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SPATIAL AND HABITAT-MEDIATED FOOD WEB DYNAMICS IN AN OYSTER-DOMINATED ESTUARY

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ABSTRACT Understanding spatial dynamics and creating spatial boundaries of marine food webs is an important topic that resource managers are beginning to understand. Food web structure, mediated by spatial and habitat differences, was examined in a subtropical estuary using stomach content and stable isotope analyses. The goal of this study was to characterize the trophic structure in subtidal oyster reef, intertidal marsh edge, and nonvegetated bottom habitats. Fish and macroinvertebrates were sampled seasonally from July 2006 to April 2007. Spatially, the lower region of the bay supported a more robust food web, with more species and links (72 and 130, respectively) than the upper bay (63 and 87, respectively). Trophic levels (determined by ^{15}N) and carbon sources (determined by ^{13}C) were combined with dietary links (determined by stomach contents), relative population levels, and linkage strength (determined by food volume) to construct 5 dimensional food web diagrams for the 2 regions and 3 habitats studied. The ^{15}N isotope indicated differences in trophic levels and probable nitrogen sources among regions whereas the ^{13}C isotope inferred differences in carbon sources among regions in the Lavaca Bay ecosystem. This evidence suggests that lower Lavaca Bay is providing an environment conducive to robust food webs, and that locations in relatively close proximities within the same estuary can have very different food web interactions. Our data suggest there are significant differences in food web structure at the spatial scales examined in Lavaca Bay, which supports the idea that food webs are compartmentalized. As resource managers move toward ecosystem-based management, they must consider the distinct communities and accompanying food webs associated with the varying habitat types and spatial scales observed in this coastal ecosystem.

KEY WORDS: food web, spatial, stable isotope, stomach contents, oyster reef, habitat

INTRODUCTION

Estuaries are one of the most productive ecosystems (Schelske & Odum 1962) and include a variety of habitat types such as intertidal marshes, seagrass beds, mangrove forests, and oyster reefs that serve as feeding areas and habitat for the many estuarine-dependent species (Minello 1999, Beck et al. 2001). Clearly, these areas are essential to estuarine organisms, because they determine their relative fitness, food selection, and ultimate survival (Beck et al. 2001). Of the putative estuarine habitat types, oyster reefs lag behind in our ecological understanding, particularly as they relate to food web dynamics.

Subtidal reefs comprised of the eastern oyster *Crassostrea virginica* (Gmelin 1791) are both a fishery resource and an important estuarine habitat. These reefs were once a prominent feature along the U.S. Gulf and Atlantic coasts. Overharvesting, disease, and other anthropogenic impacts have reduced historical coverage to a fraction of their coverage, inducing potentially major changes in marine food webs (Carpenter & Kitchell 1993, Botsford et al. 1997, Micheli & Peterson 1999, Lenihan et al. 2001). For example, the percent coverage of subtidal oyster reefs in Lavaca Bay, Texas (the focus area for this study), has decreased by approximately 60% since 1913 (Simons et al. 2004). The continued loss of estuarine habitat could disrupt the life history of numerous ecologically important species that use these areas and, ultimately, could alter the flow of nutrients and energy throughout the bay system.

Key among the ecological services these habitats provide, oyster reefs support a potentially complex, dynamic food web with a large variety of fish and macroinvertebrates (Peterson et al. 2003). Food web interactions form the basis of ecosystem processes and influence important pathways in the cycling of matter, energy, and nutrients (de Ruiter et al. 2005). Studies to understand these food web relationships more completely are commonly performed via stomach content and stable isotope analysis (Winemiller et al. 2007).

Traditional stomach content analysis in conjunction with stable isotope data can provide an estimate of the mean level of organic matter assimilated by a given species (Harrigan et al. 1989, Creach et al. 1997). Coupling both techniques is beneficial because stomach content analysis determines specific spatial feeding patterns and specific species interactions that are not readily apparent using stable isotope ratios alone (de Ruiter et al. 2005). Stomach content analysis provides a snapshot of the organism's diet, whereas stable isotope analysis gives information on food that is assimilated over time, not what is merely ingested. Nitrogen isotopic distributions are widely accepted and robust indicators of trophic position in marine ecosystems, where ^{15}N enrichment increases predictably with trophic level of consumers (Peterson & Fry 1987, Hansson et al. 1997, Kwak & Zedler 1997). Carbon isotopes have proven to be good discriminators of sources of organic carbon in the diet of estuarine and marine organisms (Peterson & Howarth 1987, Fry 2006). Stable isotopes of carbon and nitrogen have been used together to study food web structure in a number of ecosystems and communities (Fredriksen 2003, Kang et al. 2003, Kojadinovic et al. 2006, Dang et al. 2009, Lefebvre et al. 2009). Recently, food web scientists have obtained superior food web descriptions based on higher resolution data encompassing multiple techniques that allow further investigation into

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spatial variations (Cocheret de la Moriniere et al. 2003, Mantel et al. 2004, Akin & Winemiller 2006, Suzuki et al. 2008). Few studies have formulated food webs that incorporate both spatial and habitat differences (de Ruiter et al. 2005, Amarasekare 2008, but see Hansson et al. 1997, Cocheret de la Moriniere et al. 2003, Kang et al. 2003, Dang et al. 2009, Lefebvre et al. 2009), particularly in estuaries. The coupling of these techniques has the potential to provide useful insight to the highly complex and dynamic structure of estuarine food webs.

Food webs are also open systems influenced by processes in adjacent areas, making them spatially heterogeneous (Polis & Winemiller 1996). Food web theoreticians have suggested that higher order predators exert a partially stabilizing effect on a variable and expansive spatial structure (de Ruiter et al. 1995, McCann et al. 2005, Holt 2006, Rooney et al. 2006). Each food web can be defined according to habitat units nested within larger ecosystems (de Ruiter et al. 2005). Small-scale food webs are lined spatially by transient predators that connect subwebs of varying habitats into a single, complex system encompassing the entire ecosystem (Winemiller 2007, Amarasekare 2008). Spatial factors such as habitat type and proximity to other hydrodynamic systems are important factors that can influence the distribution of nekton within an estuarine food web. Thus, the purpose of this study was to define the spatial food web structure in a Texas estuary.

This study examines spatial relationships of food web structure in 2 regions and 3 habitats (subtidal oyster reefs, marsh edge, and nonvegetated bottom) in Lavaca Bay, Texas, by constructing food webs through stomach content and stable isotope (^{13}C and ^{15}N) analysis. Food web metrics such as mean gut content trophic level, $\delta^{15}N$, $\delta^{13}C$, food web species richness, number of trophic links, and food web diversity are also used to assess and segregate spatial food web modules.

MATERIALS AND METHODS

Study Area

Lavaca Bay is located in the northwest Matagorda Bay system on the central Texas coast (Fig. 1). Shallow subtropical estuaries, such as Lavaca Bay, are highly dynamic ecosystems with hydrological changes influenced by precipitation, winds, and tides (Akin & Winemiller 2006). Estuarine habitat types in the Lavaca Bay system include intertidal and subtidal oyster reefs (*Crassostrea virginica*), nonvegetated bottom (NVB), submerged aquatic vegetation (SAV) (dominated by *Halodule wrightii* Ascherson), and intertidal salt marshes (dominated by *Spartina alterniflora* Loisel). This study was conducted in 2 regions (upper and lower) and replicate habitat types (subtidal oyster reef, marsh edge [SAV occurred at marsh edge in lower bay sites], and NVB) in each region. Upper bay sites were located in the northern sector of the bay, whereas the lower bay sites in the southern sector were located inside and outside the mouth of Keller Bay (Fig. 1).

Sampling Design

In upper and lower Lavaca Bay regions, samples were collected at each of 2 replicate sites on: subtidal oyster reef (reef), NVB, and marsh-edge (marsh) habitats. In lower Lavaca Bay, the marsh was interspersed with and adjacent to SAV. Each site was sampled 4 times on a seasonal basis, with sampling trips conducted in summer (July) and fall (October) 2006, and winter (February) and spring (April) 2007.

Sampling gear included an epibenthic sled and a modified epibenthic sled for collecting small nekton over reefs (Reese et al. 2010). The epibenthic sled consists of a metal frame with an opening of 0.6 m (length) by 0.75 m (height), with a 1-mm-mesh conical plankton net. The sled was pulled ~17 m alongside marsh and through seagrass meadows, covering 10 m^2 of bottom. Six replicate tows were made at each site on each visit. This has been shown as effective and efficient gear for sampling nekton in seagrass meadows by numerous investigators (for example, see Stunz et al. [2002]). The modified epibenthic sled is similar but equipped with steel teeth designed to agitate the oyster reef surface, and an oyster exclusion net to keep oyster shells from entering the net while collecting nekton, which may be found among the oyster shells. This gear has been used successfully in sampling deep oyster reefs (Reese et al. 2010).

Large, mobile transient fish were sampled using gill nets (29 m long × 1 m deep; one half of the net was constructed from 5-cm and the other half from 2.5-cm monofilament mesh) at each site. One gill net was deployed from 2–4 h on each of the 2 replicates of the 3 habitats (marsh, NVB, and reef) in each region on all sampling trips. An oyster dredge (see Texas Parks and Wildlife Department [2002] for a detailed description) was used to collect oysters from subtidal reefs.

Stomach Content Sampling and Analysis

Fish collected by gill net were identified to species and measured to the nearest millimeter in total length. Up to 10 specimens of each species were retained for analysis from each sampling location and from each sampling event. Representative species were kept for stomach content and stable isotope analysis, and characterized the range and occurrence of these flora and fauna. For each species collected, representative sizes of both large and small individuals were sampled to incorporate multiple life history phases. Immediately on collection in the field, the entire stomach (excluding the intestines) was removed and preserved in 10% formalin. In the laboratory, all food items in the anterior half of the gut were assessed.

