.02
<i>Callinectes sapidus</i>	124	0.15	0.08	2.75	79	0.26	0.36	2.41
<i>Callinectes similis</i>	15	0.14	0.22	2.02	—	—	—	—
<i>Citharichthys spilopterus</i>	49	0.07	0.00	3.25	—	—	—	—
<i>Cynoscion arenarius</i>	8	0.39	0.00	3.14	—	—	—	—
<i>Cynoscion nebulosus</i>	50	0.04	0.00	3.18	42	0.38	0.00	3.23
<i>Cyprinodon variegatus</i>	123	0.04	0.33	2.01	17	0.06	0.69	2.00
<i>Dorosoma cepedianum</i>	111	0.09	0.59	2.24	90	0.03	0.83	2.11
<i>Elops saurus</i>	8	0.53	0.00	3.07	—	—	—	—
<i>Farfantepenaeus aztecus</i>	82	0.15	0.42	2.36	35	0.34	0.36	2.37
<i>Fundulus confluentus</i>	7	0.60	0.10	2.70	—	—	—	—
<i>Fundulus grandis</i>	108	0.18	0.83	2.54	25	0.09	0.64	2.15
<i>Fundulus pulvereus</i>	11	0.02	0.02	3.00	—	—	—	—
<i>Gobionellus boleosoma</i>	43	0.42	0.31	2.48	32	0.17	0.52	2.23
<i>Gobiosoma bosc</i>	36	0.06	0.01	3.01	129	0.10	0.16	2.85
<i>Gobiosoma robustum</i>	—	—	—	—	10	0.52	0.25	2.75
<i>Hemicaranx amblyrhynchus</i>	14	0.03	0.00	3.22	—	—	—	—
<i>Lagodon rhomboides</i>	316	0.03	0.05	2.16	48	0.07	0.04	2.74
<i>Leiostomus xanthurus</i>	265	0.17	0.00	3.21	273	0.13	0.00	2.99
<i>Litopenaeus setiferus</i>	37	0.11	0.82	2.24	52	0.03	0.83	2.03
<i>Lucania parva</i>	123	0.03	0.02	3.00	49	0.24	0.45	2.53
<i>Menidia beryllina</i>	423	0.14	0.00	2.83	196	0.20	0.03	2.52
<i>Menidia peninsulae</i>	70	0.46	0.06	2.89	—	—	—	—
<i>Microgobius gulosus</i>	6	0.63	0.00	3.06	—	—	—	—
<i>Micropogonias undulatus</i>	175	0.18	0.04	2.87	339	0.26	0.09	2.94
<i>Mugil cephalus</i>	402	0.05	0.67	2.16	115	0.10	0.59	2.07
<i>Palaemonetes pugio</i>	90	0.04	0.85	2.03	66	0.03	0.83	2.13
<i>Paralichthys lethostigma</i>	35	0.21	0.00	3.14	10	0.06	0.00	3.40
<i>Poecilia latipinna</i>	77	0.04	0.82	2.02	11	0.00	1.00	2.00
<i>Pogonias cromis</i>	43	0.06	0.76	3.15	14	0.16	0.82	2.03
<i>Sciaenops ocellatus</i>	62	0.04	0.00	3.53	33	0.11	0.00	3.27
<i>Syngnathus scovelli</i>	—	—	—	—	15	0.49	0.04	2.98

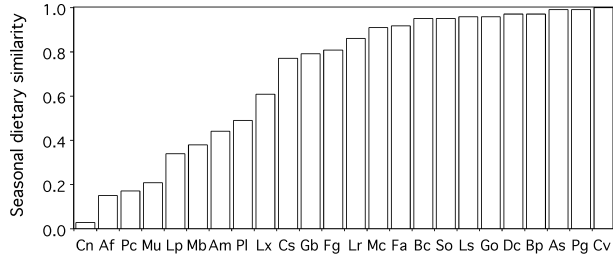


Fig. 3. Similarity (overlap) of summer and winter diets of conspecifics of common fishes and macroinvertebrates at Mad Island Marsh. Species codes are Cn = *Cynoscion nebulosus*, Af = *Arius felis*, Pc = *Pogonias cromis*, Mu = *Micropogonias undulatus*, Lp = *Lucania parva*, Mb = *Menidia beryllina*, Am = *Anchoa mitchilli*, Pl = *Poecilia latipinna*, Lx = *Leiostomus xanthurus*, Cs = *Callinectes sapidus*, Gb = *Gobiosoma bosc*, Fg = *Fundulus grandis*, Lr = *Lagodon rhomboides*, Mc = *Mugil cephalus*, Fa = *Farfantapenaeus aztecus*, Bc = *Bairdiella chrysoura*, So = *Sciaenops ocellatus*, Ls = *Litopenaeus setiferus*, Go = *Gobionellus boleosoma*, Dc = *Dorosoma cepedianum*, Bp = *Brevoortia patronus*, As = *Atractosteus spatula*, Pg = *Palaemonetes pugio*, and Cv = *Cyprinodon variegatus*.

and alligator gar) ranged from 0.04 to 0.11 seasonally, whereas the darter goby (*Gobionellus boleosoma*) ranged from 0.17 to 0.42, and the inland silverside ranged from 0.14 to 0.20. Sample size (number of stomachs examined) did not affect diet breadth during summer ($r = 0.041$, $p = 0.813$) or winter ($r = 0.247$, $p = 0.215$).

Mean dietary overlap values for summer and winter communities were 0.17 and 0.27, respectively. Dietary similarity (overlap) for conspecifics during the two seasons was compared in order to indicate the degree of seasonal diet shift (Fig. 3). Most species had high between-season dietary similarity (two thirds of species with values greater than 0.6). Detritivores and algivores had relatively high intraspecific trophic overlap, indicating minor seasonal diet shifts. Some omnivores and primary carnivores, such as spotted sea trout, Atlantic croaker, and inland silverside, had low overlaps that indicated large seasonal diet shifts.

