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Feeding Habits of Red Drum (*Sciaenops ocellatus*) in Galveston Bay, Texas: Seasonal Diet Variation and Predator-Prey Size Relationships

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ABSTRACT: Feeding habits, seasonal diet variation, and predator size-prey size relationships of red drum (*Sciaenops ocellatus*) were investigated in Galveston Bay, Texas through stomach contents analysis. A total of 598 red drum ranging from 291–763 mm total length were collected and their stomach contents analyzed during fall 1997 and spring 1998. The diet of red drum showed significant seasonal patterns, and was dominated by white shrimp (*Penaeus setiferus*) during fall and gulf menhaden (*Brevoortia patronus*) during spring. Blue crab (*Callinectes sapidus*) was an important component of red drum diets during both seasons. Significant differences existed between prey types consumed during fall and spring as red drum diet reflected seasonal variation in prey availability. Predictive regression equations were generated to estimate original carapace width of blue crabs from several measurements taken from carapace fragments recovered in red drum stomachs. Regressions were highly significant ($r^2 > 0.97$) and increased the number of blue crabs with size information nearly three fold. Predator size-prey size relationships were determined for red drum feeding on white shrimp, gulf menhaden, and blue crab. Although regression slopes were statistically significant, prey sizes increased only slightly with increasing red drum size. Comparisons of prey sizes consumed by red drum with sizes occurring in the field indicate that red drum feed in nearshore shallow water habitats, which serve as nursery areas for many juvenile fishes and crustaceans. Our findings demonstrate that red drum feed on several prey species of commercial and recreational value and may have important effects on estuarine community structure.

Introduction

The effect of predaceous fishes on the composition of aquatic ecosystems can be significant. Mortality induced by predation can reduce prey abundances locally and may limit prey recruitment in some systems (Nielsen 1980; Hartman and Margraf 1993; Bailey 1994). Predation by fishes is often size-dependent leading to increased mortality at specific life stages of prey (Werner and Gilliam 1984) and to potential shifts in the size distributions of surviving individuals (Rice et al. 1993). To begin to quantify potential effects of fish predation on community structure and prey populations, detailed information is needed on the feeding habits of important predators.

The red drum (*Sciaenops ocellatus*) is an abundant estuarine-dependent fish that is widely distributed throughout the Gulf of Mexico (Pattillo et al. 1997). Adults spawn in nearshore Gulf waters close to the mouths of passes and inlets during late summer and early fall (Pearson 1929; Peters and McMichael 1987; Comyns et al. 1991). Larvae are transported through passes into estuaries via tidal currents, where they settle in shallow nursery areas and remain through the juvenile stage (Holt et al. 1989; Rooker and Holt 1997). Although older red drum typically migrate to offshore waters during fall and winter, fish at least as old as age four commonly occur in Gulf of Mexico estuaries (Pattillo et al. 1997).

Past research on red drum feeding habits along the Gulf coast indicates that red drum diets are fairly heterogeneous with several crustaceans and juvenile fishes being important dietary components (Boothby and Avault 1971; Bass and Avault 1975; Overstreet and Heard 1978). The diet of red drum in estuaries along the Texas coast is similar to that found in other Gulf coast regions, however, information is limited and dated (Pearson 1929; Gunter 1945; Knapp 1950; Miles 1950). Previous research demonstrates that commercially important species of shrimp, crabs, and fishes can be abundant in red drum diets in Gulf coast estuaries,

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and that red drum feeding patterns may have a strong seasonal component.

We determined the diet and feeding habits of age one and older red drum during fall and spring in Galveston Bay, Texas, a large estuary on the north-central Gulf coast. Seasonal variation in diet composition was examined and related to temporal patterns in prey availability. The relationship between red drum size and prey size was examined for important prey species. Selective feeding patterns of red drum were assessed through comparisons of prey types and sizes consumed with those available in the estuary. We generated a series of allometric equations used to estimate carapace width of blue crab (*Callinectes sapidus*) from distances between orbital and frontal teeth and assess the potential for these equations to improve size-based dietary information for predators feeding on blue crabs.

Materials and Methods

Red drum (age 1–4) were captured in monofilament gill nets between September 16–November 21, 1997 (fall) and between April 14–June 17, 1998 (spring). During each season, 45 gill nets were set throughout Galveston Bay, each net being set within a one square nautical mile grid containing shoreline that was chosen randomly from all available grids that contained shoreline (Fig. 1). Gill nets measured 183 m long × 1.2 m deep and consisted of four separate sections (each of 45.7 m length) of 7.6 cm, 10.2 cm, 12.7 cm, and 15.2 cm stretched mesh. Gill nets were set within one hour of sunset and were retrieved the following day between sunrise and four hours past sunrise. Gill nets were set perpendicular to shore with the section consisting of the smallest mesh (7.6 cm) being positioned closest to the beach (see Fuls and McEachron 1997 for more detail on gill net sampling). Upon retrieval of each gill net, red drum were measured and the stomachs removed and kept on ice until they could be frozen at the laboratory. At the laboratory, stomachs were thawed and the contents identified to the lowest possible taxon, counted, measured to the nearest mm, and weighed wet to the nearest 0.01 g.

Prey availability and size structure were assessed by sampling with bag seines at random stations (one square nautical mile grids containing shoreline) throughout the bay during each season. Bag seines measured 18.3 m long × 1.8 m deep, with 1.9 cm and 1.3 cm stretched nylon mesh in the wings and bag, respectively. Each bag seine was pulled approximately 15.2 m parallel to shore at each station. For each seine haul, all fish and invertebrates captured were counted and measured (total length in mm). Twenty bag seines were completed monthly resulting in approximately 60 seine hauls during each season.

Diet composition was evaluated using a variety of indices. These included: a numerical index (% N) = the number of prey in a specific prey category as a percentage of the total number of all prey items; a gravimetric index based on prey wet weight (% W) = the weight of all prey in a specific prey category as a percentage of the total weight of all prey; and a percent frequency of occurrence index (% FO) = the percentage of all stomachs containing food that contained a specific prey category. An estimate of accuracy in describing the diet (Ferry and Cailliet 1996) was generated by plotting the cumulative number of stomachs analyzed in a random order along the x-axis and the cumulative number of new prey items encountered in the stomachs along the y-axis. The asymptotic stabilization of the curve indicates that a sufficient number of stomachs has been analyzed to produce an accurate description of diet breadth.

Seasonal variation in red drum diet composition was assessed using contingency table analysis. Chi-square statistics were calculated for each combination of season and prey type, with a significant grand total χ^2 statistic indicating a significant difference in the proportions of specific prey species consumed between fall and spring seasons. Because the random sampling design resulted in regional differences within the bay in the number of red drum captured and the potential existed for site-specific differences in prey availability, we compared red drum diet composition between seasons in a single region of the bay (West Bay region, see Fig. 1) wherein sampling effort was nearly equal. Further, within season comparisons were made between separate bay regions to determine if red drum diet composition was fairly homogeneous throughout the bay.