Stomach contents were identified to the lowest possible taxon, enumerated, and measured volumetrically based on the methods used by Akin and Winemiller (2006). Prey items were assigned to 1 of 65 categories, with variable levels of taxonomic aggregation ranging from species to orders and functional groups. Volumetric measurement of large prey items (>0.1 mL) was accomplished by dry-blotting and measuring water displacement in a graduated cylinder. For volumes of prey items less than 0.1 mL, items were placed on a glass slide and estimated visually by comparing the volume with a water droplet of known volume extracted from a graduated pipette.

Stable Isotope Sampling and Analysis

Samples of vegetation (*Halodule wrightii* and *Spartina alterniflora*), particulate organic matter (POM; mostly phytoplankton), benthic algae, benthic organic matter (BOM), oysters, macroinvertebrates, and fish tissue were collected on each sampling trip and at each site where applicable for carbon and nitrogen stable isotope analysis. Water column POM samples (100 mL) were filtered through precombusted glass

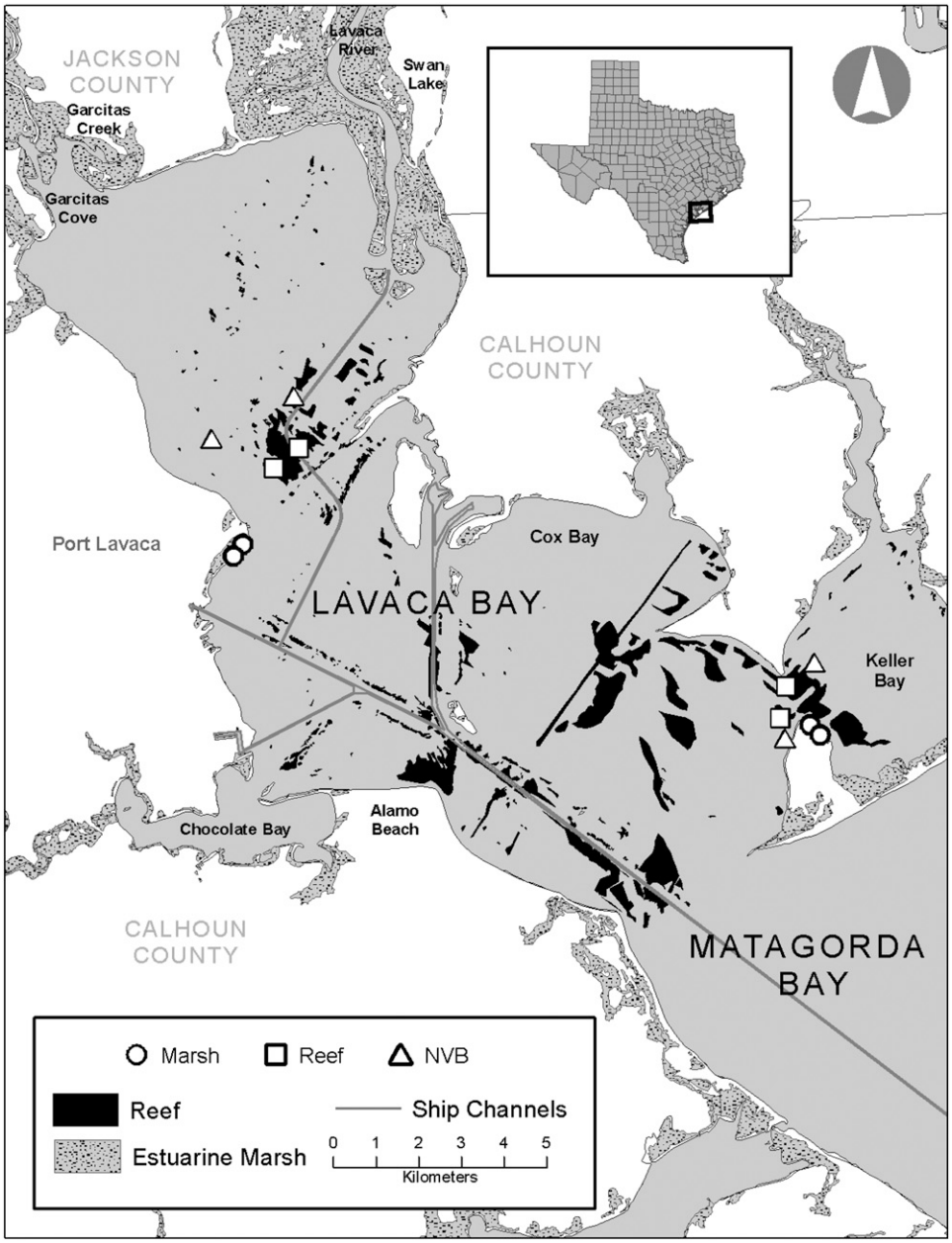

Figure 1. Map of sampling locations in Lavaca Bay, Texas, where marsh sites (circles), reef sites (squares), and nonvegetated bottom sites (triangles) were sampled from July 2006 to April 2007. Underlying substrate/habitat layers were determined by sidescan sonar (Simons et al. 2004).

microfiber filters (Whatman GF/F) and stored in precombusted aluminum foil packets. Sediment samples for the purpose of collecting benthic algae and BOM were collected with a modified Van Veen grab. Fish collected by gill net, and epibenthic and modified epibenthic sleds were processed in the field to remove approximately 10 g of dorsal epaxial white muscle tissue. All plant and fish tissue samples for stable isotope analysis were rinsed thoroughly with DI water in the field and were frozen immediately on dry ice in the field for transport to the laboratory, where they were stored in a freezer at –80°.

Fish and macroinvertebrate tissue, BOM, and vegetation samples were freeze-dried for approximately 48 h or until all moisture was removed. Dried samples were ground to a fine powder with a precombusted mortar and pestle (with the exception of POM), and then stored in precombusted glass vials. Organic samples were analyzed for stable isotope ratios ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) at the Analytical Chemistry Laboratory, Institute of Ecology, University of Georgia, Athens, Georgia. All samples were weighed to 10^{-6} g and pressed into Ultra-Pure tin capsules (Costech). The BOM samples and macroinvertebrate samples with suspected inorganic carbon present were acidified with 20% HCl and redried. Samples were then dry-combusted (micro Dumas technique) with a Carlo Erba CHN elemental analyzer. Purified gases (CO_2 and N_2) were introduced into a Finnigan Delta C mass spectrometer, and the isotopic composition was quantified relative to a standard reference material: carbon in the PeeDee Belemnite and molecular nitrogen gas in the air. For this study, the δC values reported

are actual and have not received lipid-rich correction. Results were reported as parts per thousand (‰) differences from the corresponding standard:

$$\delta X = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}}\right) - 1\right] \times 10^3,$$

where X is ^{13}C or ^{15}N and R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$.

Data Analysis

Stomach Content Analysis

Trophic level of fish was calculated using the following formula, presented in Adams et al. (1983):

$$TL_i = 1.0 + \sum_{j=1}^{n} TL_j(P_{ij}),$$

where TL_i is the trophic level of consumer species i, TL_j is the trophic level of prey item j, and P_{ij} is the fraction of the consumed food (volume) of species i consisting of prey species j. Prey item trophic level was calculated as the mean trophic level values of values from researched sources (Hobson 1993, Christian & Luczkovich 1999, Cortes 1999, Milessi et al. 2005, Froese & Pauly 2010).

The index of relative importance (IRI) was calculated and can be defined as

$$IRI = (\%N + \%V)\%FO,$$

where $\%N$ is the percent number of a prey item, $\%V$ is the percent volume, and $\%FO$ is the percent frequency of occurrence (Pinkas et al. 1971). The IRI values were calculated for each prey item in the stomach contents of each fish examined.

Food web diversity was calculated using the Shannon-Weiner diversity index H′:

$$H' = -\sum p_i \ln p_i,$$

where p_i is the proportion of the i^{th} item in the food web, and ln p_i is the natural log of the proportion. Because of very large numbers in a small number of stomachs, the Dendrobranchiata larvae (3,870 total in 3 stomachs) were not included in the H′ calculations.

Stable Isotope Analysis

The trophic levels of consumers were calculated using the formula described in Jepsen and Winemiller (2002):

$$TL = \left(\frac{\delta^{15}N_{\text{consumer}} - \delta^{15}N_{\text{reference}}}{3.3}\right) + 1,$$

where $\delta^{15}N_{\text{reference}} = 5.97$, which was the mean of all vegetation, sediment/BOM, and phytoplankton/POM samples; and the denominator value (3.3) was the estimated mean trophic enrichment (fractionation) of $\delta^{15}N$ between consumers and their food sources as defined in Winemiller et al. (2007).

Statistical Analysis

Differences in mean isotopic signatures and calculated trophic levels were tested among spatial regions and habitats. A generalized linear model was used to conduct analysis of variance (SAS Institute Inc. 1989) because of unbalanced sample sizes. When data did not meet the assumptions of normality, a 1-way nonparametric analysis of variance (NPAR1WAY) was used (SAS Institute Inc. 1989). Significant differences among treatments were evaluated post hoc using Tukey's HSD (Zar 1999). All values were considered significant at $\alpha = 0.05$. Preliminary analysis of replicates showed no site effect; thus, these areas were pooled for all analyses in this study.