PCA species ordination based on dietary data also revealed patterns of seasonal dietary shifts (Fig. 4). The first two axes explained 43.4% of the total variation (Table 3). During summer, high scores on the first axis were positively associated with detritus, centric and pennate diatoms, other algae, and gastropods, and negatively associated with amphipods, blue crab, mysid shrimp, shrimp larvae, grass shrimp, white shrimp, and brown shrimp (Table 3). Higher scores on axis 2 were positively associated with amphipods, detritus, algae, and chironomid larvae, and negatively associated with blue crab, mollusks, striped mullet, and other fishes (Table 3). Algivores and detritivores clustered in the upper right quadrat indicating selective feeding on detritus and algae (Fig. 4). Rainwater killifish (*Lucania*

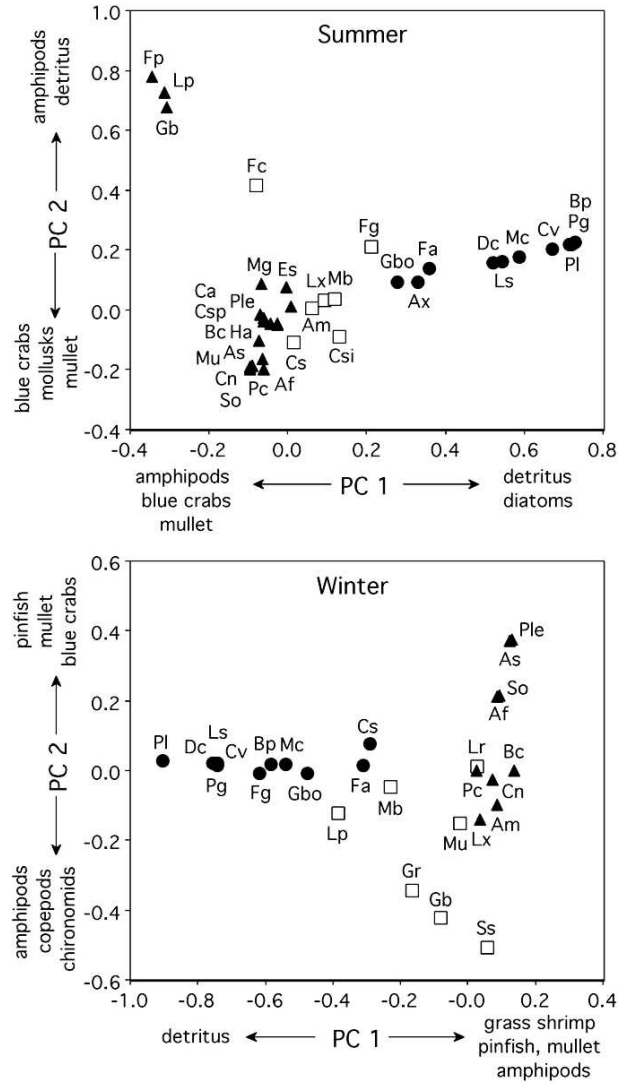


Fig. 4. PCA ordination plots based on volumetric proportion of consumed foods during summer and winter at Mad Island Marsh. Species are coded as in Fig. 3 and Akin and Winemiller (unpublished data); + designates herbivores and detritivores (trophic level = 1.0–1.5), ■ designates omnivores (trophic level = 1.5–2.0), ● designates primary carnivores (trophic level = 2.0–2.5), and Δ designates secondary carnivores (trophic level > 2.5).

parva), bayou killifish (*Fundulus pulvereus*), and naked goby (*Gobiosoma bosc*) clustered in the upper left quadrat, which indicated selective feeding on amphipods and chironomid larva. Omnivores, primary carnivores and secondary carnivores clustered tightly in the lower left quadrat, an indication of high dietary overlap among these species. Larger fish (e.g., red drum, spotted sea trout, alligator gar) were slightly separated from other species towards the lower left quadrat, which indicated feeding on larger prey, such as striped mullet, blue crab, and mollusks (Fig. 4). The remaining species clustered

TABLE 3. PCA axis loadings for major diet items from stomachs of common Mad Island Marsh macroconsumers during summer and winter seasons.

	Summer		Winter	
	Axis 1	Axis 2	Axis 1	Axis 2
Eigenvalue	0.096	0.057	0.120	0.036
Proportion of total variation	0.271	0.163	0.389	0.118
Detritus	0.90	0.22	-0.94	0.01
Diatoms	0.01	0.00	-0.03	0.01
Pennate diatoms	0.09	0.01	-0.03	0.01
Centric diatoms	0.03	0.01	-0.05	0.01
Vascular plants	0.00	-0.01	0.03	0.10
Nematodes	0.00	0.00	0.02	-0.03
Calanoid copepods	-0.03	-0.03	0.09	-0.25
Chironomid larvae	-0.02	0.08	0.04	-0.17
Polychaete worms	-0.01	0.00	-0.01	-0.04
Amphipods	-0.34	0.87	0.11	-0.76
Gastropod mollusks	0.06	0.01	-0.02	0.01
Oysters	0.00	-0.01	0.05	0.02
Other bivalve mollusks	-0.08	-0.24	0.00	0.01
Crab zoea	-0.02	-0.02	0.00	0.00
Mysid shrimp	-0.06	-0.04	0.00	0.00
Shrimp larvae	-0.07	-0.09	0.03	-0.01
Grass shrimp	-0.07	-0.05	0.17	0.01
White shrimp	-0.02	-0.03	0.07	0.12
Brown shrimp	-0.01	-0.03	0.01	0.01
Blue crab	-0.13	-0.25	0.10	0.24
Mullet	-0.12	-0.22	0.12	0.34
Gulf menhaden	-0.03	-0.05	0.06	-0.03
Sheepshead minnow	-0.02	-0.02	0.00	0.00
Bay anchovy	-0.01	-0.02	0.01	0.00
Pinfish	-0.02	-0.03	0.13	0.37
Rainwater killifish	-0.02	-0.02	0.00	0.00

above these large fishes, which indicated consumption of mysid shrimp, juvenile menhaden, brown shrimp, white shrimp, and grass shrimp.

During winter, the first two axes explained 50.7% of the total variation (Table 3). High scores on the first PCA axis were associated with greater consumption of grass shrimp, mullet, pinfish, amphipods, blue crab, calanoid copepods, white shrimp, menhaden, and chironomid larvae, and less consump-

tion of detritus, gastropods, diatoms, and other algae (Fig. 4). The second PCA axis was associated with more pinfish, striped mullet, blue crab, white shrimp, and widgeon grass in the diet, and less amphipods, calanoid copepods, chironomid larvae, and annelid worms (Table 3). Detritivores and algivores (e.g., striped mullet, Gulf menhaden, gizzard shad, and shrimp) had negative scores on PCA1 and scores near 0 on PCA2. Omnivores clustered on the lower right quadrat that was influenced by consumption of amphipods and other benthic invertebrates (Fig. 4). Primary carnivores that consumed shrimp larvae, grass shrimp, copepods, and other benthic invertebrates had positive scores on PCA1. Piscivores were located at the upper right quadrat and consumed mostly striped mullet, pinfish, and macroinvertebrates, such as blue crab and white and brown shrimp (Fig. 4).

