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Body size and trophic position in a temperate estuarine food web

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ABSTRACT

We used stomach contents and stable isotope ratios of fishes and macroinvertebrates, collected bi-monthly over 18 months from Mad Island Marsh, a small tidal estuary on the northwestern Gulf of Mexico coast, to examine potential body size–trophic position relationships. Mean body size (length) of predator taxa yielding measurable prey items were significantly correlated with body size (length) of their prey and mean volume of their stomach contents, however, the strength of the correlation was greater when two larger detrivores (i.e., striped mullet and gizzard shad) were excluded from the analysis. Similarly, trophic positions estimated by volumetric stomach contents were also significantly related to predator body size but not related to mean volume of stomach contents, but again excluding those detrivores from the analyses increased the strength of the relationship. Trophic positions estimated from stable isotopes and $\delta^{15}N$ as an index of trophic position were also unrelated to predator body length, but significantly related to predator body mass. Although estimates of trophic positions in this tidal estuary using both methods were largely concordant, there were some exceptional zooplanktivorous and detritivorous species that had higher trophic levels according to nitrogen isotope ratios. Excluding those species from the analyses increased the strength of relationships between size and trophic positions of predators. A significant relationship between body sizes of consumers and their prey supports the view that body size is a key variable influencing trophic interactions and the structure of aquatic food webs. Our results also suggest that body size (especially consumer mass) is a good predictor of trophic levels estimated by stable isotopes, whereas consumer length is an important trait predicting the trophic level estimated from stomach contents in this tidal estuarine system.

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1. Introduction

Body size is an important feature influencing ecological interactions among animals (Peters, 1983; Cohen et al., 1993).

Body size directly influences physiological and ecological traits, including metabolic rate (Hemmingsen, 1960), growth and mortality (Peters, 1983), clutch size, egg mass, breeding time, survivorship and other life histories traits (Loeuille and

Loreau, 2006 and references cited therein), population density (Peters, 1983; Marquet et al., 1990; Blackburn et al., 1993; Damuth, 1993; Schmid et al., 2000; Cohen et al., 2003; Brown and Gillooly, 2003; Ackerman et al., 2004), species distributions (Brown et al., 1993; Greenwood et al., 1996) and secondary production (Jennings et al., 2002).

Large variation in the sizes of coexisting organisms, as well as robust correlations between body size and many life history traits, suggest that variation in body size can potentially affect biological patterns at levels ranging from individuals to ecosystems (Woodward et al., 2006). Ecosystem components are interconnected as a network of individual and population interactions (i.e. food webs) that dictate fluxes of energy or matter (Woodward et al., 2006). Many theoretical food web studies, stimulated by May's (1973) study on the relationships between stability and diversity, have sought to answer how food webs are structured and what determines this structure. Theoretical analyses of food web data gathered from different ecosystems have revealed that food webs have non-random structure (Pimm, 1982). Two models have been frequently cited—the cascade and niche models (Cohen and Newman, 1985; Williams and Martinez, 2000)—to explain how food webs are structured. Although both models are essentially based on the concept of ecological niche, and assume a trophic hierarchy in which species cannot consume other species positioned above them in a food chain, these models do not specify mechanisms that constrain feeding interactions.

Many ecologists have suggested that body size can influence trophic hierarchies (Warren and Lawton, 1987; Lawton, 1989; Cohen et al., 1993; Memmott et al., 2000; Neubert et al., 2000; Woodward and Hildrew, 2002). If we exclude parasites from our discussion, most predators are larger than their prey, and larger individuals would be expected to feed at higher trophic levels. Many studies have reported results confirming this expectation (Cohen et al., 1993; France et al., 1998; Jennings et al., 2001; Woodward and Hildrew, 2002; Jennings and Mackinson, 2003). Layman et al. (2005) examined fish dietary data derived from stomach contents analysis and demonstrated that body sizes of predators and their prey were significantly correlated, but trophic level was not significantly associated with body size. They interpreted the lack of association between trophic level and body size to the diverse species assemblage with primary consumers encompassing a broad range of body sizes. To further elucidate the role of body size in structuring food webs, additional studies from a variety of ecosystems are needed.

In the present study, we examined the relationships between trophic position, calculated both from stomach contents and stable isotope data, and body size for fishes and macroinvertebrate (crabs and shrimps) of a temperate tidal estuary. We specifically asked: (1) Do sizes of predators and their prey vary in a predictable pattern? (2) Are predator body size and trophic level interrelated? (3) Does trophic level increase with greater volume of stomach contents?

2. Methods

Mad Island Marsh Preserve contains the estuary of a creek draining into Matagorda Bay, Texas on the northwestern coast of the Gulf of Mexico. The preserve is managed by the Nature Conservancy of Texas. The area is relatively shallow ranging from 0.14 to 0.74 m. Descriptions of physicochemical and ecological characteristics of the estuary appear in Akin et al. (2003). Fish and macroinvertebrate specimens for stomach contents were collected bimonthly from March 1998 to August 1999 from six sites located along the longitudinal estuarine gradient using a bag seine (6×1.2 m, 4.5 mm mesh, bag 1.2×1.2 m). Tissue samples for isotopic analysis were collected during August 1999 (plant tissues were collected during August 1999 and February 1999, and values were averaged). Captured fish and macroinvertebrates were anesthetized in MS-222 and then fixed in a 10% formalin solution in the field. In the laboratory, specimens were identified, counted, measured (standard length, SL, to nearest 0.1 mm), and weighed (to nearest 0.1 g).