An analysis of similarities (ANOSIM) was performed using PRIMER 6 software (Clarke & Gorley 2006). The ANOSIM was based on a Bray-Curtis similarity matrix calculated from the log(1 + x)-transformed IRI. The ANOSIM significance test compared similarities of diet composition through the IRI of food items between samples. This calculation gives evidence of differences in diet composition. The global R indicates the degree of similarity between the tested groups and ranges from –1 to 1. If all replicates within a site are more similar to each other than any other replicate from a different site, the value of R is 1. Values of R close to 0 indicate the similarity between sites is very high (Clarke & Gorley 2006).

To calculate the contribution of diet items in the food webs from different regions and habitats of Lavaca Bay, an analysis of similarity percentages (SIMPER) was performed using PRIMER 6 software (Clarke & Gorley 2006). The SIMPER was based on the log(1 + x)-transformed IRI data matrix. SIMPER was used to reveal the mean Bray-Curtis dissimilarity between groups of diet items.

A principle components analysis (PCA) was performed using PRIMER 6 software (Clarke & Gorley 2006). The PCA was run on a 4th root transformation of 7 of the food web metrics derived from the stomach content and stable isotope data.

Food Web Statistics

The number of species (S) or nodes in the food webs included all species or higher level taxonomic groups into which organisms were identified. The number of trophic interactions or links (L) was the number of non-0 elements in the community matrix. The linkage density for each community food web was defined as $D = \frac{L}{S}$. Connectance, which is a measure of the system complexity or the degree to which organisms interact in the web, can be defined in at least 3 ways. Trophic connectance (Warren 1989) is the number of links divided by the number of possible links: $C_T = \frac{L}{S(S-1)}$. Lower connectance (Pimm et al. 1991), defined as $C_L = \frac{2L}{S(S-1)}$, takes into account that $S(S-1)$ is the correct estimate of possible links only when cannibalism is excluded. Directed connectance (Martinez 1991), defined as $C_D = \frac{L}{S^2}$, takes into account both cannibalism and mutual predation between species.

RESULTS

Overall Food Web Structure

We examined the stomach contents of 24 species of fish from 15 families from which a total of 483 stomachs were analyzed throughout all habitat types, regions, and seasons combined (Table 1). Only 13.5% of the stomachs investigated were empty. The Gulf menhaden *Brevoortia patronus* (25.5%) represented the largest percentage of stomachs examined whereas *Bagre marinus* (16.9%) and *Ariopsis felis* (15.5%) also comprised a high percentage of the stomachs examined. Two shark species,

Sphyrna tiburo (Linnaeus, 1758) and *Carcharhinus limbatus* (Müller & Henle, 1839), which were captured only in the lower region of the bay during summer over subtidal oyster reefs and NVB habitats, were also examined.

A total of 60 species of plants, invertebrates, and fish from 41 different families were sampled for carbon and nitrogen stable isotopic signatures. The prominent vegetation (*Halodule wrightii* and *Spartina alterniflora*) had mean $\delta^{13}C$ values of –11.74‰ and –13.25‰, respectively. Other sources of primary production, BOM and POM, had mean $\delta^{13}C$ values of –17.61‰ and –20.34‰ (Table 2). It is important to note that $\delta^{13}C$ values were not lipid corrected. As a result, tissues rich in lipids may be depleted in $\delta^{13}C$ relative to those rich in proteins. Fish occurring in trophic levels 2–3 or between $\delta^{15}N$ values of 9‰ and 12‰ include mostly planktivorous and herbivorous species, whereas progressive delineations in trophic levels represent omnivorous and finally piscivorous fish. Fish such as *Cynoscion nebulosus* (Cuvier, 1830) (8.74‰), *Bairdiela chrysoura* (Lacepède, 1802) (7.01‰), *Leiostomus xanthurus* (Lacepède, 1802) (6.75‰), and *Mugil cephalus* (Linnaeus, 1758) (6.15‰), exhibited a wide range of $\delta^{15}N$ values, whereas species such as *Gobius* sp. (0.26‰), *Orthopristis chrysoptera* (Linnaeus, 1766) (0.08‰), and *Sphyrna tiburo* (0.40‰) displayed a very narrow range of $\delta^{15}N$.

A bivariate scatterplot of the generalized taxonomic groups (primary producers, invertebrates, and fish) of the Lavaca Bay food web indicated that fish were usually more enriched in terms of $\delta^{15}N$ relative to invertebrates and primary producers, whereas invertebrates were generally more enriched in $\delta^{15}N$ relative to producers (Fig. 2). Inferences can be made about the carbon sources of many of the fauna by placement of $\delta^{13}C$ values along the *x*-axis relative to the flora represented. Particulate organic matter, which is mostly phytoplankton, was least enriched whereas *Halodule wrightii* was the most enriched of the primary producers. A large portion of the consumer species were located between $\delta^{13}C$ values of –16‰ to –21‰, which are generally centered over POM and BOM on the *x*-axis (Fig. 2).

Spatially Mediated Food Web Structure

The mean trophic level based on stomach content data between the upper (TL = 2.50) and lower (TL = 2.58) regions was not significantly different (NPAR1WAY, $F_{1,999} = 1.59$, $P < 0.2082$). The top trophic level predators based on mean trophic level using stomach contents in the upper region of Lavaca Bay were *Cynoscion arenarius* (Ginsburg, 1930) (TL = 3.93), *Bagre marinus* (TL = 3.86), *Caranx hippos* (Linnaeus, 1766) (TL = 3.86), and *Sciaenops ocellatus* (Linnaeus, 1766) (TL = 3.93), whereas the top trophic level predators in the lower region of the bay were *C. hippos* (TL = 4.08), *Carcharhinus limbatus* (TL = 4.07), *C. arenarius* (TL = 3.96), *B. marinus* (TL = 3.83), *Cynoscion nebulosus* (TL = 3.81), *Sphyrna tiburo* (TL = 3.77), and *S. ocellatus* (TL = 3.76). The most notable regional difference was the presence of sharks in the lower region's food web.

TABLE 1.

List of families and species examined in stomach content analysis, size range (in millimeters total length), season, region of the bay, habitat types where they were collected, number of stomachs examined, and the number of those that were empty for the fishes collected from Lavaca Bay, Texas, from July 2006 to April 2007.

Family	Species	Size range (mm)	Season	Region	Habitat	No. examined	No. empty
Sphyrnidae	*Sphyrna tiburo*	600–652	SU	L	R, NVB	4	0
Carcharhinidae	*Carcharhinus limbatus*	407–606	SU	L	R, NVB	4	1
Dasyatidae	*Dasyatis sabina*	137–137	SP	U	M	1	0
	Elops saurus	348–348	SU	U	NVB	1	0
Clupeidae	*Brevoortia patronus*	136–355	SU, WI, FA, SP	U, L	R, NVB, M	123	6
Polynemidae	*Polydactylus octonemus*	155–203	SU, WI, FA, SP	U, L	R, NVB, M	34	18
Ariidae	*Ariopsis felis*	152–402	SU, FA, SP	U, L	R, NVB, M, M/SAV	75	3
	Bagre marinus	207–625	SU, FA, SP	U, L	R, NVB	82	3
Mugilidae	*Mugil cephalus*	213–430	SU, FA, SP	U, L	M, M/SAV	5	1
Sparidae	*Archosargus probatocephalus*	235–502	FA	U, L	M, M/SAV	8	1
	Lagodon rhomboides	126–126	FA	L	NVB	1	0
Haemulidae	*Orthopristis chrysoptera*	163–163	FA	L	R	1	0
Stromateidae	*Peprilus paru*	76–213	SU, FA	U, L	R, NVB	3	0
Sciaenidae	*Bairdiella chrysoura*	170–196	FA, WI, SP	U, L	R, NVB, M/SAV	8	0
	Cynoscion arenarius	216–371	SU, FA, SP	U, L	R, NVB	17	6
	Cynoscion nebulosus	221–465	SU, FA, SP	U, L	R, NVB, M, M/SAV	13	2
	Leiostomus xanthurus	140–197	FA, WI, SP	U, L	R, NVB, M/SAV	39	16
	Menticirrhus littoralis	197–273	SU, FA, SP	U, L	R, NVB, M, M/SAV	37	4
	Micropogonias undulatus	174–176	SU	L	R	3	0
	Pogonias cromis	296–370	FA, SP	U, L	M, M/SAV	6	0
	Sciaenops ocellatus	355–568	FA, SP	U, L	M, M/SAV	6	2
Pomatomidae	*Pomatomus saltatrix*	183–183	SP	U	M	1	1
Carangidae	*Caranx hippos*	141–175	SU	U, L	R, NVB, M/SAV	7	0
Scombridae	*Scomberomorus maculatus*	534–560	SU, SP	U, L	R, NVB	4	1
Total						483	65

FA, fall; L, lower; M, marsh; M/SAV, marsh/submerged aquatic vegetation; NVB, nonvegetated bottom; R, oyster reef; SP, spring; SU, summer; U, upper; WI, winter.

TABLE 2.

$\delta^{13}C$ and $\delta^{15}N$ values in ‰ of flora and fauna collected in Lavaca Bay, Texas, among all seasons, habitat types, and regions.