FOOD WEB COMPOSITION

Corresponding original and composite food webs contained the same number of species (nodes, including species in upper levels and aggregate taxa in low levels; Table 4). The number of fish and invertebrate species in the winter web were 23 and 10, respectively, with the numbers in the summer web increasing to 30 and 11, respectively. The code goby (*Gobiosoma robustum*) and gulf pipefish were absent from the summer web. The clown goby (*Microgobius gulosus*), diamond killifish (*Adinia xenica*), ladyfish (*Elops saurus*), bay whiff, tidewater silverside, bluntnose jack, bayou killifish, marsh killifish (*Fundulus confluentus*), and lesser blue crab (*Callinectes similis*) were absent from the winter web.

The winter and summer webs each had five secondary predators, and the annual web had six. Red drum, southern flounder, alligator gar, and hardhead catfish were secondary predators in all three webs. These predators had relatively low

TABLE 4. Food web statistics of original and composite food webs at Mad Island Marsh.

Properties	Original			Composite		
	Winter	Summer	Annual	Winter	Summer	Annual
Number of links, L	394	562	700	704	925	1094
Number of nodes, S	75	86	92	75	86	92
Linkage density, D	5.25	6.53	7.61	9.39	10.76	11.89
Lower connectance, CL	0.14	0.15	0.17	0.25	0.25	0.26
Trophic connectance, CT	0.07	0.08	0.08	0.13	0.13	0.13
Directed connectance, CD	0.07	0.08	0.08	0.13	0.13	0.13
SC (nodes × connectance)	5.32	6.61	7.69	9.51	10.88	12.02
Number of top species	5	5	6	5	5	6
Number of basal species	14	16	16	14	16	16
Number of intermediate species	56	65	70	56	66	70
Predator:prey links	0.47	0.51	0.53	0.86	0.85	0.85
Fraction of top species	0.07	0.06	0.07	0.07	0.06	0.07
Fraction of basal species	0.19	0.19	0.17	0.19	0.19	0.17
Fraction of intermediate species	0.75	0.76	0.76	0.75	0.77	0.76

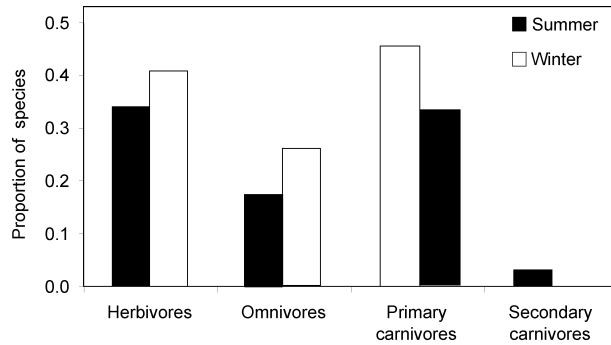


Fig. 5. Proportions of species at four trophic intervals during summer and winter at Mad Island Marsh.

trophic levels ranging from 3.1 to 3.5, which reflected consumption of species low in the food chain. The alligator gar's diet consisted mostly of striped mullet that had a trophic level of 2.06 and 2.16 for winter and summer, respectively. Red drum fed mainly on blue crab and striped mullet during winter and blue crab during summer.

Although species trophic levels tended to be higher during summer (Table 2), the distribution of trophic levels was similar during the two seasons. Both seasonal webs were dominated by primary carnivores (TL = 3.0–3.5) and herbivores (2.0–2.5), with omnivores (2.5–3.0) less common (Fig. 5). Proportions of herbivores and omnivores were slightly lower during summer, and proportions of primary and secondary carnivores were higher. None of the species fell within the secondary-carnivore interval during winter, and only one species (red drum) fell within the secondary-carnivore interval during summer (Fig. 5). Trophic levels of herbivores revealed little variation, but omnivores and primary carnivores tended to have higher trophic levels during summer.

Original food webs had far fewer links than their corresponding composite webs (Table 4). Most links were very weak (low p_{ij}). When links with $p_{ij} < 0.05$ were eliminated from matrices, all three of the original webs had about 200 links. Original and composite webs had remarkably consistent proportions of top, intermediate, and basal species for winter, summer, and annual webs. Linkage density revealed strong seasonal variation in both original and composite webs, with winter having the lowest value and the annual web having highest. The addition of links for small invertebrates greatly increased linkage density. Predator : prey ratios for composite webs were greater than those of original webs, and these ratios varied little with seasons.

For both original and composite webs, all three measures of connectance (all weak links included) revealed little seasonal variation (Table 4). Lower

connectance was twice as high as the two other connectance metrics, with the latter being identical in each case. When weak links ($p_{ij} < 0.05$) were eliminated, the three measures of connectance declined by nearly one half, and all three webs converged to a value of about 0.04 for lower connectance and 0.02 for trophic and directed connectance. Predictably, all three measures of connectance had higher values for composite webs.

Discussion

SEASONAL VARIATION IN WEB STRUCTURE

The food web paradigm seeks to understand the influence of community trophic structure on ecological dynamics, yet few empirical studies have explored temporal variation on food web structure (Warren 1989; Winemiller 1990; Closs and Lake 1994; Tavares-Cromar and Willams 1996; Thompson and Townsend 1999). We analyzed large samples of consumer stomach contents to explore seasonal variation in the food web of a temperate estuary, a type of ecosystem known for large seasonal variation in abiotic conditions and community structure. Compared to previous studies of food webs of larger estuarine systems in which most feeding interactions were inferred indirectly (e.g., Chesapeake Bay [Baird and Ulanowicz 1989]; Ythan estuary [Hall and Raffaelli 1991]), the MIM food web contains a similar number of species but more links.

Compositional changes in the MIM community were heavily influenced by several common marine species that migrated into the estuary during early life stages. Both environmental factors and species-specific, endogenous reproductive cycles probably influenced these movements into the estuary. Akin et al. (2003) reported that a suite of environmental variables (salinity, temperature, vegetation cover, dissolved oxygen, and water depth) was associated with two fairly distinct seasonal assemblage structures (winter and summer) at MIM. The winter community was dominated by spot, Atlantic croaker, and Gulf menhaden, species that enter the estuary as postlarvae. During late spring-early summer, community composition changed as resident species, such as bay anchovy, pinfish, striped mullet, and killifishes, became numerically dominant. Low dissolved oxygen (2.7 mg l^{-1}) in the upper reaches of the estuary during late summer and early fall was associated with a spatial gradient in assemblage structure, but overall, the structure of fishes and macroinvertebrates species assemblages at MIM varied according to seasons to a much greater extent than space (Akin et al. 2003). The MIM estuary does not exhibit characteristics of a degraded estuarine ecosystem, i.e., planktonic algal blooms,

low abundance of submerged aquatic plants and benthic microalgae, depleted apex predators, and depletion of oyster stocks (Baird et al. 2004). Even during late summer and early fall, apex predators, such as alligator gar and red drum, were captured throughout the system.