Volumetric quantification of stomach contents was performed following the method given in Winemiller (1990). Prey items with volumes larger than 0.1 ml were quantified in graduated cylinders in the laboratory. For volumes less than 0.1 ml, items were placed on a glass slide and visually compared with a water drop of known volume extracted from a pipette. Most of the identifiable prey items were macroinvertebrate (crabs, shrimp, and worms) and fishes, so we restrict size-based analysis of prey to these taxa. Most fishes and macroinvertebrate were identified to species level, but some prey items were partially digested and could only be identified to genus. Standard length was recorded for both predatory fishes and their fish prey. Carapace length and the total length (excluding antenna) of crabs and shrimps, respectively, were recorded for use as the measure of body size in the analysis. Using volumetric proportional dietary data from stomach contents analysis, the trophic position of each consumer species was calculated from the formula given by Adams et al. (1983):

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

where T_j is the trophic position of prey species j, and p_{ij} is the fraction of the consumed food (volume) of species i consisting of prey species j. The equation assumes no cannibalism or feeding loops. Trophic positions based on estimation from stomach contents were calculated for only those species with sample sizes having at least 6 specimens with stomachs containing food. For some species occurring in the estuary throughout the year, two temporal (summer and winter) trophic positions were calculated, and mean trophic positions of these species were estimated by taking the average of summer and winter trophic positions.

Collection and processing of tissue samples for stable isotope analyses and estimation of consumer trophic position follow methods in Jepsen and Winemiller (2002) and Winemiller et al. (2007). The formula for calculations of trophic position (TP) was:

$$TP = \left(\left(\delta^{15}N_{consumer} - \delta^{15}N_{reference} \right) / 3.35 \right) + 1$$

where $\delta^{15}N_{reference}$ (5.6) was the mean of all C_4 plants, sediments, phytoplankton, periphyton, macroalgae, and filamentous algae, and the denominator value (3.35) was an estimated mean trophic enrichment (fractionation) of δ^{15} N between

consumers and their food sources (see Table 1). The trophic enrichment estimate was calculated using dietary data from the pinfish (*Lagodon rhomboides*). We chose this abundant species for estimating trophic fractionation because we possessed nitrogen isotopes values for all its food resources including aquatic macrophytes (widgeon grass), vegetative detritus, filamentous algae, and amphipods. The mean nitrogen isotopic signature of these food items (5.66) was subtracted from the mean δ^{15}N value of pinfish (9.01) (Table 1). The resulting estimate of 3.35 closely approximates the trophic fractionation value of 3.4 obtained from laboratory studies of several animal taxa (DeNiro and Epstein, 1981; Minagawa and Wada, 1984; Vander Zanden and Rasmussen, 1996, 2001). This obviously is an estimated value, and may not be the actual universal value of fractionation, even assuming that there is one. As indicated by Jennings et al. (2002), estimation of an organism's trophic level requires that trophic levels of a group of organisms closer to the base of the food chain also are known. Assignment of trophic levels to phytoplankton, zooplankton, or species that consume them is extremely difficult because pure phytoplankton tissue cannot be extracted from plankton samples to make δ^{15} N measurements and trophic level of zooplankton can vary by two or more trophic levels due to the effects of microbial food loop (Jennings et al., 2001). In addition to trophic level estimated with the formula used above, nitrogen stable isotope values (δ^{15}N) as suggested by Jennings et al. (2001) were also used as an index of trophic level to explore the relationships with body size (length and weight).

We used regression analyses to explore relationships among related parameters such as predator and prey size (length and weight), trophic level, δ^{15}N values, and volume of stomach contents. All statistical analyses were performed using Minitab 13.1.

3.   Results

3.1.   Predator vs. prey size

Analyses of the relationship between predator size (standard length) and prey size (length) were based on the 16 piscivores (see Table 1). From the stomachs of 242 specimens of these 16 predatory fish species (Table 1), 38 measurable prey taxa, totaling 310 prey items (mostly fish, shrimp, and blue crabs) were recovered and their lengths were measured. The length of fish (measured as SL), shrimp (measured as total length excluding antenna), and crab (measured as carapace length) were used as the size of prey species. The length of prey taxa ranged from 1.5 mm to 326 mm. The most common prey taxa in the stomachs of consumers having measurable prey were blue crabs (37.60%), followed by grass shrimp (23.14%), brown shrimp (11.60%), white shrimp (10.33%), Gulf menhaden (9.50%), and mullet (8.68%). The number of measurable prey taxa per species ranged from 1.0 to 2.5 with a mean of 1.33 (Table 1).

The association between raw values of body size of 16 piscivores and their prey length (mm) was modeled by a linear equation (prey length = 11.96 + 0.12(predator length)) and this was significant ($F_{1,308} = 93.82$, $P < 0.001$, $R^2 = 0.23$)

(Fig. 1). The association between mean length of these 16 piscivores and their prey size (length) was even stronger and modeled with an exponential equation (prey length = 24.313 exp(0.002(predator length)); $F_{1,14} = 34.46$, $P < 0.001$, $R^2 = 0.71$) (Fig. 2). In order to explore the relationship between the mean volume of prey (an additional measure of prey size) and mean length of the all consumers (see Table 1), dietary data from the 16 piscivorous species were combined with those from the other 29 fish and 5 macroinvertebrate species for which diets were only quantified volumetrically (Table 1). The strongest association between these two variables (i.e., mean volume stomach contents and standard length of all species) was modeled with an exponential function (volume of stomach contents = 0.00002(predator length)$^{2.45}$) that was significant ($F_{1,48} = 140.17$, $P < 0.001$, $R^2 = 0.75$) (Fig. 1). The relationship between the mean volume of stomach contents, most of which consisted of measurable prey taxa, of 16 predatory species and mean predator length was also examined. This association was best modeled with an exponential function (volume of stomach contents = 0.00002(predator length)$^{1.97}$) that was even stronger ($F_{1,14} = 124.32$, $P < 0.001$, $R^2 = 0.90$) and which yielded further evidence emphasizing the importance of body size in determining hierarchy in food web structure (Fig. 2).