Sample Type	Family	Species	Code	$\delta^{13}C$	$\delta^{15}N$	*n*
Vegetation	BOM	Benthic organic matter	BOM	–17.61 ± 0.60	5.57 ± 0.18	36
	Cymodoceaceae	*Halodule wrightii*	HABE	–11.74 ± 0.20	3.50 ± 0.62	4
	Poaceae	*Spartina alterniflora*	SPAL	–13.25 ± 0.17	6.01 ± 0.66	12
	POM	Particulate organic matter	POM	–20.34 ± 0.99	6.47 ± 0.34	24
	Ulvaceae	*Ulva lactuca*	ULLA	–18.54 ± 0.00	5.96 ± 0.00	1
Invertebrate	Alpheidae	*Alpheus heterochaelis*	APHE	–18.26 ± 3.75	11.36 ± 0.24	2
	Diogenidae	*Clibanarius vittatus*	CLVI	–13.93 ± 0.00	7.33 ± 0.00	1
	Hippolytidae	*Tozeuma carolinense*	TOCA	–13.11 ± 0.00	7.47 ± 0.00	1
	Menippidae	*Menippe adina*	MEAD	–17.55 ± 1.13	9.18 ± 0.81	9
	Ostreidae	*Crassostrea virginica*	CRVI	–22.79 ± 0.38	9.29 ± 0.24	10
	Palaemonidae	*Palaemonetes vulgaris*	PAVU	–16.54 ± 0.56	9.35 ± 0.42	21
	Porcellanidae	Porcellanidae spp.	POSP	–18.47 ± 2.38	9.40 ± 2.90	2
	Portunidae	*Callinectes sapidus*	CASA	–17.32 ± 0.65	9.58 ± 0.52	15
	Xanthidae	Xanthidae spp.	XASP	–22.00 ± 0.29	11.99 ± 0.66	2
	Peneaidae	Peneaidae spp.	PESP	–17.10 ± 0.48	9.84 ± 0.90	3
		Farfantepenaeus aztecus	FAAZ	–16.56 ± 0.60	8.65 ± 0.37	16
		Farfantepenaeus spp.	FASP	–17.39 ± 0.59	9.99 ± 0.51	10
		Litopenaeus setiferus	LISE	–17.45 ± 0.81	9.93 ± 0.50	10
Fish	Ariidae	*Ariopsis felis*	ARFE	–19.23 ± 0.37	14.05 ± 0.22	24
		Bagre marinus	BAMA	–18.62 ± 0.20	15.53 ± 0.23	21
	Atherinopdisae	*Menidia menidia*	MEME	–17.70 ± 0.00	10.13 ± 0.00	1
	Carangidae	*Chasmodes bosquianus*	CHBO	–22.00 ± 0.00	14.59 ± 0.00	1
	Carcharhinidae	*Caranx hippos*	CAHI	–18.65 ± 0.78	14.47 ± 0.51	4
	Clupeidae	*Carcharhinus limbatus*	CALI	–17.01 ± 0.50	16.16 ± 0.30	2
	Cynoglossidae	*Brevoortia patronus*	BRPA	–19.96 ± 0.20	13.47 ± 0.21	36
	Cyprinodontidae	*Symphurus plagiusa*	SYPL	–19.14 ± 0.28	11.79 ± 0.47	3
	Dasyatidae	*Cyprinodon variegatus*	CYVA	–14.47 ± 1.36	7.06 ± 0.27	3
	Elopidae	*Dasyatis sabina*	DASA	–17.88 ± 0.00	14.09 ± 0.00	1
	Engraulidae	*Elops saurus*	ELSA	–18.54 ± 0.05	13.94 ± 1.50	2
	Gerreidae	*Anchoa mitchilli*	ANMI	–21.00 ± 0.59	13.43 ± 0.36	10
	Gobiesocidae	*Eucinostomus argenteus*	EUAR	–17.47 ± 0.00	10.55 ± 0.00	1
	Gobiidae	*Gobiesox* spp.	GOS1	–21.01 ± 0.14	13.98 ± 0.35	2
		Gobiosoma bosc	GOBO	–18.32 ± 0.85	11.92 ± 0.54	16
		Gobius spp.	GOS2	–21.00 ± 0.07	14.49 ± 0.13	2
		Microgobius gulosus	MIGU	–17.84 ± 3.68	11.98 ± 1.89	2
		Microgobius thalassinus	MITH	–18.65 ± 0.00	13.29 ± 0.00	1
	Haemulidae	*Orthopristis chrysoptera*	ORCH	–18.49 ± 0.22	13.70 ± 0.04	2
	Lutjanidae	*Lutjanus argentimaculatus*	LUAR	–15.15 ± 0.00	11.51 ± 0.00	1
	Mugilidae	*Mugil cephalus*	MUCE	–16.14 ± 0.94	9.36 ± 1.32	4
	Paralichthyidae	*Citharichthys spilopterus*	CISP	–18.50 ± 0.58	12.28 ± 0.30	7
		Paralichthys lethostigma	PALE	–16.54 ± 0.00	10.36 ± 0.00	1
	Polynemidae	*Polydactylus octonemus*	POOC	–17.50 ± 0.00	15.12 ± 0.00	1
	Pomatomidae	*Pomatomus saltatrix*	POSA	–17.23 ± 0.00	15.27 ± 0.00	1
	Sciaenidae	*Bairdiella chrysoura*	BACH	–18.79 ± 0.79	16.16 ± 1.11	5
		Cynoscion arenarius	CYAR	–18.12 ± 0.28	15.20 ± 0.15	7
		Cynoscion nebulosus	CYNE	–17.45 ± 0.69	13.71 ± 0.71	12
		Leiostomus xanthurus	LEXA	–19.36 ± 0.53	13.78 ± 0.42	16
		Menticirrhus littoralis	MELI	–17.08 ± 0.35	13.94 ± 0.24	13
		Micropogonias undulatus	MIUN	–17.37 ± 0.47	12.82 ± 0.37	13
		Pogonias cromis	POCR	–17.06 ± 1.35	12.03 ± 1.14	4
		Sciaenops occelatus	SCOC	–15.78 ± 1.08	12.38 ± 1.01	4
	Scombridae	*Scomberomorus maculatus*	SCMA	–19.17 ± 0.29	15.93 ± 0.52	3
	Sparidae	*Archosargus probatocephalus*	ARPR	–18.57 ± 0.74	13.09 ± 0.76	6
		Lagodon rhomboides	LARH	–16.59 ± 0.56	11.03 ± 0.50	10
	Sphyrnidae	*Sphyrna tiburo*	SPTI	–16.74 ± 0.01	13.94 ± 0.20	2
	Stromateidae	*Peprilus paru*	PEPA	–20.66 ± 0.71	14.35 ± 1.07	2
	Syngnathidae	*Syngnathus* spp.	SYSP	–19.29 ± 1.40	9.41 ± 1.03	5
Total						430

The species code in this table is used in subsequent figures. Values are mean ± SE with sample size (*n*).

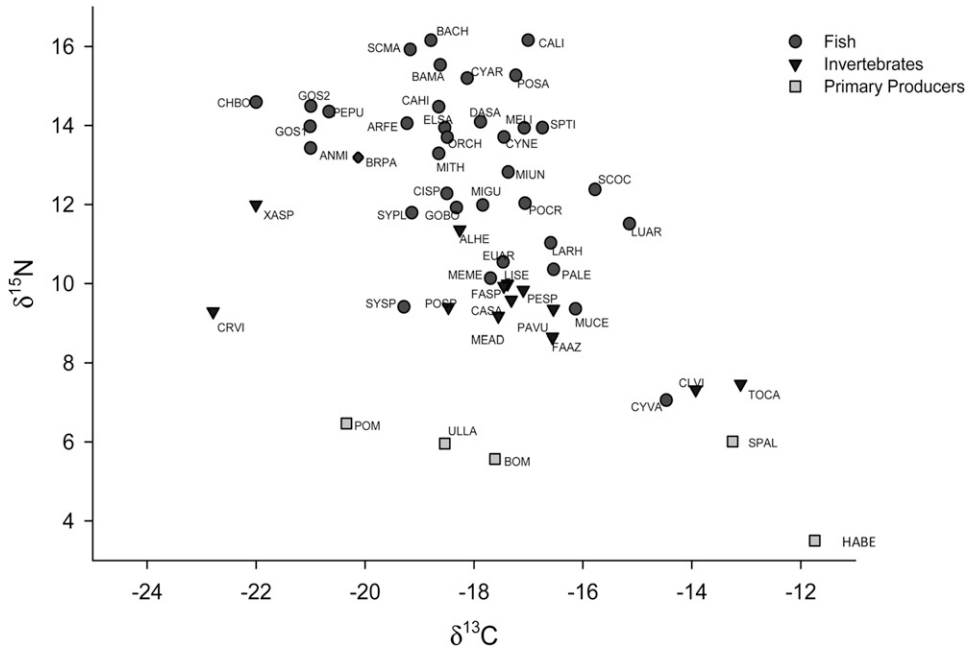

Figure 2. $\delta^{15}N$ and $\delta^{13}C$ values for major food web elements in the Lavaca Bay system. Species codes are listed in Table 2. Potential assimilation of carbon sources by consumers is indicated by degree of alignment among taxa relative to the *x*-axis, and trophic level by relative position on the *y*-axis.

The mean $\delta^{13}C$ signatures of the fishes and macroinvertebrates collected in the lower region were significantly more enriched (–16.90‰) than the upper region (–19.08‰) of Lavaca Bay (ANOVA, $F_{1,92} = 25.35$, $P < 0.001$). The frequency distribution of the $\delta^{13}C$ values by region appears to be disjointed, suggesting a difference in the major contributing carbon source for each region (Fig. 3A). The mean $\delta^{15}N$ values of the fish and macroinvertebrates collected in the upper region (12.00‰) were significantly more enriched than those from the lower region (10.20‰) (NPAR1WAY, $F_{1,428} = 29.63$, $P < 0.001$). The frequency distribution highlights the skewed, more enriched distribution of $\delta^{15}N$ in the upper region compared with the more normally distributed values in the lower region (Fig. 3B). Mean trophic levels determined with $\delta^{15}N$ values indicated a significant difference between the upper (TL = 2.76) and lower (TL = 2.32) regions of Lavaca Bay (NPAR1WAY, $F_{1,430} = 22.08$, $P < 0.0001$). The top trophic level predators for the upper region were *Scomberomorus maculatus* (Mitchill, 1815) (TL = 4.30), *Bairdiella chrysoura* (TL = 4.33), *Bagre marinus* (TL = 3.98), *Cynoscion arenarius* (TL = 3.88), and *Cynoscion nebulosus* (TL = 3.78) whereas the top trophic level predators for the lower region were *Carcharhinus limbatus* (TL = 4.09), *B. marinus* (TL = 3.80), *S. maculatus* (TL = 3.87), and *C. arenarius* (TL = 3.78). An analysis of similarities of diet IRI had a global *R* value of 0.005 and a significance level of 23.3%, indicating no significant differences in diet composition between the upper and lower regions of Lavaca Bay.