Web size increased from winter (75 nodes) to summer (86 nodes), which was expected since the number of species in the estuary increased during summer when temperature and salinity were higher (Akin et al. 2003). The summer increase in species richness was largely due to the addition of fishes at intermediate trophic levels, since numbers of lower level consumers (e.g., zooplankton and benthic invertebrates and top predators) varied little. Studies of lotic freshwater systems also have revealed strong seasonal variation in food web structure in relation to environmental conditions, such as hydrology and temperature, as well as life history characteristics (Winemiller 1990, 1996; Closs and Lake 1994; Tavares-Cromar and Williams 1996; Peterson 1997). Shallow temperate estuaries are highly dynamic ecosystems with hydrologic changes influenced by precipitation, wind, and tides. Hydrologic variation was relatively low at MIM during our study (Akin et al. 2003), and most of the seasonal variation in community composition probably was caused by combined effects of endogenous migration cycles by estuarine-dependent species and associated trophic dynamics (i.e., functional response, prey switching).

Seasonal dietary shifts were common in both fishes and macroinvertebrates in MIM. In general, there was little indication of dietary shifts for herbivores, but seasonal changes in diet were evident for omnivores and carnivores. The diet of juvenile spotted sea trout in winter consisted mostly of zooplankton, amphipods, mysid shrimp, and small fishes, such as Gulf menhaden and bay anchovy; larger fish and invertebrates, including striped mullet, pinfish, white shrimp, and blue crabs, dominated its diet during summer when its mean standard length had increased to 102 mm. The same was true for Atlantic croaker with a diet shifting from copepods, amphipods, chironomid larvae, and small fishes during winter when mean standard length was 23.5 mm, to blue crabs and larger polychaete worms during summer when mean standard length was 43.7 mm.

In addition to ontogenetic dietary shifts, diet composition shifts seasonally in response to changes in food resource availability at MIM. More amphipods were consumed by rainwater killifish and other small fishes during summer when amphipods comprised half of the total benthic fauna in core samples. An increase in direct consumption of vascular plants (mostly submerged widgeon grass)

also can be attributed to greater availability of this resource during summer. The greater summer consumption of mollusks was largely attributed to increased abundance of black drum and hardhead catfish, given that the abundance of mollusks in core samples was similar during winter and summer. An increase in piscivory during summer was associated with greater summertime abundances of piscivores, such as alligator gar.

An increase in trophic level of consumers and the proportion of primary carnivores during summer provides additional evidence that diet shifts were common features of consumers in MIM. During winter, many fishes were postlarvae of estuarine-dependent marine species that fed on zooplankton and benthic invertebrates. By summer these fishes had grown and became major food resources for piscivores, which caused increases in both mean trophic level and the proportion of primary carnivores in the web.

Seasonal variation in consumption of detritus was apparent in the MIM web. Fishes and invertebrates in our samples were estimated to consume six times more detritus (volumetrically) during summer. This estimate even takes into account the observation that the frequency of occurrence of detritus in the stomachs was slightly higher during winter (79%) than summer (72%). The increase in volume of detritus consumed during summer was influenced by a summertime increase in abundance of adult size classes of striped mullet, a major detritivore in coastal ecosystems. Greater stomach fullness also could reflect greater energy demands of fishes during warmer summer months (Baird et al. 2004).

SOURCES OF PRIMARY PRODUCTION AND DETRITUS

Benthic microalgae and macroalgae, phytoplankton, and vascular plants are sources of primary production for estuarine food webs. Several studies have concluded that vascular plants and plant detritus are the principal basal resource supporting fish production in coastal systems (Darnell 1961; Canuel et al. 1995; Currin et al. 1995; Creach et al. 1997). Other research has revealed greater assimilation of algal production by estuarine consumers (Peterson et al. 1985; Page 1997; Stribling and Cornwell 1997; Riera et al. 1999; Currin et al. 2003). Studies using stable isotope techniques have revealed that carbon derived from C4 grasses, such as saltwater cordgrass, is assimilated in variable proportions into elements of marsh food webs (Haines 1977; Currin et al. 1995; Kwak and Zedler 1997). Widgeon grass has been inferred to be a significant carbon source for some consumers in coastal food webs (Harrigan et al. 1989). Evidence from stomach contents analysis and sediment samples suggests that widgeon grass is a significant production source

supporting fishes and invertebrates in MIM. In addition to its role as a physical refuge for fishes, widgeon grass (both living and dead tissue) serves as food and habitat for benthic invertebrates that in turn are food resources for almost all juvenile fishes in the system. Availability of these invertebrates increased greatly during summer.

Consistent with other estuarine studies, detritus (originating from either algae or macrophytes) was the most important food source for the MIM macrofauna. Microscopic examination of detritus recovered from stomachs indicated mostly fine particulate matter of unknown origin. It may be assumed that this material contains variable fractions of microbial and fungal biomass, although these materials could not be quantified from our method. Consumption of detritus was not limited to detritivores, but also consumed to a lesser extent by primary carnivores and even secondary carnivores. Consumption of detritus by carnivores probably was incidental with questionable nutritional contribution. The most important foods of primary and secondary consumers were benthic organisms that feed on detritus, either suspended or deposited particles, and live aquatic vegetation. Herbivores and detritivores comprised almost half of the total fish and macroinvertebrate community during both seasons. As reported by Odum and Heald (1975) for an Atlantic coast estuary, detritivorous fishes and invertebrates link detritus to top predators via short food chains that presumably yield high ecological efficiency.

Based on dietary analysis, diatoms are another important production source supporting estuarine consumers in MIM. Since stomach contents analysis only quantifies ingested material, it is difficult to ascertain whether or not algae, cordgrass, or widgeon grass is the main source of carbon for consumers. Phytoplankton are ubiquitous at MIM, and cordgrasses (*Spartina alterniflora*, *S. patens*, *S. spartinae*) fringe the entire study reach, with a thin layer of benthic algae generally covering submerged stems and leaves. By providing estimates of assimilated (not just ingested) time-integrated diet of an animal, stable isotope ratios of consumer tissues can be used to infer primary production sources of assimilated carbon (Peterson and Fry 1987). A recent study comparing dietary and stable isotope ratios of MIM food web elements (Winemiller and Akin unpublished data) indicated that most consumer taxa probably are supported to some extent by algae, a finding consistent with other estuarine studies (e.g., Currin et al. 1995; Moncreiff and Sullivan 2001). Several species associated with shallow marginal areas of the estuary were estimated to assimilate larger fractions of carbon from isotopically heavier sources, such as cordgrass or

widgeon grass (Winemiller and Akin unpublished data).