3.2.   Trophic position vs. body size and stomach contents volume

Trophic position estimated from stomach contents were calculated for those species with sample sizes having at least 6 specimens with stomachs containing food during summer and winter (Table 1). Mean trophic positions were relatively low ranging from 2.0 (SD ± 0.00) to 3.4 (SD ± 0.19), with a mean of 2.7 (SD ± 0.48). Mean length of all species used for stomach contents analysis varied from 11.0 to 703.0 mm (SD ± 201.0) (Table 1).

The association between trophic position estimated by stomach contents and body length was best described by a logarithmic equation (trophic position = 1.99 + 0.174 ln(consumer length)), this was weakly significant ($F_{1,60} = 9.06$, $P = 0.004$, $R^2 = 0.13$) (Fig. 3). The curve representing the association between trophic position and predator size gradually increased with increasing size and started to level off approximately at TL = 3.0. In order to evaluate the effects of two outlying large detrivores (i.e., striped mullet and gizzard shad) on the relationship between trophic position and consumer size, striped mullet and gizzard shad were excluded from the analysis. Excluding these two fish species from the analysis made the relationship stronger (trophic position = 1.77 + 0.25 ln(consumer length); $F_{1,56} = 19.44$, $P < 0.001$, $R^2 = 0.26$).

Trophic positions estimated by nitrogen stable isotopes and stomach contents yielded fairly concordant results, with the exceptions of four species including Gulf menhaden, gizzard shad, grass shrimp, and ladyfish (Table 1). The former three species had higher trophic levels calculated from the stable isotope analysis compared to estimates based on stomach contents analysis, whereas the latter species had lower isotopic estimates of trophic level. Using the same data set, Winemiller et al. (2007) showed that removing these

Table 1 – Species or taxa for which stomach contents and/or stable nitrogen isotope analyses were performed

Species or taxa	Stomach contents									Stable isotopes				
	Mean Standard length (mm)	N	Mean weight (g)	Mean volume of stomach contents (ml)	% of empty stomach	NSCMP	NMPR*	Percent occurrence as measurable prey	Mean trophic position	Mean standard length (mm)	N	Mean δ^{15}N	Mean weight (g)	Trophic position
Atractosteus spatula	703.0 ± 201.0	30	2251.85 ± 1337.96	12.2 ± 25.3	33	18	18 (1)	–	3.17 ± 0.15	762.50 ± 10.66	2	13.2 ± 0.28	3250 ± 353.55	3.27
Achirus lineatus	26.3 ± 14.2	6	0.09 ± 0.08	0.002 ± 0.002	0	–	–	–	–	–	–	–	–	–
Adinia xenica	21.9 ± 2.8	59	0.26 ± 0.13	0.011 ± 0.008	5	–	–	–	2.02	–	–	–	–	–
Anchoa mitchilli	30.8 ± 7.7	911	0.60 ± 0.74	0.004 ± 0.018	15	–	–	3.30	3.17 ± 0.20	37.22 ± 4.44	9	12.80 ± 0.85	0.71 ± 0.27	3.15
Archosargus probatocephalus	272.5 ± 31.8	3	832.28 ± 237.39	12.0 ± 17.00	33	–	–	–	–	–	–	–	–	–
Arius felis	241.7 ± 45.7	77	264.74 ± 170.98	1.8 ± 2.6	17	40	57 (1.42)	0.41	3.27 ± 0.11	231.33 ± 36.21	6	13.75 ± 1.02	36.21 ± 584.2.18	3.43
Bairdiella chrysoura	36.4 ± 18.1	197	3.22 ± 11.83	0.027 ± 0.102	18	21	24 (1.19)	–	3.16 ± 0.07	96.00 ± 58.44	4	14.69 ± 1.98	47.02 ± 40.93	3.71