We combined population, stomach content, and stable isotope data to construct a food web diagram for the upper and lower regions of Lavaca Bay (Fig. 4). This diagram shows only a fraction of the species and trophic interactions because simplification was necessary to show only the most abundant species and the most important trophic links. A general trend was that many species had a higher $\delta^{15}N$ trophic level in the upper region compared with the lower region. The lower region of the bay, with 72 species and 130 links, supports a richer, more complex food web than the upper region, which had only 63 species and 87 links (Table 3). In addition, linkage density for the lower region was 1.806 whereas it was only 1.381 for the upper region. Trophic connectance and directed connectance were identical in the lower ($C_T = 0.022$) and upper ($C_D = 0.025$) regions, whereas lower connectance was about twice ($C_L = 0.045$ and 0.051, respectively) that for each region (Table 3).

Habitat-Mediated Food Web Structure

Mean $\delta^{13}C$ values of fish and macroinvertebrates captured in the 3 habitats were significantly different (ANOVA, $F_{2,428} = 52.93$, $P < 0.0001$; Fig. 5A). Pairwise comparisons showed that the marsh (–16.5‰) was significantly more enriched than NVB (–19.1‰; Tukey, $q_{428,3} = 11.61$, $P < 0.001$) and reef (–19.2‰; Tukey, $q_{428,3} = 13.00$, $P < 0.001$) habitats. However, NVB and reef were not significantly different (Tukey, $q_{428,3} = 0.36$, $P > 0.50$).

Mean $\delta^{15}N$ values of fish and macroinvertebrates collected in the 3 habitats were significantly different (NPAR1WAY, $F_{2,427} = 23.59$, $P < 0.0001$; Fig. 5B). A pairwise comparison indicated that reef (12.1‰; Tukey, $q_{427,3} = 9.205$, $P < 0.001$) and NVB (11.7‰; Tukey, $q_{427,3} = 6.880$, $P < 0.001$) habitats were significantly more enriched than those found in the marsh (9.7‰). However, NVB and reef were not significantly different (Tukey, $q_{427,3} = 1.576$, $P > 0.5$).

There was no significant difference in trophic levels determined by stomach content for the marsh (TL = 2.43), NVB (TL = 2.51), and reef (TL = 2.62) habitats (NPAR1WAY, $F_{2,998} = 2.97$, $P < 0.0519$). Top trophic level predators on NVB, based on stomach contents data, were *Carcharhinus limbatus*

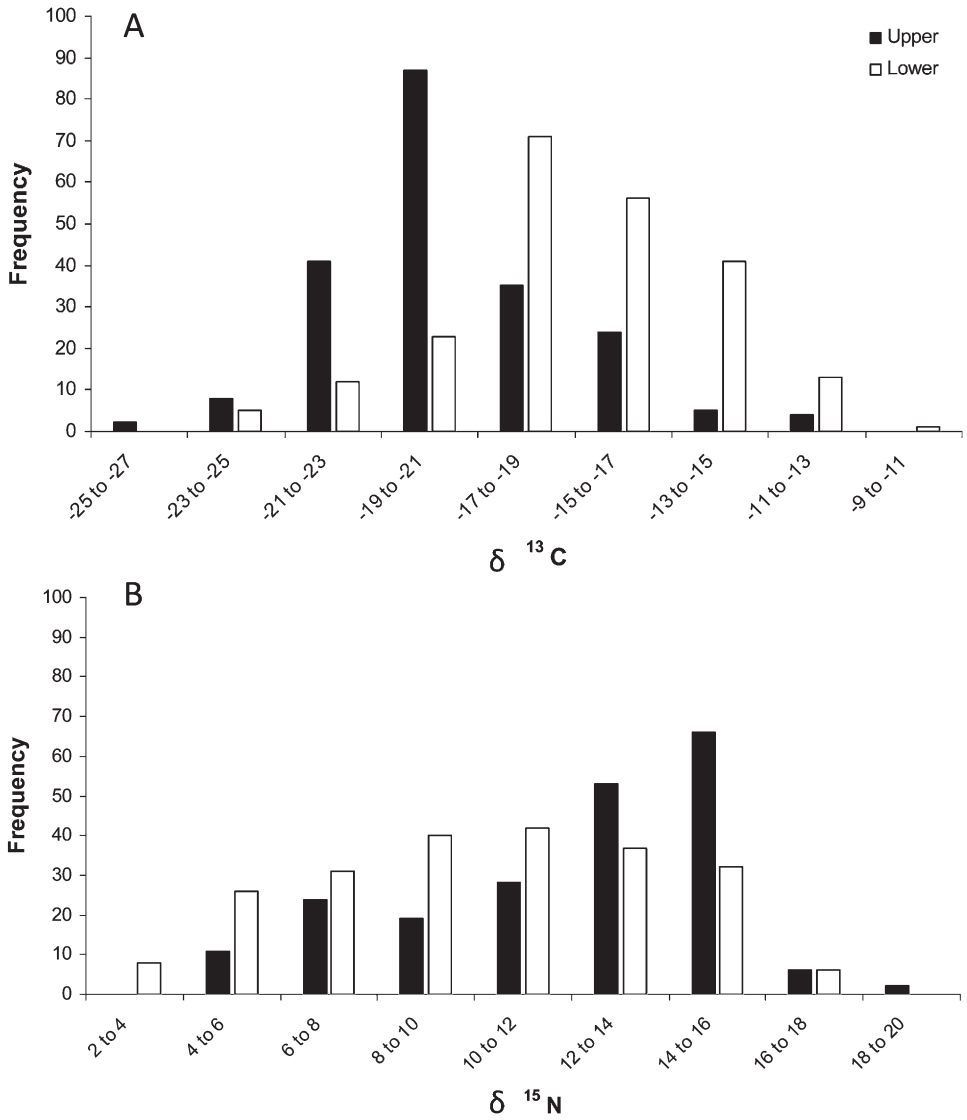

Figure 3. (A, B) Frequency distributions of $\delta^{13}C$ (A) and $\delta^{15}N$ (B) values for organisms from the upper region (filled bars) and the lower region (open bars) of the Lavaca Bay ecosystem.

(TL = 4.84), *Caranx hippos* (TL = 4.24), *Bagre marinus* (TL = 3.86), *Bairdiella chrysoura* (TL = 3.86), and *Sphyrna tiburo* (TL = 3.77); reef habitats were *C. hippos* (TL = 3.97), *Cynoscion nebulosus* (TL = 3.96), *Cynoscion arenarius* (TL = 3.95), *Sphyrna tiburo* (TL = 3.77), and *Carcharhinus limbatus* (TL = 3.68); whereas the top trophic level predators in the marsh habitat were *Sciaenops ocellatus* (TL = 3.80), *C. nebulosus* (TL = 3.65), *Ariopsis felis* (TL = 3.58), and *Menticirrhus littoralis* (Holbrook, 1847) (TL = 3.54).

Mean trophic levels determined with $\delta^{15}N$ values indicated there was a significant difference among habitats (NPAR1WAY, $F_{2,429} = 21.87$, $P < 0.0001$; Fig. 6B). A pairwise comparison indicated that reef (TL = 2.84; Tukey, $q_{429,3} = 8785$, $P < 0.001$) and NVB (TL = 2.73; Tukey, $q_{429,3} = 6.748$, $P < 0.001$) habitats had significantly different mean trophic levels than marsh (TL = 2.15). However, NVB and reef were not significantly different from each other (Tukey, $q_{429,3} = 1.297$, $P > 0.5$). The top trophic level predators for the NVB were *Bairdiella chrysoura* (TL = 4.66), *Carcharhinus limbatus* (TL = 4.18), *Cynoscion nebulosus* (TL = 4.02), *Bagre marinus* (TL = 3.77), and *Cynoscion arenarius* (TL = 3.75), whereas for the reef habitat the top trophic level predator species were *Bagre marinus* (TL = 4.01), *B. chrysoura* (TL = 4.00), *C. limbatus* (TL = 3.99), *Scomberomorus maculatus* (TL = 3.87), and *C. arenarius* (TL = 3.81). The top trophic level predators in the marsh habitat were *Menticirrhus littoralis* (TL = 3.39), *Ariopsis felis* (TL = 3.17), *Micropogonias undulates* (Linnaeus, 1766) (TL = 2.99), *Sciaenops ocellatus* (TL = 2.94), and *C. nebulosus* (TL = 2.96).

An analysis of similarities of diet composition among the 3 habitats resulted in a global R of 0.048 and a significance level (SL) of 0.1%, indicating a significant difference in the diet composition among the 3 habitats. Pairwise analyses indicated significant differences between the marsh and NVB ($R = 0.062$, SL = 0.8%) and the marsh and reef ($R = 0.101$, SL = 0.1%). There was no significant difference between the NVB and reef ($R = 0.012$, SL = 5.6%).