Prey species selection by red drum was evaluated by comparing the proportional contribution of individual prey species to red drum diets with the proportional contribution of the same prey species to the available prey population in the estuary. Dominant prey species were evaluated during fall and spring separately. Chesson's selectivity index (Chesson 1978) was calculated using prey species proportions consumed by red drum captured in gill nets and prey species proportions in the field captured in bag seines. Field prey proportions were calculated from bag seines performed 2–4 h prior to setting of the gill net in the same sampling grid and the neighboring grids. Chesson's indices were calculated for several dates with sufficient and coinciding data on diet and prey availability. For each date, calculation of the selectivity index generates a value of alpha (α), which were then aver-

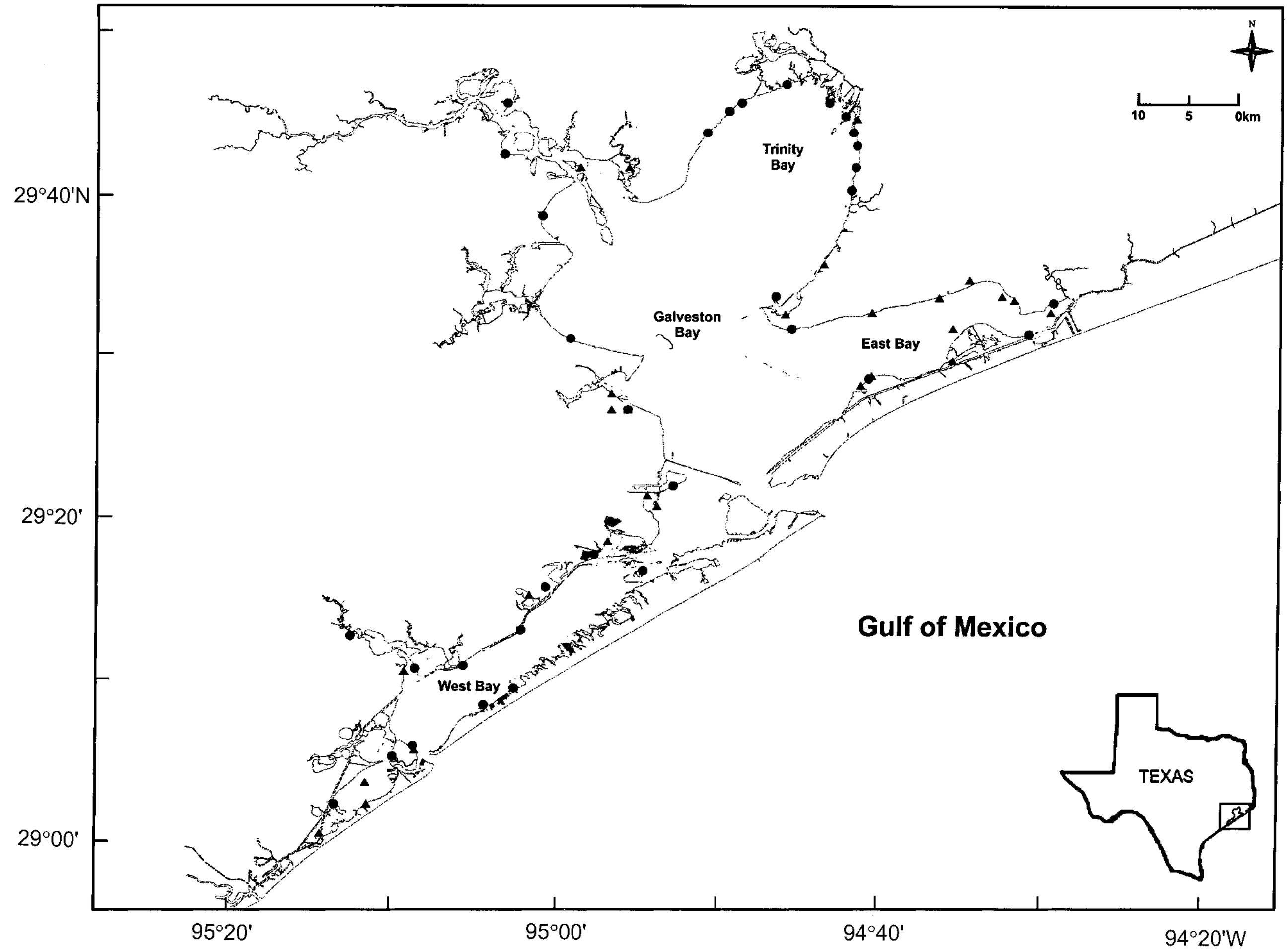

Fig. 1. Map of Galveston Bay, Texas illustrating the sample locations for red drum captured during fall 1997 (▲) and spring 1998 (●).

aged and compared statistically (*t*-test) to an expected value. Mean α-values were calculated for each of nine sets of dates during fall (September 15–16, 23–24, 25–26; October 16–17, 21–22; November 6–7, 11–12, 18–19, 20–21) and for each of nine sets of dates during spring (April 20–21, 22–23, 27–28, 29–30; May 4–5, 6–7, 11–12, 13–14; June 8–9).

A series of allometric equations was generated using regression analysis to estimate original carapace width of blue crabs from partial carapace remains recovered from red drum stomachs. For diet analyses, it was assumed that if carapace fragments were recovered from a given red drum stomach, then the entire crab was consumed. This assumption could not be made if only chelipeds or walking legs were recovered as crab escapement could have occurred. Further, because of the ability of crabs to regenerate lost limbs, predictions of original size based on measurements from regenerated appendages may not be accurate. For each red drum stomach examined, all carapace fragments recovered were assumed to be from a single crab unless two or more identical carapace fragments were recovered (i.e., frontal section containing orbital teeth), which were then each counted as a separate crab. Three measurements were regressed against total carapace width. These were: the distance between the outer and inner orbital teeth; the distance between the inner orbital tooth and the adjacent frontal tooth; and the distance between the two frontal teeth (Fig. 2).

Predator size-prey size relationships were examined by plotting red drum total length (TL) versus prey TL measurements (carapace width for crabs). For all prey pooled and for several important prey species, ontogenetic changes in minimum, mean, and maximum prey sizes consumed by red drum were estimated using least squares and quantile regression techniques (Scharf et al. 1998a). Quantiles used to represent maximum and minimum

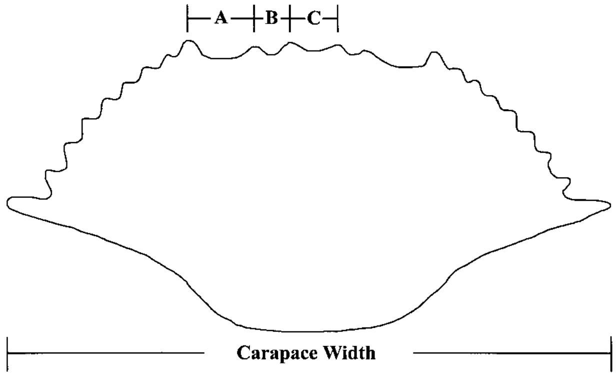

Fig. 2. Illustration of blue crab carapace indicating measurements used to generate predictive regression equations relating the measurements indicated and blue crab carapace width. A = distance between the outer and inner orbital teeth; B = distance between the inner orbital tooth and the adjacent frontal tooth; C = distance between the two frontal teeth.