Brevoortia patronus	27.3 ± 6.0	525	0.72 ± 0.81	0.064 ± 0.071	0	–	–	9.50	2.02 ± 0.00	30.70 ± 10.80	4	14.47 ± 0.42	1.01 ± 0.64	3.65
Carrcharhinus limbatus	450.0	1	1800	7	0	1	2 (2)	–	–	–	–	–	–	–
Citharichthys macrops	11.6	1	0.18	0.0007	0	–	–	–	–	–	–	–	–	–
Citharichthys spilopterus	24.3 ± 10.0	49	0.65 ± 1.00	0.006 ± 0.008	4	–	–	–	3.25	–	–	–	–	–
Cynoiscon nebulosus	89.2 ± 109.4	92	135.73 ± 297.67	0.28 ± 1.89	21	32	34 (1.06)	0.41	3.20 ± 0.04	190.75 ± 158.67	8	13.23 ± 2.21	234.50 ± 403.14	3.28
Cynoscion arenurius	41.4 ± 55.8	10	0.10 ± 0.08	0.04 ± 0.097	10	–	–	–	3.14	–	–	–	–	–
Cyprinodon variegatus	24.0 ± 8.5	140	3.48 ± 14.94	0.071 ± 0.093	7	–	–	1.24	2.00 ± 0.00	30.4	1	9.59	0.98	2.19
Dasyatis sabina	207 ± 37.7	6	547 ± 403.33	0.4 ± 0.5	33	3	3 (1)	–	–	–	–	–	–	–
Dorosoma cepedianum	232.6 ± 30.5	201	241.17 ± 91.89	3.1 ± 3.6	7	–	–	–	2.17 ± 0.17	236.25 ± 12.74	8	12.48 ± 0.82	258.51 ± 33.22	3.05
Elops saurus	205.3 ± 92.2	10	75.53 ± 109.16	1.4 ± 3.1	40	6	8(1.33)	–	3.07	200.63 ± 129.00	4	9.35 ± 1.51	165.37 ± 110.09	2.12
Eucinostomus argenteus	19.6 ± 2.4	2	0.37 ± 0.34	0.001 ± 0.000	0	–	–	–	–	–	–	–	–	–
Fundulus confluentus	34.8 ± 9.8	7	0.99 ± 0.86	0.006 ± 0.003	0	–	–	–	2.70	–	–	–	–	–
Fundulus grandis	33.3 ± 11.4	133	1.85 ± 3.96	0.009 ± 0.022	28	–	–	1.65	2.34 ± 0.28	44.38 ± 10.07	4	11.07 ± 0.38	2.22 ± 1.90	2.09
Fundulus mojalis	45.8	1	2.08	0.0001	0	–	–	–	–	–	–	–	–	–
Fundulus pulvereus	28.7 ± 8.00	11	0.57 ± 0.46	0.017 ± 0.051	9	–	–	–	3.00	–	–	–	–	–
Gobiesox strumosus	18.5 ± 7.8	6	0.14 ± 0.08	0.002 ± 0.004	50	–	–	–	–	–	–	–	–	–
Gobioenellus boleosoma	23.7 ± 4.3	75	0.24 ± 0.18	0.002 ± 0.001	5	–	–	–	2.36 ± 017	–	–	–	–	–
Gobiosoma bosc	21.7 ± 5.0	165	0.24 ± 0.30	0.002 ± 0.008	27	–	–	–	2.93 ± 0.11	26.55 ± 1.06	2	9.10 ± 0.51	0.47 ± 0.18	2.04
Gobiosoma robustum	17.9 ± 2.3	10	0.47 ± 0.09	0.001 ± 0.001	10	–	–	–	2.75	–	–	–	–	–
Hemicaranx amblyrhynchus	28.7 ± 4.7	14	1.08 ± 0.05	0.039 ± 0.036	7	–	–	–	3.22	–	–	–	–	2.02
Lagodon rhomboides	38.4 ± 17.7	364	2.95 ± 2.67	0.051 ± 0.140	4	3	3 (1)	4.13	2.45 ± 0.41	56.67 ± 5.32	12	9.01 ± 1.72	5.32 ± 2.22	–
Leiostomus xanthurus	38.8 ± 15.7	538	3.10 ± 3.12	0.06 ± 0.011	8	8	8 (1)	0.41	2.93 ± 0.09	28.75 ± 2.52	2	13.34 ± 1.99	0.53 ± 0.18	3.31
Lepisosteus oculatus	488.3 ± 53.3	5	784.71 ± 349.28	4.5 ± 9.3	20	4	10 (2.5)	–	–	590	1	12.45	1400	3.04
Lepisosteus platostomus	455.0	1	540	4.5	0	1	2 (2)	0.41	–	–	–	–	–	–
Lucania parva	24.00 ± 5.4	173	0.26 ± 0.20	0.002 ± 0.003	30	–	–	–	2.76 ± 0.33	38.2	1	9.49	0.13	2.16
Menida penunsilae	30.6 ± 8.5	70	0.37 ± 0.28	0.001 ± 0.002	36	–	–	–	2.89	–	–	–	–	–
Menidia berylina	38.3 ± 12.1	619	1.20 ± 1.00	0.004 ± 0.010	22	7	7 (1)	0.41	2.68 ± 0.23	37.74 ± 2.81	6	11.07 ± 0.38	0.35 ± 0.07	2.64
Microgobius gulosus	26.7 ± 5.5	9	0.72 ± 0.82	0.001 ± 0.001	22	–	–	–	3.06	–	–	–	–	–
Micropogonias undulatus	30.5 ± 19.3	515	4.83 ± 19.28	0.01 ± 0.056	14	10	10 (1)	0.41	3.07 ± 0.19	–	–	–	–	–
Mugil cephalus	148.0 ± 109.1	514	211.60 ± 263.20	3.7 ± 8.5	17	–	–	8.68	2.11 ± 0.06	234.29 ± 75.58	8	10.45 ± 1.80	306.76 ± 266.46	2.45