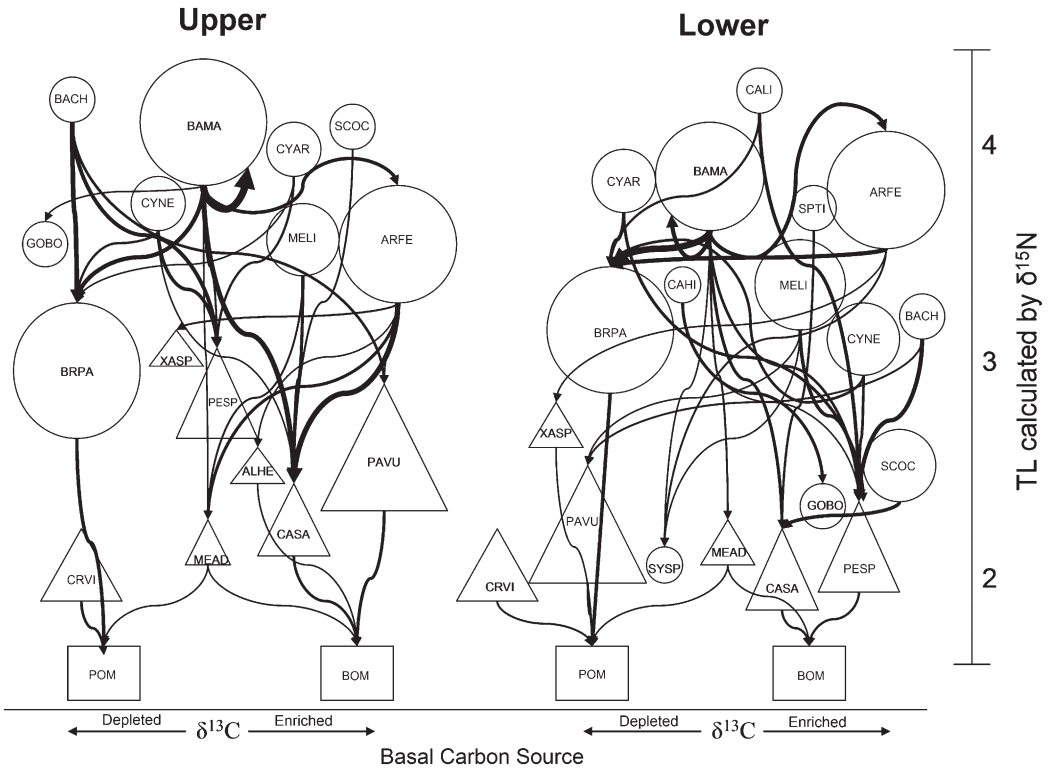

Figure 4. Spatial food web diagram for Lavaca Bay, Texas, constructed from field collection, stomach content, and stable isotope analysis. Position on the *x*-axis is based on the $\delta^{13}C$ value and region of the bay; position on the *y*-axis is based on the trophic level (TL) ($\delta^{15}N$). Relative sizes of nodes (circle, fish; triangle, invertebrate; square, basal carbon source) depict abundance. Relative thickness of links is an interpretation of the numerical and volumetric contribution of prey in the diet of each consumer. Species codes are listed in Table 2. NVB, nonvegetated bottom.

An analysis of similarity percentages indicated that *Actinopterygii* spp. contributed greatly to the average similarity of diet in each of the 3 habitats, and especially for the NVB and reef. Because the *Actinopterygii* spp. category is very general and could represent a number of different species of fish, it is not a very good discriminator and was dropped from the analysis. The SIMPER run without *Actinopterygii* spp. indicated that *Halodule wrightii* (34.43%) and Callianassidae sp. (19.10%) contributed more than 50% of the cumulative average similarity to the marsh diet matrix, and a total of 7 diet items made up more than 90% of the cumulative average similarity (Table 4). The NVB diet matrix was dominated by *Callinectes sapidus* (Rathbun, 1896) (32.66%) and, along with Pleocymata spp. (8.2%), *Brevoortia patronus* (6.56%) and Decapoda spp. (5.82%), made up more than 50% of the cumulative average similarity. A total of 15 food items were required to account for greater than 90% of the cumulative average similarity for the NVB diet matrix (Table 4). Last, the reef diet matrix was dominated by *Menippe adina* (Williams and Felder, 1986) (26.81%) and *C. sapidus* (22.12%), and, along with *B. patronus* (12.87%), made up more than 60% of the cumulative average similarity. A total of 7 food items made up 90% of the cumulative percent similarity (Table 4).

TABLE 3.

Food web statistics for habitats and regions studied in Lavaca Bay, Texas.

	Habitat									Region		
	Marsh			Nonvegetated bottom			Reef					
	Upper	Lower	Total	Upper	Lower	Total	Upper	Lower	Total	Upper	Lower	Total
S	38	31	53	27	55	59	39	45	55	63	72	87
L	39	36	69	33	63	84	47	64	88	87	130	170
D	1.026	1.161	1.302	1.222	1.146	1.424	1.265	1.422	1.600	1.381	1.806	1.954
C_T	0.027	0.039	0.025	0.047	0.021	0.025	0.032	0.032	0.030	0.022	0.025	0.023
C_L	0.056	0.077	0.050	0.094	0.042	0.049	0.063	0.065	0.059	0.045	0.051	0.045
C_D	0.027	0.038	0.025	0.045	0.021	0.024	0.031	0.032	0.029	0.022	0.025	0.023

C_D, directed connectance; C_L, lower connectance; C_T, trophic connectance; D, linkage density; L, number of links; S, number of nodes (species or taxonomic groups).

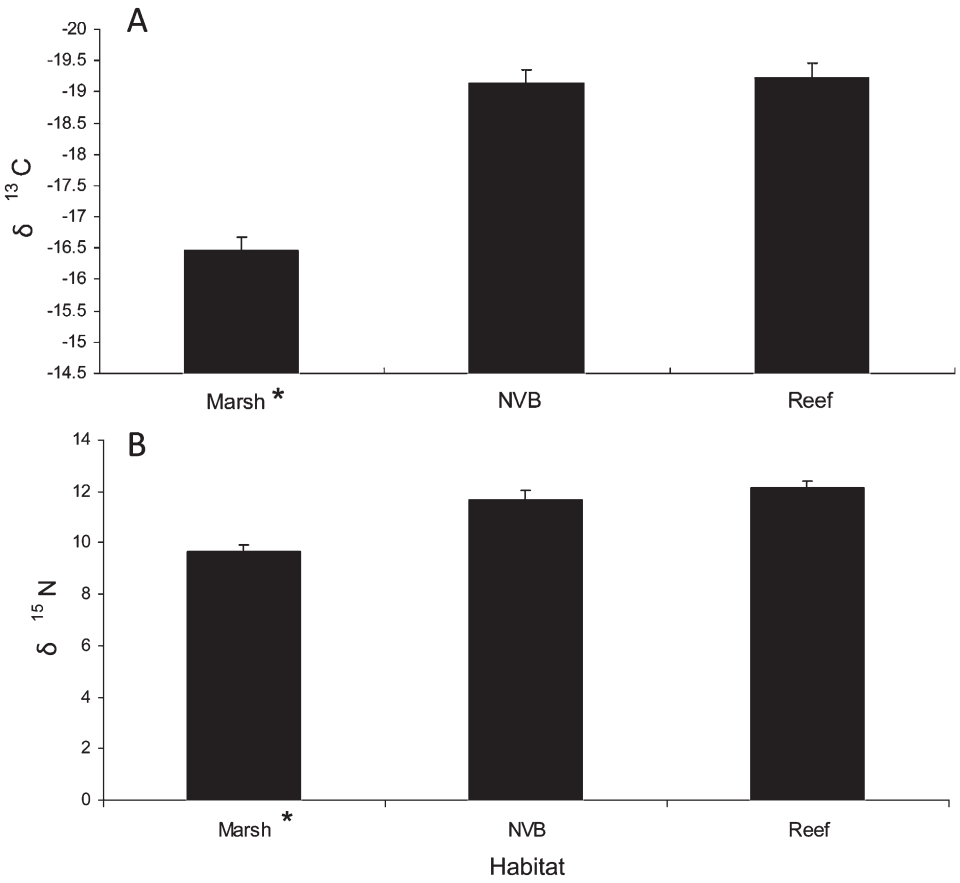

Figure 5. (A, B) Bar charts indicating the mean and SD of the $\delta^{13}C$ (A) and $\delta^{15}N$ (B) values for the upper and lower regions of the marsh, nonvegetated bottom (NVB), and reef habitats. * Significant difference in means.

We combined population, stomach content, and stable isotope data to construct a food web diagram of the 3 habitat types in Lavaca Bay (Fig. 7). Only a fraction of the species and interactions are pictured because simplification of the web was necessary to show only the most abundant species and most important trophic links. Species and trophic interactions by habitat varied greatly. For example, the marsh habitat supports a generally lower trophic level system (TL = 2.43, stomach content; TL = 2.15, $\delta^{15}N$) compared with the NVB (TL = 2.51, stomach content; TL = 2.73, $\delta^{15}N$) and the reef (TL = 2.62, stomach content; TL = 2.82, $\delta^{15}N$) habitats. The NVB and reef food webs had a greater number of species ($n = 59$ and $n = 55$, respectively) than were found near the marsh ($n = 53$), and supported a greater number of trophic links ($n = 84$ and $n = 88$, respectively) than were found on the marsh ($n = 69$). The NVB food web appears to be lacking many of the middle trophic level consumers that are present in the reef food web, suggesting that the higher level predators are using prey sources from other habitats (namely, the reef; Fig. 7). Linkage density was greatest over the reef (D = 1.60) habitat compared with the NVB (D = 1.42) and marsh (D = 1.30) habitats (Table 3). Comparison of all 3 connectance values between the marsh and NVB habitats were nearly identical, whereas those for the reef habitat differed by about 20% (Table 3). In addition, upper and lower marsh and NVB connectance values differed greatly on a regional basis for all 3 measures, but were nearly identical for the upper and lower reef (percent difference between reef habitats in the upper and lower regions: $C_T = 0\%$, $C_L = 3\%$, $C_D = 3\%$; Table 3).