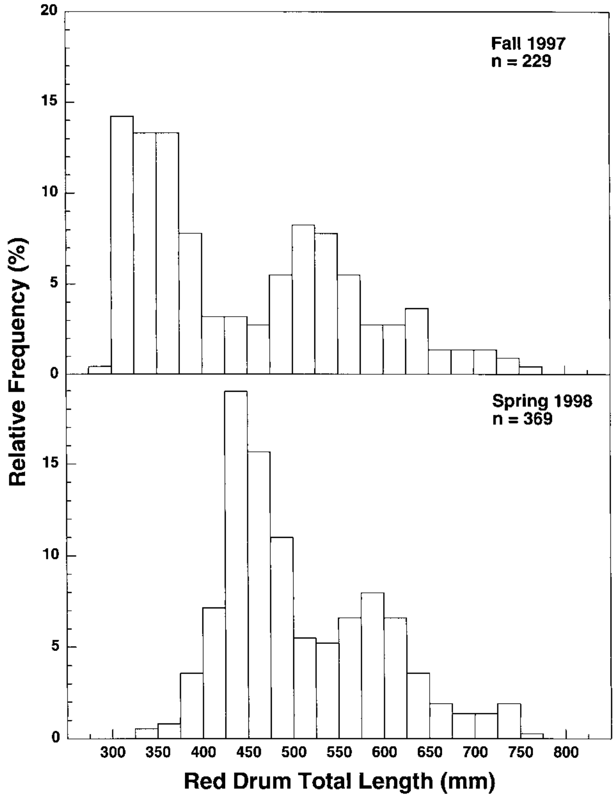

Fig. 3. Length frequency distributions of red drum examined for stomach contents during fall 1997 and spring 1998. Length modes during fall represent ages 1–4; length modes during spring represent ages 1.5–3.5.

prey sizes were selected based on sample size considerations (Scharf et al. 1998a).

Size-selective feeding patterns of red drum were examined by comparing length frequencies of important prey species recovered from red drum stomachs with length frequencies of those same prey species occurring in Galveston Bay during fall and spring. Bag seine samples were used to construct length frequencies of prey species in the estuary. Length frequency distributions for prey species captured using bag seines were compared to length frequency distributions for prey species consumed by red drum using a Kolmogorov-Smirnov two sample test.

Results

A total of 598 red drum stomachs were collected and examined (229 during fall; 369 during spring); 383 red drum stomachs contained food (168 [73.4%] during fall; 215 [58.3%] during spring). Red drum stomachs were collected from 27 locations in fall and 33 locations in spring (Fig. 1). Red drum size ranged from 291–763 mm during fall and from 345–751 mm during spring. Clear modes in the length frequency plots represented ages 1–3 (Fig. 3), with some larger individuals potentially representing age 4 fish in each season based upon previously constructed length-at-age plots (Colura and Buckley 1996). Plots of the cumulative number of prey types recovered from red drum stomachs versus the cumulative number of stomachs examined showed trends toward asymptotic stabilization for each season (Fig. 4). This result indicates that, for age 1–4 red drum in Galveston Bay, Texas, a sufficient number of red drum stomachs were examined to produce an accurate estimate of diet breadth.

The fall diet of red drum was dominated primarily by decapod crustaceans with teleost fishes being of secondary importance (Table 1). Decapods occurred in nearly 83% of red drum stomachs examined that contained food with crabs and shrimp occurring in approximately 40% and 60% of stomachs, respectively. Of the crabs consumed, blue crab was most commonly eaten, occurring in 25% of red drum stomachs and accounting for nearly 20% of the diet by weight. White shrimp (*Penaeus setiferus*) were the single most important dietary item of red drum in fall, occurring in nearly 23% of stomachs examined and accounting for nearly 40% of the diet by number. In addition, most unidentified shrimp were likely white shrimp based on relative proportions of the three shrimp species recovered in red drum diets in fall. Therefore, white shrimp likely represented nearly 60% of the diet of red drum by number and occurred in over 60% of red drum stomachs during fall. Other decapods that occurred in fall red drum diets in relatively small proportions included lesser blue crab (*Callinectes similis*), brown shrimp (*Penaeus aztecus*), several xanthid crabs, grass shrimp

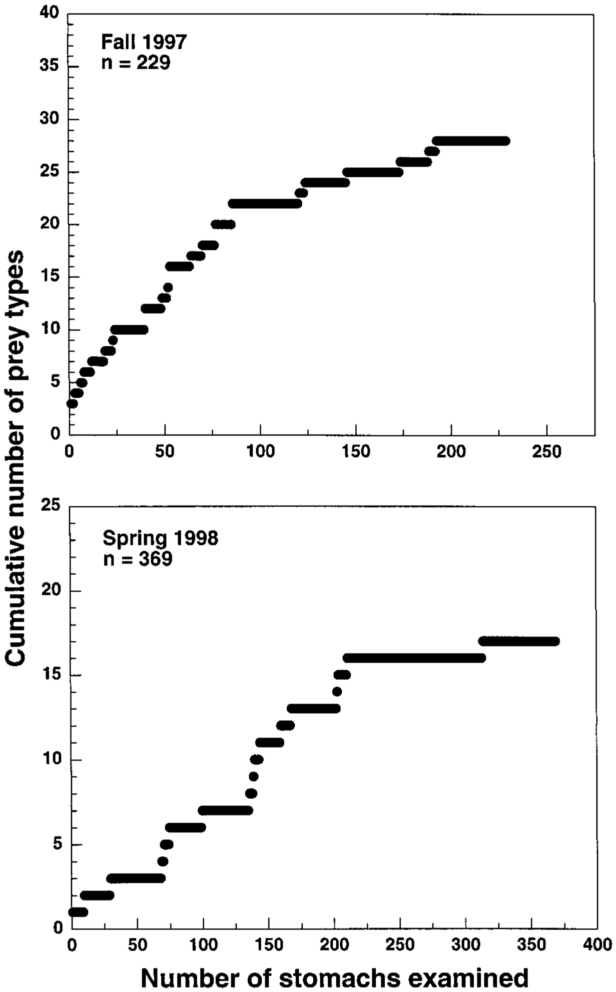

Fig. 4. The cumulative number of prey types recovered from red drum stomachs versus the total number of stomachs examined during fall 1997 and spring 1998. Asymptotic stabilization of the number of new prey types recovered is indicative of a sufficient number of stomachs examined to obtain an accurate estimate of diet breadth.

(*Palaemonetes* spp.), green porcellain crabs (*Petrolisthes armatus*), and estuarine snapping shrimp (*Alpheus estuariensis*).

Teleost fishes occurred in slightly over 40% of the stomachs examined in fall and represented about 40% of the diet by weight, with most fish being unidentified (Table 1). The most prevalent fish species were black cheeked tonguefish (*Symphurus plagiusa*), shrimp eels (*Ophichthus gomesi*), and gulf menhaden (*Brevoortia patronus*). Other fish species eaten in fall included bay anchovy (*Anchoa mitchilli*), hardhead catfish (*Arius felis*), mullet (*Mugil* spp.), least puffer (*Sphoeroides parvus*), midshipman (*Porichthys plectrodon*), and sea robin (*Prionotus* spp.). Sea anemones, isopods, and oyster shell were also recovered in trace amounts.

TABLE 1. 1997 fall diet composition of red drum (*Sciaenops ocellatus*) in Galveston Bay, Texas expressed as percent frequency of occurrence (% FO), percent number (% N), and percent wet weight (% W). UID = unidentified; NA = not applicable.