Table 1 (continued)

Species or taxa	Stomach contents									Stable isotopes				
	Mean Standard length (mm)	N	Mean weight (g)	Mean volume of stomach contents (ml)	% of empty stomach	NSCMP	NMPR*	Percent occurrence as measurable prey	Mean trophic position	Mean standard length (mm)	N	Mean δ^{15}N	Mean weight (g)	Trophic position
Oligoliptes saurus	43.1 ± 16.4	4	0.21 ± 0.03	0.06 ± 0.06	25	–	–	–	–	–	–	–	–	–
Parachlithys lethostigma	224.6 ± 136.1	43	439.74 ± 403.32	0.7 ± 1.9	44	21	25 (1.14)	–	3.27 ± 0.18	297.50 ± 45.96	2	13.22 ± 1.68	507.65 ± 274.16	3.27
Poecila latipinna	26.5 ± 22.6	89	0.24 ± 0.15	0.04 ± 0.045	4	–	–	0.41	2.00 ± 0.01	–	–	–	–	–
Pogonias cromis	260.1 ± 134.4	57	577.74 ± 517.74	0.8 ± 2.00	35	12	14 (1.16)	0.41	3.09 ± 0.08	299.37 ± 69.42	8	12.91 ± 1.07	708.92 ± 584.03	3.18
Sciaenops ocellatus	425.1 ± 99.5	94	1328.36 ± 976.36	4.1 ± 9.1	32	55	87 (1.58)	–	3.40 ± 0.19	425.41 ± 99.91	13	13.29 ± 0.87	1790 ± 956.50	3.29
Sphoeroides pachygaster	29.3 ± 1.9	3	4.83 ± 19.29	0.002 ± 0.001	0	–	–	–	–	–	–	–	–	–
Synathus louisanae	121.7 ± 17.4	4	0.60 ± 0.57	0.009 ± 0.008	0	–	–	–	–	–	–	–	–	–
Syngnathus scovelli	68.1 ± 21.9	16	0.15 ± 0.15	0.002 ± 0.003	19	–	–	–	2.98	73.9	1	10.77	0.2	2.54
Neopanope sayi	–	–	–	–	–	–	–	3.30	–	–	–	–	–	–
Myrophis punctatus	–	–	–	–	–	–	–	4.96	–	–	–	–	–	–
Callinectes sapidus	62.92 ± 56.91	203	30.83 ± 59.17	0.06 ± 0.024	29	–	–	37.60	2.58 ± 0.24	138.33 ± 13.52	7	11.14 ± 2.31	124.76 ± 37.43	2.66
Callinectes similis	13.96 ± 4.48	16	0.09 ± 0.03	0.002 ± 0.002	25	–	–	–	2.02	–	–	–	–	–
Palaemonetes pugio	31.66 ± 4.66	155	0.26 ± 0.30	0.031 ± 0.096	23	–	–	23.14	2.08 ± 0.07	–	4	11.0 ± 1.81	–	2.89
Farfantepenaeus aztecus	64.36 ± 12.12	117	1.13 ± 0.69	0.37 ± 0.002	8	–	–	11.16	2.36 ± 0.00	71.69 ± 3.06	9	8.02 ± 0.40	2.68 ± 0.75	1.72
Penaeus setiferus	59.06 ± 20.54	90	1.65 ± 3.47	0.39 ± 0.02	10	–	–	10.33	2.14 ± 0.14	69.44 ± 8.01	5	9.00 ± 2.81	2.25 ± 1.49	2.02
Others as prey	–	–	–	–	–	–	–	6.61	–	–	–	–	–	–
Mud	–	–	–	–	–	–	–	–	–	–	2	8.67 ± 1.04	–	–
Filamentous algae	–	–	–	–	–	–	–	–	–	–	4	6.31 ± 0.14	–	–
Periphyton	–	–	–	–	–	–	–	–	–	–	3	2.82 ± 0.21	–	–
Phytoplankton	–	–	–	–	–	–	–	–	–	–	3	3.51 ± 0.74	–	–
Widgeaon grass	–	–	–	–	–	–	–	–	–	–	4	4.58 ± 0.39	–	–
Sea weed	–	–	–	–	–	–	–	–	–	–	4	6.47 ± 0.44	–	–
Sediment	–	–	–	–	–	–	–	–	–	–	6	5.34 ± 0.37	–	–
Spartina alterniflora	–	–	–	–	–	–	–	–	–	–	5	6.55 ± 4.07	–	–
Spartina spartinae	–	–	–	–	–	–	–	–	–	–	3	5.42 ± 0.28	–	–
Amphipoda	–	–	–	–	–	–	–	–	–	–	2	6.42 ± 0.06	–	–

Mean standard length, mean length of individuals for which stomach contents and stable isotopes analyses were performed; N, the number of individuals analyzed for stomach contents and stable isotope analyses; mean weight (for stomach contents), mean weight of the sampled individuals; mean weight for stable isotope, mean weight of individuals on which stable isotope analyses were performed; mean volume of stomach contents, mean volume of stomach contents including both measurable prey items that were used in the regression analyses in Figs. 1 and 2 and non-measurable prey item; % of empty stomachs, number of empty stomachs divided by the total number of stomach examined and multiplied by 100; NSCMP, the number of stomachs containing measurable prey item; NMPR, the number of measurable prey item recovered from the stomachs (*number in parentheses is the mean prey item per stomach containing measurable prey item); percent occurrence as measurable prey items, calculated as the number of occurrences of a given measurable prey item in the stomach of predators divided by the total number of individuals (242) of 16 predatory fish species yielding measurable prey items × 100; mean trophic position, mean of winter and summer trophic position of species. Trophic position without standard deviation represents the trophic position calculated either for winter or summer; trophic position, trophic position estimates from stable nitrogen isotope; ±SD, standard deviation.
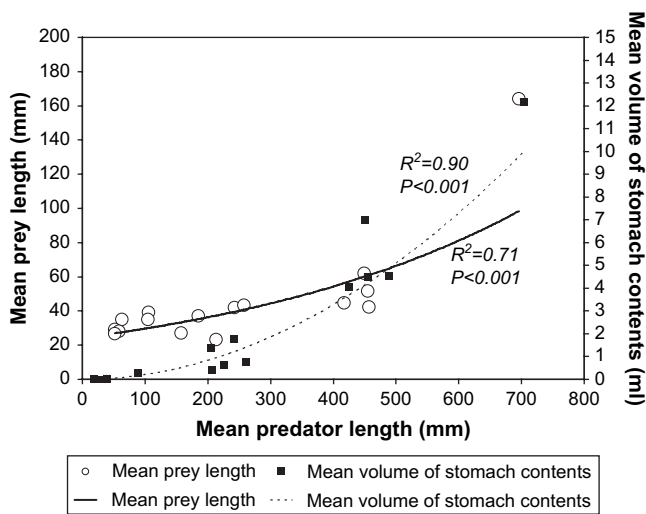
Fig. 1 – Relationships between the length of 242 specimens of 16 predatory species and 310 prey items, and between the mean volume of stomach contents of 50 fish and macroinvertebrate species and their size.

organisms from the linear regression analysis of trophic level calculated from stomach contents with that derived from stable isotopes increased the coefficient of determination from 0.19 to 0.55.