Ecosystem Food Web Structure

We used the food web metrics (Table 5) to analyze the spatial food web topology in multivariate space. The PCA revealed that 79% of the variance was explained by the first principle component, which loads heaviest on the links (–0.735) and WebSR (–0.647) metrics. The second principle component, which accounts for 16.8% of the variation, loaded heaviest on the $\delta^{13}C$ (0.694), $\delta^{15}N$ (0.504), and WebH′ (–0.487) metrics. The first 2 principle component accounted for 96.4% of the variance. In general, food webs from habitats in the upper region of Lavaca Bay were located in the northeastern half of the principle component space (Fig. 8), whereas those from the lower region occupied the southwestern half of principle component space. There is, in general, a wide dispersion among all 6 of the food webs.

DISCUSSION

Spatially Mediated Food Web Structure

The food web in Lavaca Bay, Texas, is dynamic, supporting a variety of organisms from primary producers to tertiary consumers. The magnitude of trophic levels among habitat

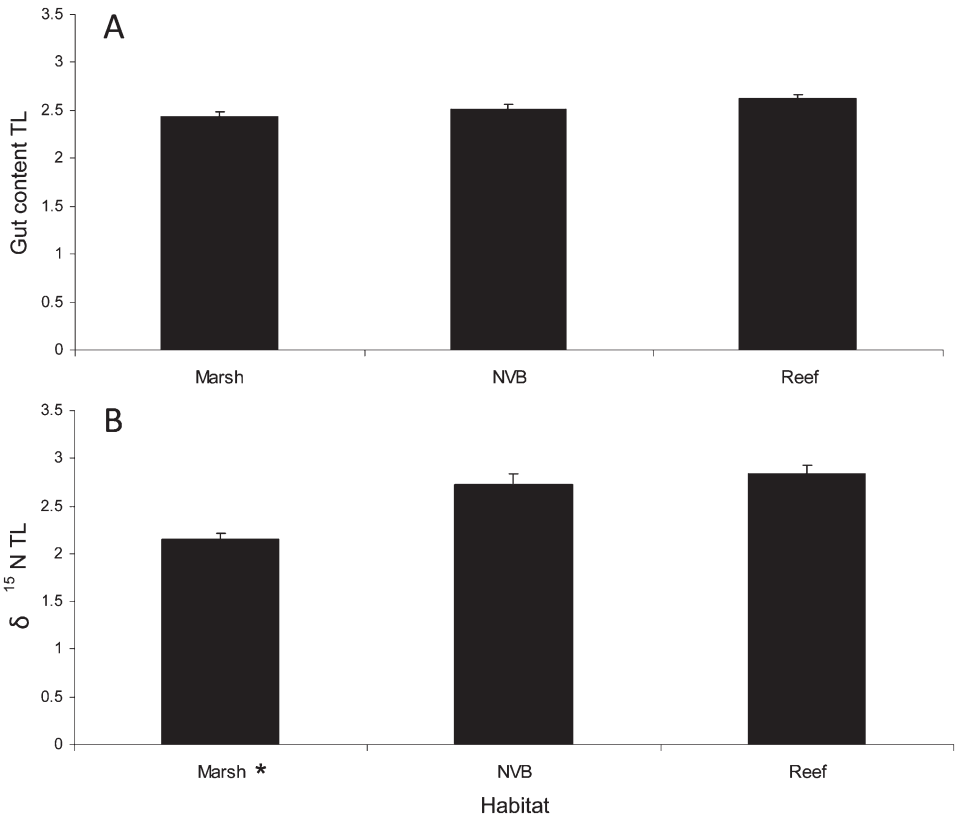

Figure 6. (A, B) Bar charts indicating the mean and SD of the trophic levels calculated using stomach contents (A) and $\delta^{15}N$ values (B) for the upper and lower regions of the marsh, nonvegetated bottom (NVB), and reef habitats. * Significant difference in means.

types varied, with the reef and NVB habitats supporting more robust food webs compared with the marsh. This might suggest that species using the reef and NVB habitats together may be somewhat disjointed from those using marsh habitats. Spatially, the lower region of the bay supported a more robust food web with more species and links. The apparent variability of trophic structure at different spatial scales and between habitat types found in this study provides new information on the dynamic nature of food webs. Although it was not investigated in this study, there are likely seasonal shifts in the food webs in the Lavaca Bay system. The spatially mediated food web structure was assessed by comparing 2 regions of Lavaca Bay that differed primarily in mean salinity (Reese et al. 2010). They found that the lower region food web was more robust with more species and more links than the upper region, but with a slightly lower mean trophic level based on $\delta^{15}N$. Care must be taken when using trophic levels determined from $\delta^{15}N$ because these differences may reflect different anthropogenic sources of nitrogen. Indeed, the upper region of Lavaca Bay is more influenced by riverine inputs from the Lavaca River draining rangeland ($\delta^{15}N$ range, 7–11‰) and is located adjacent to the municipalities of Port Lavaca and Point Comfort, likely sources of sewage ($\delta^{15}N$ from 7–11‰) outfalls. The lower region is more influenced by marsh plants ($\delta^{15}N$ range, 1–10‰) and phytoplankton ($\delta^{15}N$ range, 0–9‰) inputs from Matagorda Bay and the Gulf of Mexico.

The species composition of the food webs between the upper and lower regions of Lavaca Bay are very similar; however, a few rarely occurring species, such as *Carcharhinus limbatus*, *Sphyrna tiburo*, and *Orthopristis chrysoptera*, were found in the lower region of the bay, closer to the bay's connection to Matagorda Bay. Two shark species, *S. tiburo* and *C. limbatus*, were captured only in the lower region of the bay, consistent with recent research on shark distributions in Texas coastal waters (Froescke et al. 2010). The occurrence of submerged aquatic vegetation and the proximity to the tidal inlet and Matagorda Bay in the lower region of the bay may both be contributing factors to the richer food web, greater linkage, density and trophic connectance found in the lower region of Lavaca Bay. By incorporating spatial variation in their food webs, a potential source of bias in food web studies is reduced (Winemiller et al. 2007).

The disjointed frequency distribution of $\delta^{13}C$ values by region (Fig. 3) suggests a difference in the major contributing carbon source in each region. The lower region appears to have a greater C_4 plant and BOM influence than the upper region of the bay. These differences are attributed to greater coverage of seagrass habitat observed in the lower bay. The upper region appears to have a greater C_3 plant and phytoplankton influence, which can be attributed to riverine POM and greater growth of phytoplankton in response to riverine input of nutrients. It is important to note that $\delta^{13}C$ values were not lipid corrected. As a result tissues rich in lipids may be depleted in $\delta^{13}C$ relative to those rich in proteins (Post et al. 2007).

Physical parameters such as salinity, dissolved oxygen, and water temperature are likely influences on the food web structure of the upper and lower regions of Lavaca Bay. There were significant differences in salinity, water, temperature and

TABLE 4.

Results of SIMPER analysis indicating the taxonomic groups that collectively contributed 90% of the mean similarity to the diets of each of the 3 habitats.

Taxonomic group	Mean IRI	Mean similarity	Contributed %	Cumulative %
Marsh; mean similarity, 11.03				
Halodule wrightii	2.21	3.80	34.43	34.43
Callianassidae spp.	1.69	2.11	19.10	53.53
Peneaidae spp.	1.52	1.62	14.73	68.27
Callinectes sapidus	1.41	1.18	10.72	78.99
Gastropoda spp.	0.94	0.64	5.78	84.76
Palaemonetes vulgaris	0.85	0.42	3.84	88.60
Mysidae spp.	0.81	0.41	3.70	92.30
Nonvegetative bottom; mean similarity, 3.45				
Callinectes sapidus	1.14	1.13	32.66	32.66
Pleocyemata spp.	0.57	0.28	8.20	40.86
Brevoortia patronus	0.42	0.23	6.56	47.43
Decapoda spp.	0.39	0.20	5.82	53.25
Dendrobranchiata spp.	0.42	0.20	5.69	58.94
Polycheate spp.	0.48	0.17	5.05	63.99
Dendrobranchiata spp. (larvae)	0.46	0.15	4.32	68.31
Hymenoptera spp.	0.38	0.14	4.11	72.42
Halodule wrightii	0.43	0.13	3.89	76.31
Menippe adina	0.35	0.12	3.39	79.69
Nemertea spp.	0.39	0.11	3.32	83.01
Peneaidae spp.	0.28	0.08	2.33	85.35
Pectinariidae spp.	0.28	0.07	2.03	87.38
Sygnathus spp.	0.29	0.06	1.84	89.22
Amphipoda spp.	0.29	0.06	1.63	90.85
Reef; mean similarity, 6.79				
Menippe adina	1.44	1.82	26.81	26.81
Callinectes sapidus	1.35	1.50	22.12	48.93
Brevoortia patronus	0.89	0.87	12.87	61.80
Peneaidae spp.	0.93	0.86	12.65	74.45
Pleocyemata spp.	0.89	0.61	9.03	83.48
Decapoda spp.	0.43	0.25	3.73	87.21
Sygnathus spp.	0.48	0.20	3.02	90.23

IRI, index of relative importance.

dissolved oxygen between regions of the bay (Reese et al. 2010). The upper region is highly influenced by freshwater inflow from the Lavaca River, reducing the salinity, whereas the lower region, although influenced by freshwater inflow, is more so by the exchange of higher salinity water from Matagorda Bay and Gulf of Mexico. The upper bay was characterized by lower and more extreme fluctuations in water temperatures, and higher levels of dissolved oxygen compared with the lower region, which had warmer water temperatures and lower dissolved oxygen. This is likely a result of the geographic influence of this region by land-based temperatures and shallower depths, whereas the lower region is more influenced by inputs of Matagorda Bay water, which tend to remain more moderate across seasons.