COMPARISONS WITH OTHER FOOD WEBS

Due to inconsistent criteria that have been used to compile food webs based on information in the literature (Paine 1988) as well as the sensitivity of web properties to methods (Winemiller 1990; Polis 1991; Hall and Raffaelli 1993), we consider comparisons of webs from field studies using different methods and criteria to be tenuous. Food webs can be compared if similar methods are used to sample habitats, quantify feeding interactions, and designate prey categories. We compared the MIM original web with those from studies by Winemiller (1990), Peterson (1997), and Link (2002) that used similar methods and followed most of the criteria proposed by Cohen et al. (1993). For heuristic purposes, we also compared several properties of our composite webs with food webs created from literature data and that only characterize web topology (e.g., Little Rock Lake [Martinez 1991] and topological webs compiled in ECOWEB [Cohen et al. 1993]).

The number of species in our original and composite annual food webs was greater than most of the ECOWEB webs. Exceptions were Ythan estuary ($S = 134$; Hall and Raffaelli 1991), Little Rock Lake ($S = 183$), and El Verde rainforest, Puerto Rico ($S = 136$; Regan et al. 1996). Criteria used to compile these webs vary widely. Cohen et al. (1993, p. 254) suggested "a yield-effort curve should be accompanied by an explicit report of the temporal and spatial sampling frame, the sampling plan, sampling gears, and methods for preserving samples in the field." Our MIM composite annual web had more links (1,094) than the Ythan estuary web (500) and all of the other webs from ECOWEB (average 34, range 3–138), except for the Little Rock Lake (2,366), El Verde (1,428), and marine coastal shelf webs (1,562; Link 2002). The Ythan estuary web included 1 mammal and 18 bird species, and some data were gathered from the literature. The greater number of links in the MIM web seems to be derived from finer taxonomic resolution among primary producers and invertebrates.

Winemiller's (1990) tropical stream webs contained an average of 514 links when all interactions were included, and 99 links when weak interactions with $p_{ij} < 0.05$ were eliminated from the web. MIM original webs contained an average of 552 links with all interactions included and 144 links when weak links ($p_{ij} < 0.05$) were excluded. A potential explanation is that these webs have similar ranges for web size (number of nodes), and consumers in both types of aquatic systems tend to have fairly

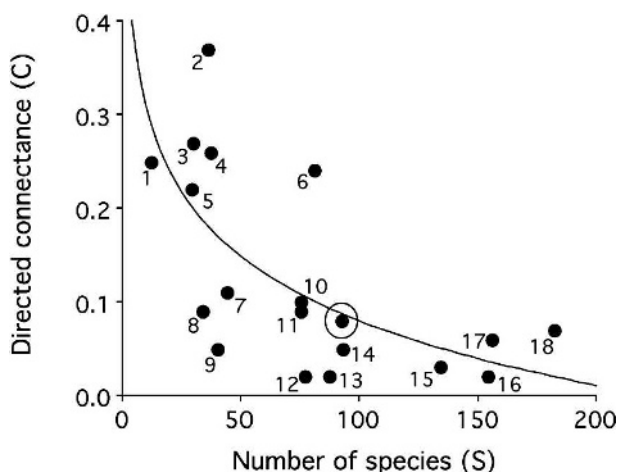


Fig. 6. Directed connectance plotted in relation to the number of species of the Mad Island Marsh food web (symbol circled) and 19 published webs: 1) Canadian Lake (Sprules and Bowerman 1988), 2) Chesapeake Bay (Baird and Ulanowicz 1989), 3) Coachella Valley-aggregated (Polis 1991), 4) Skipwith pond (Warren 1989), 5) Benguela ecosystem (Yodzis 1988), 6) northwest U.S. shelf ecosystem (Link 2002), 7) St. Martin Island (Goldwasser and Roughgarden 1993), 8) Duffin Creek (Tavares-Cromar and Williams 1996), 9) Australian stream (Closs and Lake 1994), 10) Bridge Brook Lake (Havens 1993), 11) neotropical wetlands and streams (Winemiller 1990), 12) UK grassland (Martinez et al. 1999), 13) UK grassland (Dawah et al. 1995), 14) Ythan estuary-1 (Hall and Raffaelli 1991), 15) Ythan estuary-2 (Huxham et al. 1996), 16) Silwood park (Memmot et al. 2000), 17) El Verde rainforest (Reagen and Waide 1996), and 18) Little Rock Lake (Martinez 1991).

broad diets, with individual species consuming, on average, about 10–15% of available prey nodes.

Because it represents trophic complexity as a single value, connectance has received much attention, particularly in the context of theories predicting effects of complexity on stability (e.g., Pimm et al. 1991; Martinez 1992; Warren 1994). Early published food webs indicated that directed connectance, C_D , decreases hyperbolically with increasing number of species, S (Fig. 6). Subsequent analyses of published food webs rejected this pattern and showed that C_D increases (Winemiller 1989) or is constant (Warren 1989; Martinez 1992; Martinez et al. 1999) in relation to S . Montoya and Solé (2002) concluded that C_D is scale variant in a new collection of 12 food webs, with values ranging from 0.02 to 0.24. C_D of MIM webs only ranged from 0.07 during winter to 0.08 for the cumulative annual web, even though the number of species was 75 and 92 for these webs, respectively. Our findings agree with results obtained by Tavares-Cromar (1996) and Peterson (1997), but our C_D values were smaller than those obtained by Winemiller (1990) for tropical streams. Differences in C_D could be due to more trophic links derived from greater sampling effort in the latter study.

Briand and Cohen's (1984) link-species scaling law theorized that the average number of links per species in food webs (linkage density) is approximately constant at 1.86, with this presumed as derived from dynamic constraints on system stability. Others have claimed that linkage density increases with increasing number of species in webs (Schoener 1989; Hall and Raffaelli 1991; Martinez 1992; Havens 1993; Goldwasser and Roughgarden 1993). Linkage density, D , was higher in the MIM annual web than the time-specific webs largely because both the numbers of species and links were greater in the annual web. The average linkage density for three original MIM webs (6.4) was nearly the same as the mean of 6.3 estimated for tropical stream webs (Winemiller 1990), whereas linkage densities of composite MIM webs (9.39–11.89) were nearly twice the values of the original MIM webs, and were much higher than the value reported for Ythan estuary (4.1). Such patterns should be interpreted with caution, especially given that Martinez (1991) demonstrated the high sensitivity of linkage density to taxonomic aggregation.