The length of fish and macroinvertebrates analyzed for stable isotopes ranged from 30.4 to 762.5 mm (SD $\pm$ 10.66), and their weight varied from 0.13 to 3250 g (SD $\pm$ 353.55) (Table 1). Minimum (2.02), mean (2.77) and maximum (3.71) trophic position values estimated by nitrogen isotope data were similar to those obtained from stomach contents analysis (Table 1). Despite these fairly concordant results, the association between stable isotope estimates of trophic position and body size of consumers was not significant correlated with body length ($F_{1,23} = 3.26$, $P = 0.084$, $R^2 = 0.12$) but weakly correlated with body mass ($F_{1,23} = 8.48$, $P = 0.032$, $R^2 = 0.18$) (Fig. 4). Exclusion of the above-mentioned four species from the

Fig. 2 – Relationships between the mean length of 16 predatory species and mean length of their prey and mean volume of stomach contents.
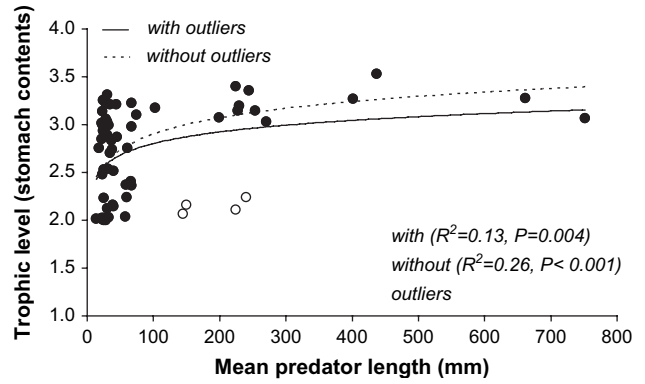
Fig. 3 – Relationships between mean consumer length and trophic level estimated from stomach contents analyses. Open circles represent two outlying species (*Mugil cephalus* and *Dorosoma cepedianum*).

analysis yielded significant and stronger logarithmic associations (trophic position = 1.54 + 0.26 ln(consumer length), $F_{1,19} = 6.83$, $P = 0.017$, $R^2 = 0.26$; trophic position = 2.47 + 0.09 ln(consumer weight), $F_{1,19} = 8.48$, $P = 0.009$, $R^2 = 0.31$) (Fig. 4).

Mean δ^{15}N ranged from 9.01 (SD $\pm$ 1.72) to 14.69 (SD $\pm$ 1.98) for 25 consumers, including four macroinvertebrate species (Table 1). In addition to exploring the relationship between trophic position estimated by stable isotopes and predator size, we also investigated the relationship between predator size (length and mass) and mean nitrogen stable isotope ratio as an index of trophic position, as suggested by Jennings et al. (2001). The results of regression analysis between nitrogen isotope ratio and mean consumer size (length) and mass revealed relationships similar to those obtained from the analyses performed between trophic position and consumer size and mass (Fig. 5). The nitrogen isotope values of consumers were not significantly associated with the length of consumers ($F_{1,23} = 3.45$, $P = 0.076$, $R^2 = 0.13$), but weakly associated with consumer mass (δ^{15}N = 10.95 + 0.25 ln(consumer weight), $F_{1,23} = 5.11$, $P = 0.034$, $R^2 = 0.18$) (Fig. 5). Nitrogen stable isotope values, on the other hand, exhibited stronger relationship with consumer length (δ^{15}N = 7.62 + 0.85 ln(consumer length), $F_{1,19} = 5.17$, $P = 0.035$, $R^2 = 0.21$) and mass (δ^{15}N = 10.78 + 0.29 ln(consumer weight), ($F_{1,19} = 6.77$, $P = 0.018$, $R^2 = 0.26$) when excluding four outlying species from the regression analysis (Fig. 5).

Trophic positions estimated from stomach contents had a positive relationship with mean volume of stomach contents ($r = 0.20$), however, the relationship was not statistically significant ($F_{1,60} = 3.81$, $P = 0.056$, $R^2 = 0.06$) (Fig. 6). Exclusion of the two large detrivores from the analysis yielded a significant relationship between these two variables ($F_{1,56} = 12.60$, $P = 0.001$, $R^2 = 0.18$).
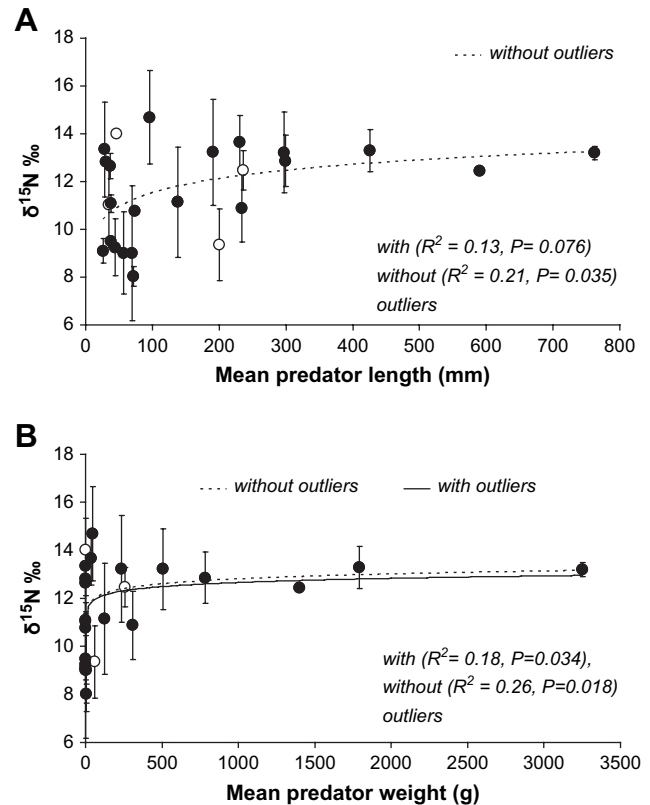
4. Discussion