Prey Category	% FO	% N	% W
Decapoda	82.74	73.14	58.01
Portunidae			
Callinectes sapidus	25.00	8.66	18.84
Callinectes similis	2.38	0.57	0.84
Callinectes spp.	2.38	0.85	0.17
Penaeidae			
Penaeus setiferus	22.62	38.49	21.19
Penaeus aztecus	1.79	0.85	0.63
Xanthidae			
Eurypanopeus depressus	1.19	0.43	0.31
Menippe adina	0.59	0.14	0.80
Xanthidae spp.	0.60	0.14	0.03
Palaemonidae			
Palaemonetes spp.	1.79	0.43	0.07
Porcellanidae			
Petrolisthes armatus	0.60	0.14	0.22
Alpheidae			
Alpheus estuariensis	1.19	0.28	0.22
UID crabs	5.36	1.14	1.28
UID shrimp	39.29	21.73	13.03
Teleostei	41.67	25.88	40.11
Culpeidae			
Brevoortia patronus	2.98	2.84	9.03
Engraulidae			
Anchoa mitchilli	1.79	0.85	0.32
Ariidae			
Arius felis	1.19	0.28	0.72
Mugilidae			
Mugil spp.	2.98	0.99	7.12
Cynoglossidae			
Symphurus plagiusa	8.33	6.25	7.57
Ophichthidae			
Ophichthus gomesi	9.52	3.69	7.56
Tetraodontidae			
Sphoeroides parvus	0.60	0.14	0.26
Batrachoididae			
Porichthys plectrodon	0.60	0.14	0.68
Triglidae			
Prionotus spp.	0.60	0.71	0.25
UID fish	23.21	10.23	7.37
Actiniaria	2.38	0.07	0.46
Isopoda	1.19	0.28	0.03
Mytiloida	2.98	NA	NA
Ostreidae			
Crassostrea virginica	2.98		
UID remains	4.17	NA	1.39

The spring diet of red drum was dominated by fishes, which represented over 97% of the diet by number and over 80% by weight (Table 2). Gulf menhaden represented the greatest proportion of fishes consumed, with 95% of the diet by number and nearly 70% of the diet by weight being gulf menhaden. The frequency of occurrence of gulf menhaden was 35%, which was low when compared to the percent of the diet by number and weight represented by this prey. However, large quantities of gulf menhaden were often recovered from individual red drum stomachs, often as high

TABLE 2. 1998 spring diet composition of red drum (*Sciaenops ocellatus*) in Galveston Bay, Texas expressed as percent frequency of occurrence (% FO), percent number (% N), and percent wet weight (% W). UID = unidentified; NA = not applicable.

Prey Category	% FO	% N	% W
Decapoda	44.19	2.51	12.25
Portunidae			
Callinectes sapidus	19.53	1.30	8.87
Callinectes similis	0.93	0.02	0.05
Callinectes spp.	1.86	0.09	0.07
Penaeidae			
Penaeus aztecus	4.19	0.33	0.59
Xanthidae			
Menippe adina	1.86	0.11	0.99
Xanthidae spp.	5.12	0.26	0.63
Palaemonidae			
Palaemonetes spp.	0.47	0.02	0.01
Machrobrachium ohione	0.47	0.02	0.05
Alpheidae			
Alpheus estuariensis	0.47	0.02	0.03
UID crabs	1.40	0.00	0.12
UID shrimp	7.91	0.33	0.82
Teleostei	63.72	97.49	82.83
Clupeidae			
Brevoortia patronus	35.35	95.22	68.82
Bothidae			
Paralichthys lethostigma	0.47	0.02	0.34
Sparidae			
Lagodon rhomboides	2.33	0.11	0.45
Mugilidae			
Mugil cephalus	0.47	0.02	2.01
Mugil spp.	1.40	0.07	0.58
Cynoglossidae			
Symphurus plagiusa	0.47	0.02	0.05
Ophichthidae			
Ophichthus gomesi	1.86	0.22	0.74
Batrachoididae			
Opsanus beta	0.47	0.02	0.58
Atherinidae			
Membras martinica	2.79	1.34	4.19
UID fish	18.14	0.44	5.08
UID remains	12.56	NA	4.92

as 100–200 per stomach, accounting for the large diet proportions by number and weight for this species. Other fish species that occurred in relatively low quantities included mullet, black cheeked tonguefish, shrimp eels, southern flounder (*Paralichthys lethostigma*), pinfish (*Lagodon rhomboides*), gulf toadfish (*Opsanus beta*), and rough silverside (*Membras martinica*).

Decapod crustaceans were of lesser importance in spring, but still occurred in nearly 45% of red drum stomachs that contained food (Table 2). Although shrimp prey declined sharply from the fall, blue crab remained an important dietary item of red drum in spring. Blue crab occurred in nearly 20% of stomachs that contained food and represented nearly 10% of the diet by weight. White shrimp were absent from the spring diets of red drum as this species is rarely found in the bay during spring. Other decapod crustaceans recovered from the stomachs of red drum in spring included lesser blue crab, brown shrimp, xanthid crabs, grass shrimp, estuarine snapping shrimp, and ohio or river shrimp (*Machrobrachium ohione*).

TABLE 3. Contingency table analysis to test for seasonal differences in diet composition of red drum in Galveston Bay, Texas. Observed values represent the number of occurrences of each prey in red drum stomachs. Expected values are based on the total number of prey occurrences (both seasons) and the number of red drum stomachs containing food in each season (168 in fall; 215 in spring). The test statistic is highly significant (** $p < 0.001$).

Prey Species	Fall Observed (Expected)	Spring Observed (Expected)	Total N_i (Both Seasons)	χ_i^2
Blue crab	42 (37)	42 (47)	84	1.29
White shrimp	38 (17)	0 (21)	38	48.62
Gulf menhaden	5 (36)	76 (45)	81	46.73
Brown shrimp	3 (5)	9 (7)	12	1.74
Mugil spp.	5 (4)	4 (5)	9	0.50
N_j	93	131	224	
χ_j^2	55.50	43.38		98.88**

Results of contingency table analysis indicated that significant seasonal differences occurred in the diet composition of red drum (Table 3). Clearly, the large numbers of white shrimp consumed during fall and the large numbers of gulf menhaden consumed during spring account for the observed seasonal differences. Comparisons restricted to the West Bay region showed similar seasonal differences. Further, within season regional comparisons (between East Bay and West Bay during fall and between Trinity Bay and West Bay during spring) resulted in only minor differences in red drum diet composition. The importance of dominant prey species (blue crab, penaeid shrimp, gulf menhaden) remained similar between separate regions within each season and any regional differences in red drum diet composition were due to site specific occurrences of relatively less common prey (atherinid fishes and xanthid crabs).

Strong seasonal patterns in estuarine abundance were evident for the important prey species of red drum (Fig. 5). During 1997–1998, gulf menhaden abundance peaked between early April and early June. The timing of the annual peak in gulf menhaden abundance matched closely with the period of the spring diet analyses of red drum in this study. Similarly, brown shrimp abundance peaked during April, May, and June, coinciding with our spring study period. The highest abundance of white shrimp in 1997–1998 occurred between mid-July and late November. Our fall study period extended over much of the same time period as the annual peak in white shrimp abundance. During our study year, blue crab abundance was fairly consistent, with slight peaks in late January and June. The abundance patterns for these four prey spe-