The fractions of top species, basal, and intermediate species are claimed to be constant at the ratio of 0.29, 0.19, and 0.52, respectively (Briand and Cohen 1984; Cohen et al. 1990), but these ratios have been criticized (Winemiller 1990; Polis 1991; Closs et al. 1993; Havens 1993). To define a top predator is not a simple matter, especially when one considers that even the fiercest predators suffer some level of predation (Winemiller 1990). In the MIM web, top, intermediate, and basal species were nearly constant between seasons. Because they sum to unity, these proportions are not independent (Closs et al. 1993), and the proportion of basal species has been shown to decrease with increasing number of species in the web (Winemiller 1990; Schoenly and Cohen 1991). Schoenly and Cohen (1991) suggested that smaller proportions of basal species in cumulative webs relative to time-specific webs are due to the fact that turnover among intermediate species and top species is much more prevalent than among basal species. This appears to be the case at MIM and estuaries in general. The number of intermediate species was greater (70) in the annual web compared to seasonal webs (56, 65), but the number of basal nodes changed little (14–16).

Average food chain length in the MIM web was low, with top species, such as alligator gar and red drum, having trophic level estimates between 3.1–3.5. These low values were strongly influenced by consumption of common detritivores, such as Gulf menhaden and striped mullet. Our small sample size for the alligator gar (30, including 12 empty stomachs) could have influenced results. Alligator

gars have been reported to feed on gizzard shad (García et al. 2001), another common detritivore in MIM, but no gizzard shad were found in our sample of alligator gar stomachs. For red drum, sample size was adequate (95, with 35 empty) to represent subadult and adult feeding habits accurately (standard length range of specimens 200–665 mm). Our estimate of the red drum diet is similar to that obtained from an investigation of stomach contents of red drum from Galveston Bay on the Texas Gulf coast (Scharf and Schlicht 2000).

Omnivory, feeding on more than one trophic level, is reported to be common in food webs (Winemiller 1990; Hall and Raffaelli 1991; Polis 1991; Havens 1993; Holyoak and Sachdev 1998). The percentage of omnivorous fish and macro-invertebrate species at MIM varied from 17% to 26%, a range that overlaps with those reported for the Ythan estuary (21–34%) and tropical streams (15–25%). A decline in omnivory in MIM during summer can be attributed to the fact that many estuarine-dependent fishes and invertebrates migrate into the estuary as postlarvae during winter and early spring. Diets of most postlarvae and juvenile estuarine fishes consisted of mixtures of detritus, diatoms, zooplankton, and other micro-invertebrates. As some of these species grow during the warmer months, they became more specialized feeders. Recent theoretical research indicates that these kinds of flexible feeding strategies (adaptive foraging) can increase food web stability (Kondoh 2005).

ACKNOWLEDGMENTS

The Nature Conservancy of Texas and M. Dumesnil provided access to field sites and facilities at Mad Island Marsh Preserve. We thank D. Arrington, J. Arrington, S. Aydin, Y. Bolek, T. Lantz, H. Lopez, M. Morgan, M. Robertson, S. Tarim, and J. Walther for assistance with field data and specimen collection. W. Neill and J. Calvin provided helpful statistical advice. Funding was provided by the Nature Conservancy of Texas, International Sportfish Fund, and a fellowship from Gaziosmanpasa University to the first author.

LITERATURE CITED

- ADAMS, S. M., B. L. KIMMEL, AND G. R. PLOSKEY. 1983. Sources of organic carbon for reservoir fish production: A trophic-dynamics analysis. *Canadian Journal of Fisheries Aquatic Sciences* 40:1480–1495.
- AKIN, S., K. O. WINEMILLER, AND F. P. GELWICK. 2003. Seasonal and spatial variation in fish and macrocrustacean assemblage structure in Mad Island Marsh estuary, Texas. *Estuarine Coastal and Shelf Science* 56:1–14.
- BAIRD, D., R. R. CHRISTIAN, C. H. PETERSON, AND G. A. JOHNSON. 2004. Consequences of hypoxia on estuarine ecosystem function: Energy diversion from consumers to microbes. *Ecological Applications* 14:805–822.
- BAIRD, D. AND R. E. ULANOWICZ. 1989. The seasonal dynamics of the Chesapeake Bay ecosystem. *Ecological Monographs* 59:329–364.
- BRIAND, F. 1983. Environmental control of food web structure. *Ecology* 64:253–263.
- BRIAND, F. AND J. E. COHEN. 1984. Community food webs have scale-invariant structure. *Nature* 307:264–266.
- BRIAND, F. AND J. E. COHEN. 1987. Environmental correlates of food chain length. *Science* 238:956–960.
- CANUEL, E. A., J. E. CLOERN, D. B. RINGELBERG, J. B. GUCKERT, AND G. H. RAU. 1995. Molecular and isotopic tracers used to examine sources of organic-matter and its incorporation into the food webs of San Francisco Bay. *Limnology and Oceanography* 40:67–81.
- CLOSS, G. P. AND P. S. LAKE. 1994. Spatial and temporal variation in the structure of an intermittent-stream food web. *Ecological Monographs* 64:1–21.
- CLOSS, G., G. A. WATTERSON, AND P. J. DONNELLY. 1993. Constant predator-prey ratios: An arithmetic artifact? *Ecology* 74:238–243.
- COHEN, J. E. 1978. *Food Webs and Niche Space*. Princeton University Press, Princeton, New Jersey.
- COHEN, J. E., R. A. BEAVER, S. H. COUSINS, D. L. ANGELIS, L. GOLDWASSER, K. L. HEONG, R. K. HOLT, A. J. KOHN, J. H. LAWTON, N. MARTINEZ, R. O'MALLEY, L. M. PAGE, B. C. PATTERN, S. L. PIMM, G. A. POLIS, M. REJMANEK, T. W. SCHOENER, K. SCHOENLY, W. G. SPRULES, J. M. TEAL, R. E. ULANOWICZ, P. H. WARREN, H. M. WILBUR, AND P. YODZIS. 1993. Improving food webs. *Ecology* 74:252–258.
- COHEN, J. E., F. BRIAND, AND C. M. NEWMAN. 1986. A stochastic theory of community food webs. III. Predicted and observed lengths of food chains. *Proceedings of the Royal Society of London B* 228:317–353.
- COHEN, J. E., F. BRIAND, AND C. M. NEWMAN. 1990. *Community Food Webs: Data and Theory*. Springer-Verlag, New York.
- CREACH, V., M. T. SCHRICKE, G. BERTRU, AND A. MARIOTTI. 1997. Stable isotopes and gut analyses to determine feeding relationships in saltmarsh macroconsumers. *Estuarine Coastal and Shelf Science* 44:599–611.
- CURRIN, C. A., S. Y. NEWELL, AND H. W. PEARL. 1995. The role of standing dead *Spartina alterniflora* and benthic microalgae in salt-marsh food webs—Considerations based on multiple stable-isotope analysis. *Marine Ecology Progress Series* 121:99–116.
- CURRIN, C. A., S. C. WAINWRIGHT, K. W. ABLE, M. P. WEINSTEIN, AND C. M. FULLER. 2003. Determination of food web support and trophic position of the mummichog, *Fundulus heteroclitus*, in New Jersey smooth cordgrass (*Spartina alterniflora*), common reed grass (*Phragmites australis*), and restored marshes. *Estuaries* 26:495–510.
- DARNELL, R. M. 1961. Trophic spectrum of an estuarine community based on studies of Lake Pontchartrain, Louisiana. *Ecology* 42:553–568.
- DAWAH, H. A., B. A. HAWKINS, AND M. F. CLARIDGE. 1995. Structure of the parasitoid communities of grass-feeding chalcid wasps. *Journal of Animal Ecology* 64:708–720.
- DEANGELIS, D. L. 1975. Stability and connectance in food web models. *Ecology* 56:238–243.
- DEANGELIS, D. L. 1992. *Dynamics of Nutrient Cycling and Food Webs*. Chapman and Hall, London.
- DE CRESPIN DE BILLY, V., S. DOLEDEC, AND D. CHESSEL. 2000. Biplot presentation of diet composition data: An alternative for fish stomach contents analysis. *Journal of Fish Biology* 56:961–973.
- DE RUITER, P. C., A.-M. NEUTEL, AND J. C. MOORE. 1995. Energetics, patterns of interaction strengths, and stability in real ecosystems. *Science* 269:1257–1260.
- DE RUITER, P. C., V. WOLTERS, J. C. MOORE, AND K. O. WINEMILLER. 2005. Food web ecology: Playing Jenga and beyond. *Science* 309: 68–69.
- GARCIA, F. J., L. GONZALES-GARCIA, J. M. HERRERA-CASTILLO, K. O. WINEMILLER, AND A. BANDA-VALDES. 2001. Ecology of the alligator gar, *Atractosteus spatula*, in the Vicente Guerrero Reservoir, Tamaulipas Mexico. *The Southwestern Naturalist* 46: 151–157.