In the cascade and niche models, predators are always positioned higher in the food chain than their prey, which yields
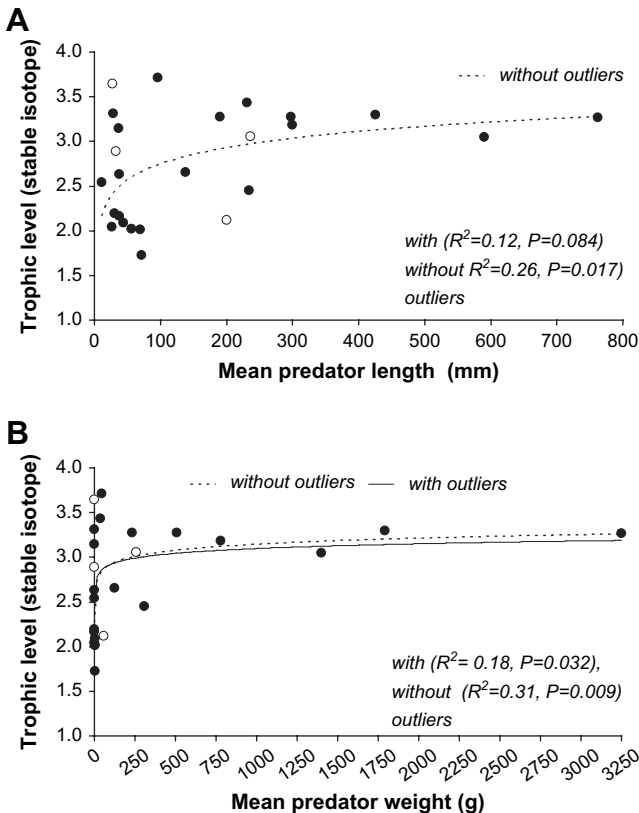
Fig. 4 – Relationships between trophic level estimated from stable isotopes and consumer length (A, upper panel) or mean weight (B, lower panel). Open circles represent the outlying species (*Dorosoma cepedianum*, *Palaemonotes pugio*, *Elops saurus* and *Brevoortia patronus*). The fitted line is for the significant relationship.


Fig. 5 – Relationships between $\delta^{15}N$ of consumers and their mean length (A, upper panel) or mean weight (B, lower panel). Open circles represent the outlying species (*Dorosoma cepedianum*, *Palaemonotes pugio*, *Elops saurus* and *Brevoortia patronus*). The fitted line is for the significant relationship.

an upper triangular predation matrix (Cohen and Newman, 1985). Several investigators have suggested that body size constraints in predator–prey interactions create consistent trophic structures in communities (Warren and Lawton, 1987; Lawton, 1989; Cohen et al., 1993; Leaper and Huxham, 2002). Our study revealed a positive relationship between predator and prey body sizes. The volume of stomach contents and the size of the consumers had a strong positive relationship that further emphasizes the importance of predator–prey size ratios in determining trophic hierarchies. Yet there are exceptions in which piscivores are not larger than their prey (Winemiller, 1990). Leaper and Huxham (2002) demonstrated that trophic hierarchies cannot be justified solely on the basis of body size when parasites and grazing insects are considered. Other exceptions include fishes that harvest scales (Peterson and Winemiller, 1997), fins (Winemiller and Kelso-Winemiller, 1993), or mucus (Winemiller and Yan, 1989).

In fishes, prey size (measured as length or volume) is largely constrained by mouth gape and/or digestive capacity, i.e., volume of the stomach (Schmitt and Holbrook, 1984; Karpouzi and Stergiou, 2003). The positive relationship between standard length of Mad Island Marsh consumers and the volume of their stomach contents suggests optimal foraging

(Pyke et al., 1977) whereby consumers attempt to maximize energy acquisition while minimizing the energetic cost of food uptake by targeting the most abundant, profitable and easily captured prey. Consumers often maximize energy assimilation by targeting the largest prey that also carry lowest relative costs in terms of searching, capture, and handling (Werner and Hall, 1977). The positive relationship between size and caloric content of prey consumed by fishes
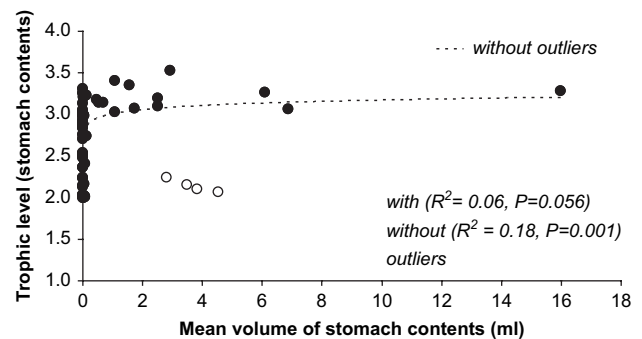
Fig. 6 – Relationship between mean volume of stomach contents and trophic levels estimated from stomach content analyses for fishes and macroinvertebrates from the tidal estuary at Mad Island Marsh.

described by Benoit-Bird (2004) supports the view of optimal foraging.

In shallow lotic and estuarine systems, food webs tend to have three or four trophic levels (Winemiller, 2005). Food chain length is constrained by predator/prey size ratios, losses of energy during its transfer from one trophic level to another (Pimm and Kitching, 1987; Jennings and Warr, 2003). The low trophic positions of top predators at Mad Island Marsh estuary were probably due to high incidence of feeding on herbivores and detritivores (i.e., mullet, menhaden, and crabs) (Akin and Winemiller, 2006). Based on estimates of trophic position from stable isotope ratios, Layman et al. (2005) did not find a significant relationship between trophic position and predator size in a tropical river food web. They interpreted the lack of association between trophic level and body size to the diverse species assemblage with primary consumers encompassing a broad range of body sizes in a species-rich community. Like Layman et al. (2005), we also found a positive but insignificant relationship between predator size (length) and trophic position estimated from nitrogen isotope data, and a significant relationship between mean body size of consumers and trophic position estimated by stomach content analysis. This relationship was stronger when the two large detrivores (mullet and gizzard shad) were excluded from the analysis ($r = 0.50$ vs. 0.36).