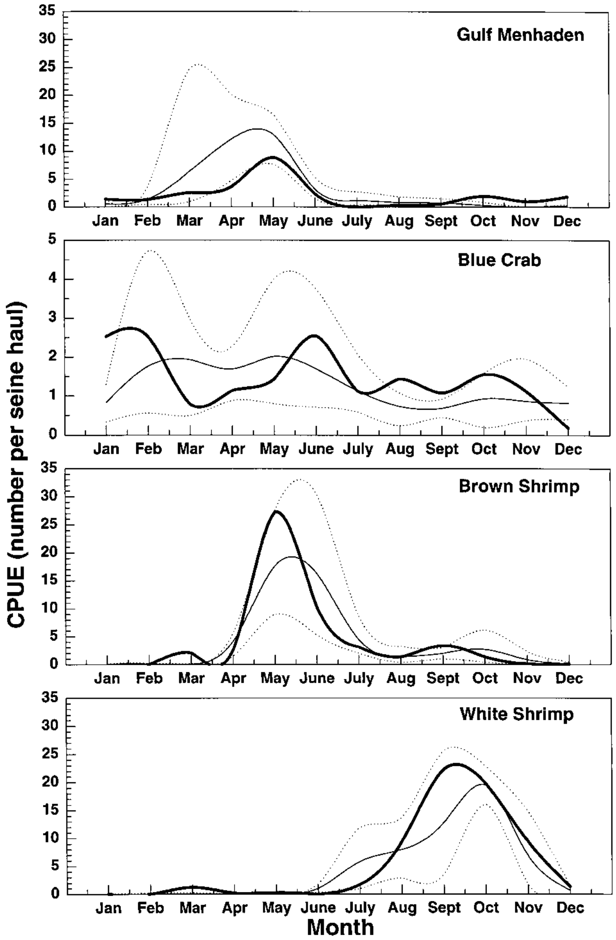

Fig. 5. Seasonal variation in catch-per-unit-effort (CPUE) of important prey species of red drum. CPUE is calculated per month as the geometric mean of number per seine haul based on 20 seine hauls per month. The thin solid line in each plot represents the average monthly catch rate for the period January 1991–December 1996. For each plot, the dashed lines above and below this 6-yr average represent the largest and smallest values of CPUE observed for each month during this time period. The thick solid line in each plot represents the CPUE values observed during this study (July 1997–June 1998). Lines represent a smoothed fit to the monthly CPUE means. Note the scale change in CPUE for blue crab.

cies observed during 1997–1998 corresponded well with a six-year average of monthly abundance estimates (1991–1996), indicating that seasonal abundance patterns and actual levels of prey abundance observed during 1997–1998 were representative of a typical year.

Results of prey species selectivity analyses indicate that red drum fed on blue crabs and white shrimp in proportion to their abundance levels in the estuary during fall (Table 4). During spring, however, red drum showed positive selection for gulf menhaden and avoidance for brown shrimp, whereas blue crab were eaten in proportions similar to those in the estuary (Table 4). The addition of prey of lesser dietary importance to the selectivity analysis did not alter our results, therefore only results for dominant prey are presented.

Allometric equations were generated using measurements taken from 110 blue crabs with carapace widths between 18–174 mm, representing the size range naturally occurring in Gulf coast estuaries (Pattillo et al. 1997). Blue crab carapace measurements taken among orbital and frontal teeth were highly significant predictors of original blue crab carapace width, with variation in each of the three measurements explaining between 97–98% of the variation in original carapace width (Fig. 6). Of 49 blue crabs recovered for which size information could be obtained, only 18 were recovered with the entire carapace intact and measurable. The additional 31 carapace width estimates were produced using the predictive regression equations.

Significant predator size-prey size relationships were observed for each important prey species and for all prey combined (Fig. 7). For all three prey species, only slight increases in mean prey size occurred with increasing red drum size, with larger red drum including several small-sized prey in the diet. Similarly, although regression slopes were statistically significant, most were less than 0.10 resulting in only small changes in maximum and minimum prey sizes consumed with increasing red drum size regardless of prey species. For all prey

TABLE 4. Values of Chesson's selectivity index for important prey species of red drum during fall and spring. Mean α = the mean value of alpha calculated from 9 dates during fall and from 9 dates during spring; s_b α = standard error of alpha; expected α based on null hypothesis of no prey selection; t = test statistic of *t*-test comparing mean α with expected α; df = degrees of freedom of *t*-test; p = probability value of *t*-test.

Prey Species	Mean α	s_b α	Expected α	t	df	p
			Fall			
Blue crab	0.6690	0.1067	0.5000	1.5848	8	0.1517
White shrimp	0.3310	0.1067	0.5000	1.5848	8	0.1517
			Spring			
Blue crab	0.2774	0.1301	0.3333	0.4297	8	0.6788
Gulf menhaden	0.7200	0.1309	0.3333	2.9538	8	0.0183
Brown shrimp	0.0026	0.0020	0.3333	166.4435	8	<0.0001

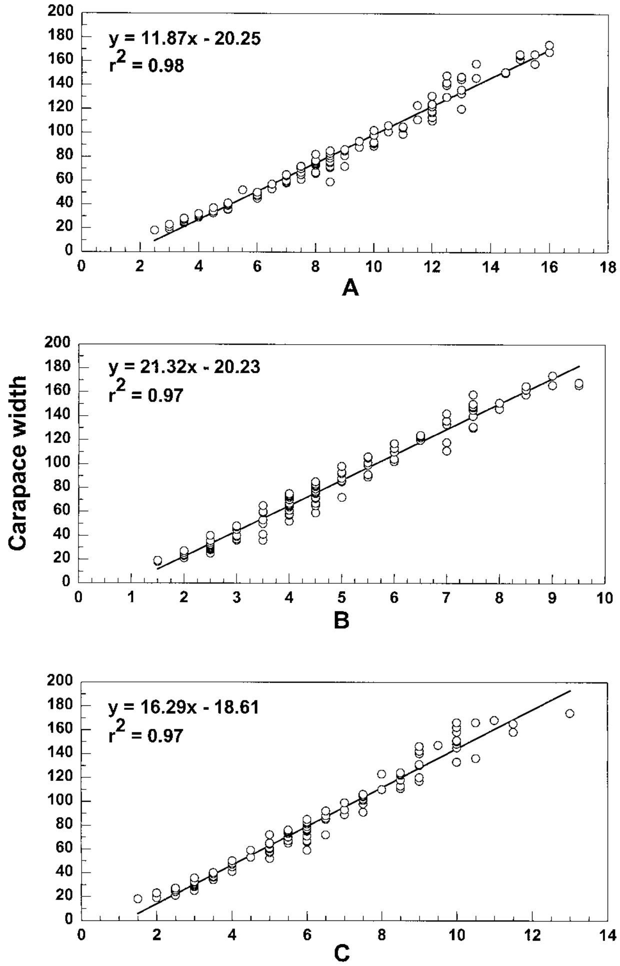

Fig. 6. Least squares regressions generated to estimate original blue crab carapace width from measurements taken from fragments of the carapace recovered from red drum stomachs. A, B, and C follow definitions from Fig. 2. All three regressions were highly significant ($p < 0.0001$). $n = 110$.