Habitat-Mediated Food Web Structure

Each habitat type exhibited a specifically structured food web, with some species occurring only in certain habitats. Reef and NVB were found to support more robust food webs with a greater number of species and links, and higher level predators compared with the marsh habitat in Lavaca Bay. Based on stomach contents, the top-level predators of both NVB and reef habitats were sharks and jacks, whereas the top-level predators in the marsh habitat were primarily sciaenids. This was not the case, though, with trophic levels determined by $\delta^{15}N$; this family of fish was prevalent in all habitat types. These differences likely reflect the difference between a brief snapshot of the stomach content diet versus the isotopes assimilated over a period of weeks to months. A comparison of trophic status between stomach content versus isotope data for this study can be found in Wrast (2007).

The prey bases found to reside in the different habitat types studied were dissimilar (Reese et al. 2010). Marsh diet items such as *Halodule wrightii* and Callianassidae sp. were major contributors to the stomach contents and are typical of marsh-edge communities. Major contributors to the reef diet included *Menippe adina* and *Callinectes sapidus*. Although *C. sapidus* is rather ubiquitous throughout Lavaca Bay, *M. adina* preferentially inhabits a reef habitat. The NVB diet was dominated by *C. sapidus* and then a large number of other food items in small numbers. Food webs are structured based on the prey base available to the system. Diverse prey bases attract an array of distinct predators to that habitat type, in turn creating a dissimilarly structured community. The habitat complexity and thus food availability associated with the habitat types create

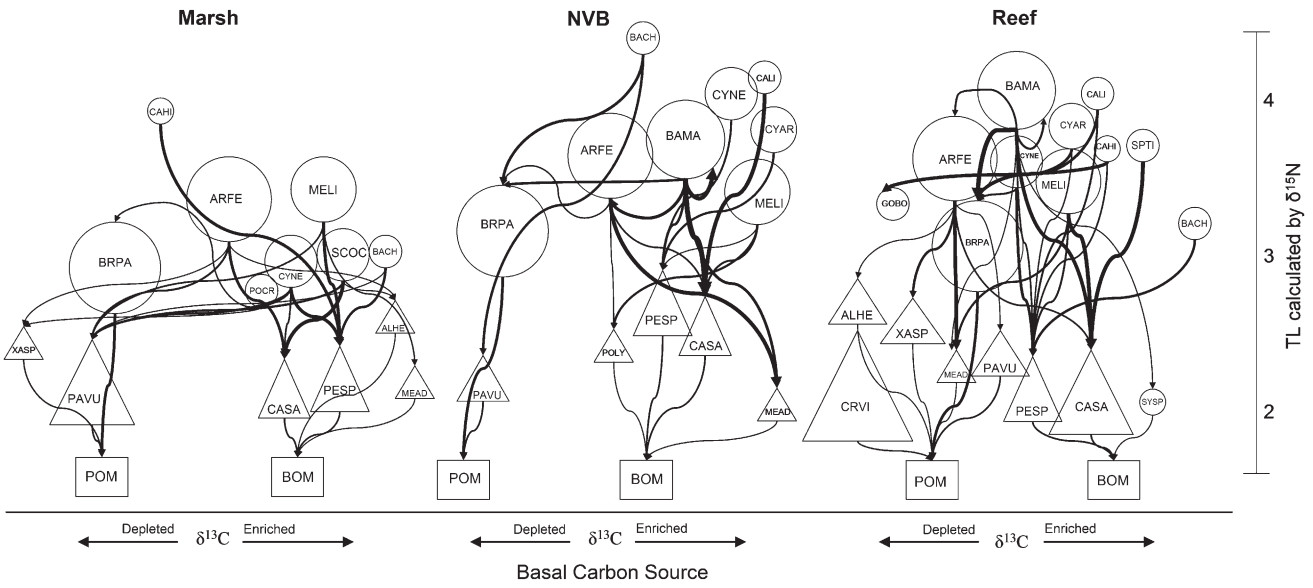

Figure 7. Food web diagram by habitat type for Lavaca Bay, Texas, constructed from field collection, stomach content, and stable isotope analysis. Position on the *x*-axis is based on the $\delta^{13}C$ value and habitat type; position on the *y*-axis is based on the trophic level (TL) ($\delta^{15}N$). Relative sizes of nodes (circle, fish; triangle, invertebrates; square, basal carbon source) depict total abundance. Relative thickness of links is an interpretation of the numerical and volumetric contribution of prey in the diet of each consumer. Species codes are listed in Table 2. NVB, nonvegetated bottom.

distinct food web modules within a larger estuarine system food web.

Differentiation in food web structures by habitat types is also evident when $\delta^{13}C$ isotope signatures are examined. The fish assemblages from both NVB and reef habitats were more depleted in $\delta^{13}C$ compared with individuals from marsh habitats. This reflects a greater input of both C_3 and C_4 detrital matter, which would occur in the marsh habitats relative to the "open-water" NVB and reef habitats, which are more dependent on POM and BOM as their food source.

Many studies have compared community assembly and food web structure among estuarine habitat types (Minello et al. 1989, Akin 2001, Simons unpubl. data); however, only a few (Plunket & La Peyre 2005, Shervette 2006) have included oyster reefs. Plunket and La Peyre (2005) studied the difference in nekton community structure of subtidal oyster reef habitat with that of NVB and found the abundance of organisms on the oyster reef was approximately twice that of NVB; however, they did not include any vegetated habitats. Shervette (2006) found an intertidal oyster reef habitat of a Mississippi estuary occupied by a distinct community of fish and invertebrates, with high densities of these residents compared with adjacent vegetated and nonvegetated habitats.

Understanding spatial dynamics and creating spatial boundaries of marine food webs is an important topic that marine ecologists are just beginning understand and generate scientific information for these complex marine ecosystems (Sogard et al. 1989, Winemiller 1990, Holt 2002, Melville & Connolly 2003, Winemiller et al. 2007, Amarasekare 2008). It is difficult to compartmentalize systems spatially that do not have obvious physical barriers (Yodzis 1993). Communities are mixes of species with different life history strategies; therefore, they experience the world at different spatial scales (Holt 1996, 2002). Resource managers should not only consider processes that vary across scales, but also consider the scales at which species can and cannot move and interact. In summary, the more robust a food web (i.e., the more redundant links that are present in the network), the more elastic the community to perturbations (de Ruiter et al. 2005).

There are many differences in the physical and biological makeup of habitats in the upper and lower regions of the Lavaca Bay system. The data suggest there are significant differences in food web structure at the spatial scales examined in Lavaca Bay, which supports the hypothesis these estuarine food webs are compartmentalized (Winemiller 2007). Assessing the food web as a whole is important in gaining an understanding of major predator–prey relationships. Differences in the food web structure by habitat types and spatial scales must be considered to gain a more complete understanding of the system. As resource managers move toward ecosystem-based

Table 5.

List of food web metrics derived from the stomach content and stable isotope data for regions studied in Lavaca Bay, Texas.

	Upper			Lower		
	M	NVB	R	M	NVB	R
WebH′	2.38	2.01	2.62	3.03	2.94	2.06
GutTL	2.52	2.47	2.51	2.29	2.53	2.71
δ^{15}NTL	2.58	2.83	2.91	1.88	2.61	2.76
WebSR	38	27	39	31	55	45
Links	39	33	47	36	63	64
$\delta^{13}C$	–17.90	–20.23	–19.99	–15.58	–17.81	–18.31
$\delta^{15}N$	11.46	12.11	12.33	8.54	11.14	11.90

δ^{15}NTL, trophic levels determined from $\delta^{15}N$; GutTL, trophic levels determined from stomach contents; Links, number of trophic links in the food web; M, marsh; NVB, nonvegetated bottom; R, oyster reef; WebH′, food web diversity index; WebSR, food web species richness.

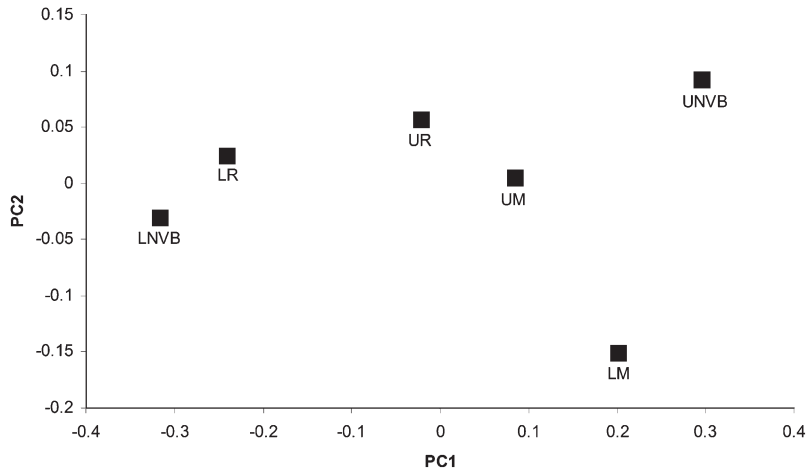

Figure 8. Plot of the first 2 principle components calculated from the food web metrics derived from stomach content and stable isotope data. LM, lower marsh; LNVB, lower nonvegetated bottom; LR, lower reef; UM, upper marsh; UNVB, upper nonvegetated bottom; UR, upper reef.

management, they must consider the distinct communities and accompanying food webs associated with the habitat types and spatial scales observed in the ecosystem.

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