We obtained a significant relationship between trophic position estimated from stomach contents and consumer size (length), but a non-significant relationship between trophic level estimated by stable isotopes or nitrogen ratio and body size (length), and this result could be attributable to methodological differences. Stable isotopes provide a continuous measure of trophic position that integrates assimilation of material from all trophic pathways leading to a top predator. On the other hand, stomach contents analysis provides an estimation of trophic level based on prey that are consumed but not necessarily assimilated in proportion to their mass in the stomach. Although both methods yielded largely concordant results for consumer trophic positions, there were some exceptional species, including Gulf menhaden (*Brevortia patranus*), gizzard shad (*Dorosoma cepedianum*), grass shrimp (*Palaemonetes pugio*) and lady fish (*Elops saurus*), that reduced the strength of the relationship between trophic level estimates from stable isotope and body size (length) ($r = 0.35$ and $r = 0.51$ with and without inclusion of these species, respectively). The former three species had higher trophic levels calculated from stable isotope data compared to estimates based on stomach contents analysis, whereas the latter species had a lower trophic level calculated from stable isotopes. The discordant results of trophic positions of these species could have been caused by differences between food consumed and assimilated. Sometimes consumed food is not assimilated and discarded as feces. For example, menhaden stomachs contained mostly fine amorphous organic material that was assumed to derive from a mixture of algal and macrophyte sources (Winemiller et al., 2007). Only trace amounts of invertebrates were recovered from stomachs. Isotopic analysis indicated that invertebrates were the primary nutritional resource for menhaden (Winemiller et al., 2007). Thus, juvenile menhaden could best be characterized as zooplanktivores positioned at trophic level 3, which is similar to the conclusion

obtained from stable isotope studies of menhaden in a coastal marsh in Georgia (Peterson and Howarth, 1987).

In addition, there could be sources of error in estimating trophic positions from either method. For example, low trophic position values assigned to species consuming large volumes of detritus could be a source of error in the diet-based estimates of trophic position. This is because detritivores are among the most abundant species in the marsh, and thus are important in diets of piscivores (Winemiller et al., 2007). Another potential source of bias in the comparison of trophic positions calculated using both methods is ''time averaging'' of assimilated material in isotopic analysis (O'Reilly et al., 2002). Our isotopic data were based on samples collected during August (plants tissues were collected during August and February and values were averaged). Species with short life cycles can show large temporal variation in isotopic signatures, whereas longer-lived species will reflect integration of signals over longer time intervals. Thus, our isotopic data may have reflected differing amounts of time integration that depended on body size and/or other ecological and physiological factors, whereas our dietary samples reflected numerical averages based on available specimens collected over the course of an 18-month field survey. In almost all cases, the sizes of specimens used for isotopic analysis closely matched the average size of conspecifics used for dietary analyses. Another factor that can increase variation in isotopic data is fish movement (Herzka, 2005). Recent immigrants may reflect a history of feeding within the habitat from which they emigrated rather than the receiving habitat (Jackson and Harkness, 1987). Given the large potential for differences in time and place to influence variation in diets and isotopic signatures, it is rather remarkable that estimates from the two methods matched closely for most of the species examined.

Despite the discordant estimates for invertivores that consume large amounts of detritus, trophic level estimates from the two methods for most species were in fairly close agreement. When these organisms were removed from the statistical analysis, the coefficient of determination for the linear regression between trophic level estimated by stable isotope and stomach contents analysis increased from 0.19 to 0.55 (Winemiller et al., 2007). This gives confidence that the trophic level algorithm and our nitrogen ratio enrichment value were reasonable.

The curve representing the relationship between consumer size and trophic position estimated by stomach contents analysis increased with increasing body size and then leveled off at approximately TL = 3.0. This relationship is consistent with other fish studies (Stergiou and Karpouzi, 2002; Karpouzi and Stergiou, 2003). Constraints on trophic structure (i.e., food chain length) in natural systems could be determined by many factors including energetic constraints (Odum, 1959), productivity (Pimm, 1982; Hairston and Hairston, 1993; Briand and Cohen, 1987; Kaunzinger and Morin, 1998), ecosystem size (Post et al., 2000), predator–prey population dynamical constraints, such as self damping (i.e., density-dependent responses; Sterner et al., 1997) or local colonization and extinction dynamics (Pimm, 1982; Holt, 2002), and environmental fluctuations and disturbance (Pimm, 1982). Due to difficulties in distinguishing only

one factor determining the limit of food chain, those factors together could operate in determining the limit of trophic position in this tidal estuary. Given that the Mad Island Marsh tidal estuary is a relatively small and dynamic habitat subject to frequent disturbances, ecosystem size and disturbance could be the main factors limiting food chain length.

Food web structure provides an important tool for fishery management. Impacts of fishing on marine fish populations frequently are associated with trophic position, with largest species at higher trophic positions usually targeted first (Pauly et al., 1998). As demonstrated by Layman et al. (2005), removal of the largest species from a species assemblage is not always followed by a reduction in mean food chain length. Removal of abundant large-bodied prey feeding at low trophic positions can result in a dietary shift by predators toward consumption prey occupying higher trophic positions. We hypothesize that reductions in populations of striped mullet (*Mugil cephalus*), Gulf menhaden (*Brevoortia patronus*), or blue crabs (*Callinectes sapidus*) at Mad Island Marsh would result in a shift by red drum (*Sciaenops ocellatus*), alligator gar (*Atractosteus spatula*), and other top predators toward greater consumption of abundant small species at higher trophic positions, such as spot (*Leiostomus xanthurus*), Atlantic croaker (*Micropogonias undulatus*), and juvenile spotted sea trout (*Cynoscion nebulosus*). This hypothesis could be tested by comparing diets and trophic positions of piscivorous fishes in Gulf coastal ecosystems during years with differential recruitment of prey taxa.

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