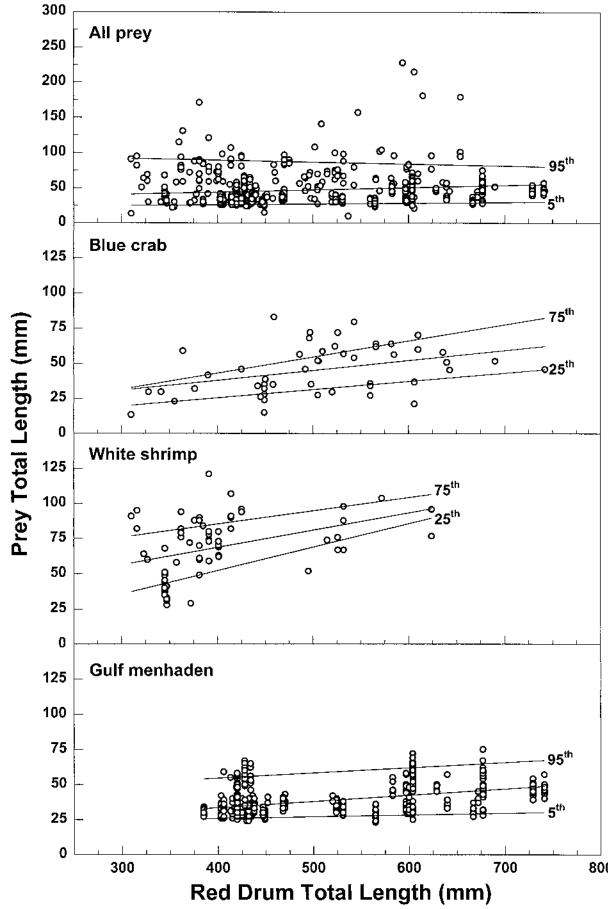

Fig. 7. Scatter diagrams illustrating the relationships between prey size and red drum size for three important prey species and for all prey combined. Upper and lower bounds for each prey represent ontogenetic changes in maximum and minimum prey size consumed with increasing red drum size. Upper and lower bound quantiles are indicated on each panel. Intermediate regression lines represent changes in mean prey size with increasing red drum size. Blue crab total length = carapace width in mm.

combined, the maximum regression slope was not significant ($p = 0.445$), suggesting no change in maximum size of prey consumed with increasing red drum size. A narrow size range of blue crabs between approximately 25–75 mm carapace width was consumed by red drum during both seasons, with only two crabs larger than 75 mm being eaten. Sizes of white shrimp consumed ranged mainly between 25–100 mm, with most being eaten by red drum less than 425 mm (the dominant size group, age one, of red drum during fall). Gulf menhaden between 25–60 mm were consumed by red drum of all sizes during spring, with only a slight increase in mean size eaten with increasing red drum size.

Red drum did not exhibit strong selectively based on prey size for any of its important prey (Fig. 8). No statistical differences could be detected between size distributions of white shrimp (fall) and gulf menhaden (spring) captured in bag seines and size distributions of each prey species eaten by red drum. Blue crab sizes consumed by red drum (both seasons) were statistically different than sizes of blue crabs captured in bag seines. Red drum consumed more larger (50–75 mm) blue crabs than expected based on field size distributions.

Discussion

The feeding habits of red drum in Galveston Bay, Texas showed strong seasonal patterns that were closely linked to temporal changes in prey availability. Past research on the diets of age one and older red drum (ages 1–4 in this study) reveal similar seasonal variation. In a study conducted in

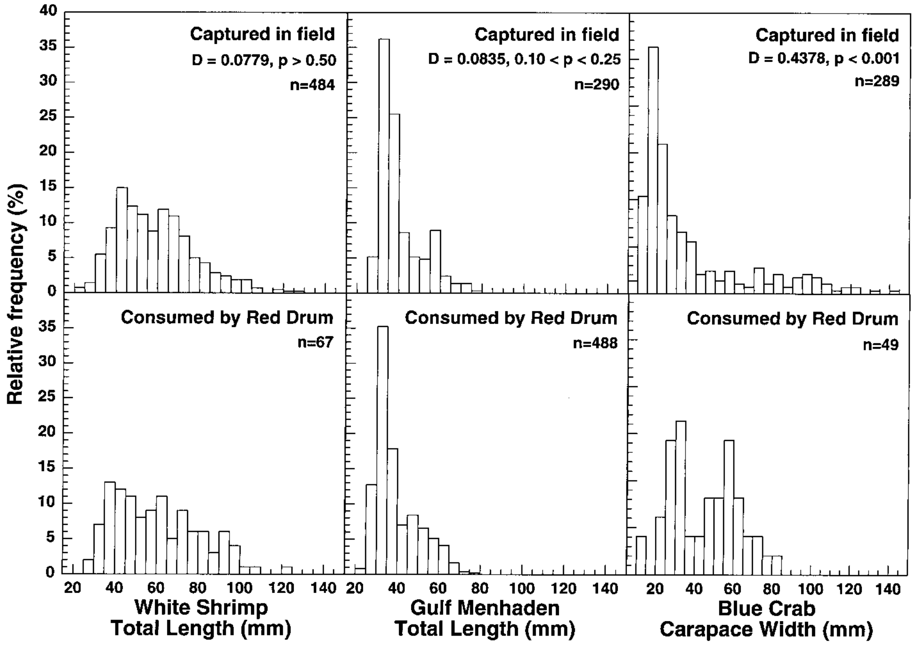

Fig. 8. Length frequency histograms for white shrimp, gulf menhaden, and blue crabs captured in bag seines (top panels) and for each prey consumed by red drum (bottom panels) during fall 1997 and spring 1998. D = largest difference between cumulative length frequencies of each prey captured in the field (bag seines) and the lengths of each prey consumed by red drum; p = probability value of the Kolmogorov-Smirnov two sample test; n = number of individual prey.

a coastal marsh in southeastern Louisiana, Boothby and Avault (1971) concluded that fish were important components of adult red drum diets during winter and spring, with crustaceans becoming more important in later spring months and dominating the diet throughout summer and fall. Overstreet and Heard (1978) also found fish to be important during winter and spring, with blue crabs being most prevalent during summer and penaeid shrimp dominating the fall diet of adult red drum in Mississippi Sound.

The results of our study indicate that single prey species can dominate red drum diets during periods of high abundance. White shrimp were found in higher abundances in the estuary than any other fish or crustacean species during fall 1997. The numbers of white shrimp consumed by red drum were also higher than any other prey species eaten during fall, especially considering that most unidentified shrimp were likely white shrimp. Similarly, Overstreet and Heard (1978) concluded that penaeid shrimp, likely white shrimp, dominated fall red drum diets and suggested that this finding was related to local patterns in shrimp abundance.

During spring, gulf menhaden and brown shrimp were two of the most abundant prey available in Galveston Bay. However, only gulf menhaden were recovered from red drum stomachs in large numbers with brown shrimp rarely being eaten. The overwhelming contribution of gulf menhaden to the diet of red drum during spring in our study has not been noted in previous examinations of red drum diets along the Gulf coast. Only Boothby and Avault (1971) found gulf menhaden to be an important component of red drum diets, occurring in 33% and 22% of stomachs during winter and spring, respectively. However, the authors found that gulf menhaden accounted for only 16% of the diet by volume during winter and only 6% by volume during spring. The fact that gulf menhaden abundance levels in Galveston Bay during spring 1998 were similar to those observed during spring months throughout the previous six years is suggestive that the large contribution of gulf menhaden to the spring diet of red drum is common. The apparent avoidance of brown shrimp by red drum during spring contrasts with the observed feeding patterns of red drum for other prey species, in which prey species were fed upon in large numbers during the time periods coinciding with their highest abundance levels. Other studies of red drum feeding habits that examined seasonal diet changes concluded that penaeid shrimp, likely brown shrimp, were important components of red drum diets during spring, occurring in 20–25% of red drum stomachs (Boothby and Avault 1971; Overstreet and Heard 1978). The potential existence of fine scale patterns in predator and prey spatial distributions may have contributed to the spring feeding patterns observed. The finding that red drum consumed gulf menhaden in proportions greater than expected based on menhaden contribution to prey populations in the estuary may have resulted from red drum encounters with dense schools of menhaden, which were observed frequently thoughout the bay during spring. During encounters with large schools of menhaden, red drum may feed exclusively on this prey while disregarding other prey in the area. Such occurrences could have facilitated the observed positive selection for gulf menhaden and avoidance of brown shrimp.