- GARCIA, A. M., J. P. VIEIRA, AND K. O. WINEMILLER. 2003. Influences of El Niño on the dynamics of an estuarine fish assemblage. *Estuarine Coastal and Shelf Science* 57:489–500.
- GELWICK, F. P., S. AKIN, D. A. ARRINGTON, AND K. O. WINEMILLER. 2001. Seasonal dynamics in abiotic factors and distribution of fishes in the Mad Island Marsh Preserve, Texas. *Estuaries* 24: 285–296.
- GOLDWASSER, L. AND J. ROUGHGARDEN. 1993. Construction and analysis of a large Caribbean food web. *Ecology* 74:1216–1233.
- HAINES, E. B. 1977. Origins of detritus in Georgia salt-marsh estuaries. *Oikos* 29:254–260.
- HALL, S. J. AND D. G. RAFFAELLI. 1991. Food web pattern: Lessons from a species rich web. *Journal of Animal Ecology* 60:823–842.
- HALL, S. J. AND D. G. RAFFAELLI. 1993. Food webs. Theory or reality? p. 187–239. *In* M. Begon and A. H. Fitter (eds.), *Advances in Ecological Research*. Academic Press, London.
- HARRIGAN, P., J. C. ZIEMAN, AND S. A. MACKO. 1989. The base of nutritional support for the gray snapper (*Lutjanus griseus*): An evaluation based on a combined stomach content and stable isotope analysis. *Bulletin of Marine Science* 44:65–77.
- HAVENS, K. E. 1993. Pelagic food web structure in Adirondack Mountain, USA, lakes of varying acidity. *Canadian Journal of Fisheries and Aquatic Sciences* 50:149–155.
- HOLYOAK, M. AND S. SAMBHAV. 1998. Omnivory and the stability of simple food webs. *Oecologia* 117:413–419.
- HUXHAM, M., S. BEANEY, AND D. RAFFAELLI. 1996. Do parasites reduce the chances of triangulation in a real food web? *Oikos* 76:284–300.
- JEFFRIES, M. J. AND J. H. LAWTON. 1985. Predator-prey ratios in communities of freshwater invertebrates: The role of enemy and free space. *Freshwater Biology* 15:105–112.
- KONDOH, M. 2005. Linking flexible food web structure to population viability: A theoretical consideration on adaptive food webs, p. 101–113. *In* P. de Ruiter, V. Wolters, and J. C. Moore (eds.), *Dynamic Food Webs: Multispecies Assemblages, Ecosystem Development, and Environmental Change*. Elsevier, Amsterdam.
- KREBS, C. J. 1999. *Ecological Methodology*, 2nd edition. Addison Wesley, Menlo Park, California.
- KWAK, T. J. AND J. B. ZEDLER. 1997. Food web analysis of southern California coastal wetlands using multiple stable isotopes. *Oecologia* 110:262–277.
- LAWTON, J. H. 1989. Food webs, p. 43–78. *In* J. M. Cherrett (ed.), *Ecological Concepts*. Blackwell Scientific, Oxford, U.K.
- LINK, J. 2002. Does food web theory work for marine ecosystems. *Marine Ecology Progress Series* 230:1–9.
- MARTINEZ, N. D. 1991. Artifacts or attributes? Effects of resolution on the Little Rock Lake food web. *Ecological Monographs* 61:367–392.
- MARTINEZ, N. D. 1992. Constant connectance in community food webs. *American Naturalist* 139:1208–1218.
- MARTINEZ, N. D., B. A. HAWKINS, H. A. DAWAH, AND B. P. FEIFAREK. 1999. Effects of sampling effort on characterization of food-web structure. *Ecology* 80:1044–1055.
- MAY, R. M. 1973. *Stability and Complexity in Model Ecosystems*. Princeton University Press, Princeton, New Jersey.
- MCCANN, K. S. 2000. The diversity-stability debate. *Nature* 405:228–233.
- MEMMOT, J., N. D. MARTINEZ, AND J. E. COHEN. 2000. Predators, parasitoids and pathogens: Species richness, trophic generality and body sizes in a natural food web. *Journal of Animal Ecology* 69:1–15.
- MERRITT, R. W. AND K. W. CUMMINS (EDS.). 1996. *An Introduction to the Aquatic Insects of North America*, 3rd edition. Kendall/Hunt Publishing Company, Dubuque, Iowa.
- MONCREIFF, C. A. AND M. J. SULLIVAN. 2001. Trophic importance of epiphytic algae in subtropical seagrass beds: Evidence from multiple stable isotope analyses. *Marine Ecology Progress Series* 215:93–106.
- MONTOYA, J. M. AND R. V. SOLE. 2002. Small world patterns in food webs. *Journal of Theoretical Biology* 214:405–421.
- ODUM, W. E. AND E. J. HEALD. 1975. The detritus based food web of an estuarine mangrove community, p. 265–286. *In* L. E. Cronin (ed.), *Estuarine Research*, Volume 1. Academic Press, New York.
- PAGE, H. M. 1997. Importance of vascular plant and algal production to macroinvertebrate consumers in a southern California salt marsh. *Estuarine Coastal and Shelf Science* 45:823–834.
- PAINE, R. T. 1988. Food webs: Road maps of interactions or grist for theoretical development? *Ecology* 69:1648–1654.
- PATTILO, M. E., T. E. CZAPLA, D. M. NELSON, AND M. E. MONACO. 1997. *Distribution and Abundance of Fishes and Invertebrates in Gulf of Mexico, Volume II: Species Life History Summaries*. ELMR Rep. No. 11. NOAA/NOS Strategic Environmental Assessments Division, Silver Spring, Maryland.
- PENNAK, R. W. 1978. *Freshwater-Invertebrates of the United States*, 2nd edition. John Wiley and Sons, New York.
- PETERSON, C. C. 1997. Food webs of two Venezuelan clear-water streams with seasonal fluctuations in hydrology. M.S. Thesis, Texas A&M University, College Station, Texas.
- PETERSON, B. J. AND B. FRY. 1987. Stable isotope in ecosystems studies. *Annual Review of Ecology and Systematics* 18:293–320.
- PETERSON, B. J., R. W. HOWARTH, AND R. H. GARRITT. 1985. Multiple stable isotopes to trace the flow of organic matter in estuarine food webs. *Science* 227:1361–1363.
- PIANKA, E. R. 1973. The structure of lizard communities. *Annual Review of Ecology and Systematics* 4:53–74.
- PIMM, S. L. 1982. *Food Webs*, 1st edition. Chapman and Hall, London, England.
- PIMM, S. L. AND R. L. KITCHING. 1987. The determinants of food chain length. *Oikos* 50:302–307.
- PIMM, S. L., J. H. LAWTON, AND J. E. COHEN. 1991. Food web pattern and their consequences. *Nature* 350:669–674.
- POLIS, G. A. 1991. Complex trophic interactions in deserts: An empirical critique of food web theory. *American Naturalist* 138: 123–155.
- POLIS, G. A., R. D. HOLT, B. A. MENGE, AND K. O. WINEMILLER. 1996. Temporal and spatial components of food webs, p. 435–460. *In* G. A. Polis and K. O. Winemiller (eds.), *Food Webs: Integration of Patterns and Dynamics*. Chapman and Hall, New York.
- REAGAN, D. P. AND R. B. WAIDE (EDS.). 1996. *The Food Web of a Tropical Rain Forest*. University of Chicago Press, Chicago, Illinois.
- RIERA, P., L. J. STAL, AND J. NIEUWENHUIZE. 1999. Determination of food sources for benthic invertebrates in a salt marsh (Aiguillon Bay, France) by carbon and nitrogen stable isotopes: Importance of locally produced sources. *Marine Ecology Progress Series* 187:301–307.
- SCHARF, F. S. AND K. K. SCHLICHT. 2000. Feeding habits of red drum (*Sciaenops ocellatus*) in Galveston Bay, Texas: Seasonal diet variation and predator-prey size relationships. *Estuaries* 23:128–139.
- SCHOENER, T. W. 1989. Food webs from the small to the large: Probes and hypotheses. *Ecology* 70:1559–1589.
- SCHOENLY, K. AND J. E. COHEN. 1991. Temporal variation in food web structure: Sixteen empirical cases. *Ecological Monographs* 61: 267–298.
- SIMPSON, E. H. 1949. Measurement of diversity. *Nature* 163:688.
- SPRULES, G. AND J. BOWERMAN. 1988. Omnivory and food chain lengths in zooplankton food webs. *Ecology* 69:418–426.
- STRIBLING, J. M. AND J. C. CORNWELL. 1997. Identification of important primary producers in a Chesapeake Bay tidal creek system using stable isotopes of carbon and sulfur. *Estuaries* 20: 77–85.
- SUGIHARA, G., K. SCHOENLY, AND A. TROMBLA. 1989. Scale invariance in food webs properties. *Science* 245:48–52.