Blue crabs were an important food item for red drum during both fall and spring in Galveston Bay. Previous Gulf coast studies reported that blue crabs were a major component of red drum diets and were consumed during all seasons. Boothby and Avault (1971) found that blue crabs occurred in 42% of red drum stomachs and were most prevalent during summer and fall, whereas Overstreet and Heard (1978) determined that blue crabs were most important during spring and summer. Based on the moderate levels of abundance maintained by blue crab in Galveston Bay throughout the year and the more pronounced seasonal abundance patterns of other important prey species, blue crab may be even more prevalent in red drum diets during time periods not examined in this study, particularly summer. However, our diet data only supports the conclusion that it is likely that blue crab represent an important part of the diet of red drum during all seasons.

Because gill nets were fished for up to 14 h, postcapture digestion may have influenced stomach contents analysis. In contrast to our findings, Overstreet and Heard (1978) recovered several soft-bodied polychaetes from the stomachs of a similar size range of red drum in Mississippi. However, during each season of our study, several red drum examined contained recently consumed prey, indicating feeding and capture just prior to gear retrieval. If soft-bodied invertebrates, such as polychaetes, contributed significantly to the diet of age 1–4 red drum in Galveston Bay, their presence should have been detected in these recently captured fish. Further, fish and shrimp contain a sufficient number of identifiable hard parts resistant to digestion that enable identification to at least order and suborder taxonomic levels. Lastly, our results, demonstrating the substantial contribution of decapod crustaceans to the diet of age 1–4 red drum, agree well with previous studies on this size group (Boothby and Avault 1971; Overstreet and Heard 1978).

Allometric equations generated to predict blue crab carapace width from measurements taken from fragmented carapace remains should yield accurate estimates of original prey size. For fish prey, diagnostic bones and external morphological measurements have often been used successfully to reconstruct original fish size from digested remains (Trippel and Beamish 1987; Hansel et al. 1988; Scharf et al. 1998b). Our results suggest that similar techniques may be applicable to crabs, such as those used by Cortés et al. (1996) to estimate blue crab carapace width from measurements of carapace length (measured front to back). Application of the equations presented in this study resulted in a nearly three-fold increase in the number of blue crabs with body size information.

The composition of red drum diets did not change appreciably with changes in red drum body size as most important prey species were eaten by all sizes of red drum. The exception was white shrimp, which were consumed mainly by red drum less than 425 mm total length. This size group of red drum represented fish of age one and was the most prevalent age class during fall. Past researchers also found very little change in adult red drum diet compostion with age (Boothby and Avault 1971; Overstreet and Heard 1978). This contrasts with the diet of red drum during the first year of life when several dietary phases are evident (Bass and Avault 1975; Soto et al. 1998).

Sizes of important prey species consumed by red drum remained relatively constant with increasing red drum size. Slope estimates representing changes in minimum, mean, and maximum prey size with increasing red drum size were mostly significant. However, most slope estimates were less than 0.10, with several less than 0.05. Minimum and maximum prey sizes scaled closely with mean sizes as red drum size increased, indicating that the size range of prey eaten remains fairly constant with age. Minimum prey size did not change substantially with increasing red drum size for all prey combined suggesting that small prey are important components of red drum diet throughout ontongeny. The small sizes of prey consumed by red drum are not likely a result of gape limitations as evidenced by the presence of several larger prey in some stomachs. Rather, sizes of prey consumed by red drum are probably due in large part to temporal and spatial overlap of red drum with commonly occurring sizes of prey species occupying nearshore habitats.

The sizes of prey consumed by red drum during fall and spring match closely with those sizes captured in bag seines in nearshore habitats, indicating that red drum in Galveston Bay may be important predators in shallow nursery habitats. When feeding on white shrimp and gulf menhaden, there is no evidence to suggest that red drum feed selectively on particular sizes of prey as length frequency distributions captured in bag seines and those consumed by red drum did not differ statistically for these two species. Blue crabs consumed by red drum were restricted to a narrower range of sizes than that available in the estuary. Blue crabs larger than 85 mm carapace width were not eaten by red drum, possibly due to gape limitations specific to the morphology of this prey species. Blue crabs less than 25 mm carapace width were most prevalent in field samples yet occurred infrequently in red drum diets. The lack of small blue crabs in red drum diets may be related to a lack of spatial overlap or difficulty in prey detection.

The prey species consumed most frequently by red drum in Galveston Bay support important commercial fisheries not only in this bay, but in many Gulf of Mexico estuaries (Pattillo et al. 1997). Food habits studies completed throughout the Gulf of Mexico have demonstrated the importance of blue crabs and penaeid shrimp to the diet of red drum (Pearson 1929; Gunter 1945; Knapp 1950; Miles 1950; Darnell 1958; Simmons and Breuer 1962; Boothby and Avault 1971; Bass and Avault 1975; Overstreet and Heard 1978). Further, our results indicate that gulf menhaden can potentially dominate red drum diets seasonally. Over the past decade, monitoring data indicates that red drum populations along the Texas Gulf coast have increased substantially (Fuls and McEachron 1997; McEachron et al. 1998). Red drum represent only one of several species of estuarine predatory fishes wherein efforts are being made to recover populations to historical levels of abundance. For example, recovery efforts are proceeding for southern flounder (*Paralichthys lethostigma*) and spotted seatrout (*Cynoscion nebulosus*) in Texas waters, both of which are thought to prey heavily on young fishes and crustaceans (Darnell 1958; Minello and Zimmerman 1984; Hettler 1989; Minello et al. 1989). The effects of increasing predator populations on prey resources is unknown, but increased predator demand may have important implications for harvest of commercially valuable prey. To quantify the potential impact of increased predator abundance levels, future research should involve field and laboratory studies to determine size-based and age-based consumption rates of predatory fishes during their residence in estuarine systems.

We have presented evidence that red drum in Galveston Bay feed on seasonally important prey species and that foraging occurs in shallow water nursery habitats. Observed feeding habits suggest that predation pressure will be highest on juvenile stages of fish and crustaceans. Predation during juvenile life stages of fishes can have significant effects on recruitment variation (Bailey 1994). Therefore, in years of high abundance, red drum may have the potential to affect prey population levels and recruitment to the adult stage for specific prey species. Multispecies approaches to managing fisheries have recently gained attention and attempts are being made to incorporate biological interactions into the modelling of fish stock dynamics (Sissenwine and Daan 1991). Interactions between red drum and their principal prey species will likely have important ramifications if ecosystem level management practices become a reality in Gulf coast estuaries. The feeding habits and abundance of red drum make it an important contributor to the structure of prey assemblages in near shore estuarine habitats.

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Literature Cited

Bailey, K. M. 1994. Predation on juvenile flatfish and recruitment variability. *Netherlands Journal of Sea Research* 32:175–189.

Bass, R. J. and J. W. Avault, Jr. 1975. Food habits, length-weight relationships, condition factor, and growth of juvenile red drum, *Sciaenops ocellata,* in Louisiana. *Transactions of the American Fisheries Society* 104:35–45.

Boothby, R. N. and J. W. Avault, Jr. 1971. Food habits, length-weight relationships, and condition factor of the red drum, *Sciaenops ocellata,* in southern Louisiana. *Transactions of the American Fisheries Society* 100:290–295.

Chesson, J. 1978. Measuring preference in selective predation. *Ecology* 59:211–215.

Colura, R. L. and R. Buckley. 1996. Comparison of Texas red drum age-length keys and von Bertalanffy growth models. Final Report: Federal Aid in Sport Fish Restoration Act, Grant No. F-36-R (Project 19). Texas Parks and Wildlife Department, Coastal Fisheries Division. Austin, Texas.

Comyns, B. H., J. Lyczkowski-Shultz, D. L. Nieland, and C. A. Wilson. 1991. Reproduction of red drum, *Sciaenops ocellatus,* in the northcentral Gulf of Mexico: Seasonality and spawner biomass. National Oceanic and Atmospheric Administration Technical Report, National Marine Fisheries Service 95:17–26.

Cortés, E., C. A. Manire, and R. E. Hueter. 1996. Diet, feeding habits, and diel feeding chronology of the bonnethead shark, *Sphyrna tiburo,* in southwest Florida. *Bulletin of Marine Science* 58:353–367.

Darnell, R. M. 1958. Food habits of fishes and larger invertebrates of Lake Pontchartrain, Louisiana, and estuarine community. *Publications of the Institute of Marine Science* 5:353–416.

Ferry, L. A. and G. M. Cailliet. 1996. Sample size and data analysis: Are we characterizing and comparing diet properly?, p. 71–80. *In* D. MacKinlay and K. Shearer (eds.), Feeding Ecology and Nutrition in Fish: Proceedings of the Symposium on the Feeding Ecology and Nutrition in Fish, International Congress on the Biology of Fishes, San Francisco, California, July 14–18, 1996. American Fisheries Society, San Francisco, California.

FULS, B. AND L. W. MCEACHRON. 1997. Trends in relative abundance and size of selected finfishes and shellfishes along the Texas coast: November 1975–December 1995. Texas Parks and Wildlife Management Data Series No. 137. Texas Parks and Wildlife, Austin, Texas.

GUNTER, G. 1945. Studies on marine fishes of Texas. *Publications of the Institute of Marine Science* 1:1–190.

HANSEL, H. C., S. D. DUKE, P. T. LOFY, AND G. A. GRAY. 1988. Use of diagnostic bones to identify and estimate original lengths of ingested prey fishes. *Transactions of the American Fisheries Society* 117:55–62.

HARTMAN, K. J. AND F. J. MARGRAF. 1993. Evidence of predatory control of yellow perch (*Perca flavescens*) recruitment in Lake Erie, USA. *Journal of Fish Biology* 43:109–119.

HETTLER, W. F. 1989. Food habits of juveniles of spotted seatrout and gray snapper in western Florida Bay. *Bulletin of Marine Science* 44:155–162.

HOLT, S. A., G. J. HOLT, AND C. R. ARNOLD. 1989. Tidal stream transport of larval fishes into non-stratified estuaries. *Rapports et Proces-Verbaux des Réunions Conseil International pour l'Exploration de la Mer* 191:100–104.

KNAPP, F. T. 1950. Menhaden utilization in relation to the conservation of food and game fishes of the Texas Gulf coast. *Transactions of the American Fisheries Society* 79:137–144.

MCEACHRON, L. W., R. L. COLURA, B. W. BUMGUARDNER, AND R. WARD. 1998. Survival of stocked red drum in Texas. *Bulletin of Marine Science* 62:359–368.

MILES, D. W. 1950. The life histories of the spotted seatrout, *Cynoscion nebulosus,* and the redfish, *Sciaenops ocellatus.* Annual Report of the Texas Game, Fish, and Oyster Commission, Rockport Marine Lab, Rockport, Texas.

MINELLO, T. J. AND R. J. ZIMMERMAN. 1984. Selection for brown shrimp, *Penaeus aztecus,* as prey by the spotted seatrout, *Cynoscion nebulosus. Contributions in Marine Science* 27:159–167.

MINELLO, T. J., R. J. ZIMMERMAN, AND E. X. MARTINEZ. 1989. Mortality of young brown shrimp *Penaeus aztecus* in estuarine nurseries. *Transactions of the American Fisheries Society* 118:693–708.

NIELSEN, L. A. 1980. Effect of walleye (*Stizostedion vitreum vitreum*) predation on juvenile mortality and recruitment of yellow perch (*Perca flavescens*) in Oneida Lake, New York. *Canadian Journal of Fisheries and Aquatic Sciences* 37:11–19.

OVERSTREET, R. M. AND R. W. HEARD. 1978. Food of the red drum *Sciaenops ocellatus* from the Mississippi Sound. *Gulf Research Reports* 6:131–135.

PATTILLO, M. E., T. E. CZAPLA, D. M. NELSON, AND M. E. MONACO. 1997. Distribution and abundance of fishes and invertebrates in Gulf of Mexico estuaries, Volume II: Species life history summaries. Estuarine Living Marine Resources Report No. 11. National Oceanic and Atmospheric Administration/National Ocean Service Strategic Environmental Assessments Division, Silver Spring, Maryland.

PEARSON, J. C. 1929. Natural history and conservation of the redfish and other commercial sciaenids on the Texas coast. *Bulletin of the U.S. Bureau of Fisheries* 44:129–214.

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

RICE, J. A., L. B. CROWDER, AND K. A. ROSE. 1993. Interactions between size-structured predator and prey populations: Experimental test and model comparison. *Transactions of the American Fisheries Society* 122:481–491.

ROOKER, J. R. AND S. A. HOLT. 1997. Utilization of subtropical seagrass meadows by newly settled red drum (*Sciaenops ocellatus*): Patterns of distribution and growth. *Marine Ecology Progress Series* 158:139–149.

SCHARF, F. S., F. JUANES, AND M. SUTHERLAND. 1998a. Inferring ecological relationships from the edges of scatter diagrams: Comparison of regression techniques. *Ecology* 79:448–460.

SCHARF, F. S., R. M. YETTER, A. P. SUMMERS, AND F. JUANES. 1998b. Enhancing diet analyses of piscivorous fishes in the Northwest Atlantic through identification and reconstruction of original prey sizes from ingested remains. *Fishery Bulletin* 96:575–588.

SIMMONS, E. G. AND J. P. BREUER. 1962. A study of redfish, *Sciaenops ocellata* Linnaeus and black drum, *Pogonias cromis* Linnaeus. *Publications of the Institute of Marine Science* 8:189–211.

SISSENWINE, M. P. AND N. DAAN. (EDS.). 1991. An overview of multispecies models relevant to management of living resources. International Council for the Exploration of the Sea Marine Science Symposium. 193:6–11.

SOTO, M. A., G. J. HOLT, S. A. HOLT, AND J. ROOKER. 1998. Food habits and dietary overlap of newly settled red drum (*Sciaenops ocellatus*) and Atlantic croaker (*Micropogonias undulatus*) from Texas seagrass meadows. *Gulf Research Reports* 10:41–55.

TRIPPEL, E. A. AND F. W. H. BEAMISH. 1987. Characterizing piscivory from ingested remains. *Transactions of the American Fisheries Society* 116:773–776.

WERNER, E. E. AND J. F. GILLIAM. 1984. The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics* 15:393–426.

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