- TAVARES-CROMAR, A. F. AND D. D. WILLIAMS. 1996. The importance of temporal resolution in food web analysis: Evidence from a detritus-based stream. *Ecological Monographs* 66:91–113.
- THOMPSON, R. M. AND C. R. TOWNSEND. 1999. The effect of seasonal variation on the community structure and food-web attributes of two streams: Implications for food-web science. *Oikos* 87:75–88.
- THOMPSON, R. M. AND C. R. TOWNSEND. 2005. Food-web topology varies with spatial scale in a patchy environment. *Ecology* 86: 1916–1925.
- WARREN, P. H. 1989. Spatial and temporal variation in the structure of a freshwater food web. *Oikos* 55:299–311.
- WARREN, P. H. 1994. Making connections in food webs. *Trends in Ecology and Evolution* 9:136–141.
- WERNER, E. E. AND J. F. GILLIAM. 1984. The ontogenetic niche and species interactions in size structured populations. *Annual Review of Ecology and Systematics* 15:393–425.
- WINEMILLER, K. O. 1989. Must connectance decrease with species richness? *American Naturalist* 134:960–968.
- WINEMILLER, K. O. 1990. Spatial and temporal variation in tropical fish trophic networks. *Ecological Monographs* 60:331–367.
- WINEMILLER, K. O. AND C. A. LAYMAN. 2005. Food web science: Moving on the path from abstraction to prediction, p. 10–23. In P. C. de Ruiter, V. Wolters, and J. C. Moore (eds.), *Dynamic Food Webs: Multispecies Assemblages, Ecosystem Development and Environmental Change*. Elsevier, Amsterdam.
- WINEMILLER, K. O. AND G. A. POLIS. 1996. Food webs: What can they tell us about world? p. 1–22. In G. A. Polis and K. O. Winemiller (eds.), *Food Webs: Integration of Patterns and Dynamics*. Chapman and Hall, New York.
- YODZIS, P. 1988. The indeterminacy of ecological interactions as perceived through perturbation experiments. *Ecology* 69:508–515.
- YODZIS, P. 1993. Environmental and trophodiversity, p. 26–38. In R. E. Ricklefs and D. Schluter (eds.), *Species Diversity in Ecological Communities*. University of Chicago Press, Chicago, Illinois.

Received, September 15, 2005

Revised, February 27, 2006

Accepted, February 28, 2006