Seasonal and Size Specific Diet and Prey Demand of Red Snapper on Alabama Artificial Reefs

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Abstract.—Red snapper, *Lutjanus campechanus*, is a heavily exploited reef fish that is harvested in the Gulf of Mexico from both natural and artificial reefs. Since regulations were imposed in 1990, the stock has begun to recover; this recovery has also been attributed in part to an increase in artificial habitats/reefs. However, little is known about the role artificial reefs play in the trophic dynamics of the species. To this end, the seasonal and size-specific diet of red snapper was examined through stomach content analysis of individuals collected from artificial reefs in the north-central Gulf of Mexico off Alabama between May 1999 and April 2000. Diet information was subsequently combined with data from the literature to obtain a first-order estimate of prey demand of the red snapper population on artificial reefs off Alabama. Results indicate both that diet varied with season and red snapper size and that the overall diet was comprised primarily of demersal crustaceans, fish, and pelagic zooplankton. Annual prey demand of the red snapper population on Alabama artificial reefs was estimated to be over 31 million kg. Red snapper derived most of their nutrition from sand/mud- and water column-associated organisms, not from organisms associated with reefs. Based on these results, and the results from other red snapper studies off Alabama, Alabama artificial reefs may be attracting, not producing red snapper.

Introduction

Red snapper *Lutjanus campechanus* (Poey, 1860) supports the most important recreational and commercial offshore finfish fishery in the northern Gulf of Mexico

(Fischer et al. 2004). Knowledge of the role artificial habitats play in the life history of this species is crucial to making informed management decisions about this fishery. Since 1990, regulations imposed by National Marine Fisheries Service, including size and bag limits and total allowable catches, have

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helped the overexploited stock begin to recover (Schirripa and Legault 1997; Patterson 1999); despite these actions, Gulf of Mexico red snapper continue to be overfished and are undergoing overfishing (Goodyear 1995; Schirripa and Legault 1999; SEDAR 2005). The recovery of the stock has also been attributed in part to an increase in artificial habitats in the form of oil and gas platforms and artificial reefs (Bailey et al. 2001). However, some scientists question whether these structures are a positive influence because of doubts about whether they produce or attract fish (see *Fisheries* Vol. 22, April 1997).

The Alabama shelf, one of the centers of red snapper abundance in the northern Gulf of Mexico (Goodyear 1995; Schirripa and Legault 1997; Patterson 1999; Patterson et al. 2001), has over 4000 km^2 of artificial reef permit area (Shipp 1999), where anywhere from 8,000 (Minton and Heath 1998) to 20,000 (Patterson 1999; Bailey et al. 2001) artificial reefs have been deployed to enhance fishing. According to Strelcheck (2001), red snapper are the most abundant finfish on artificial reefs in the Hugh Swingle permit area off Alabama. By examining factors that might be enhanced by artificial reefs, such as food availability, the production versus attraction debate can be addressed (Vose et al. 1997). The type and amount of food necessary to support the most abundant species on the reefs must first be quantified (Meier and Steimle 1997), after which prey supply versus prey demand can be addressed empirically. Estimating the diet composition and prey demand of the red snapper population is a first step toward the resolution of the production versus attraction debate off Alabama.

Little is known about the foraging habits of reef fishes on temperate artificial reefs (Bohnsack and Sutherland 1985; Howe 2001; Appendix 1 for review), especially off Alabama. Of diet studies on red snapper in Alabama waters, two had small sample sizes (Siegel 1983; Bailey 1995), one sampled primarily juveniles (Szedlmayer and Lee 2004), another focused on red snapper from deep, natural reefs (Pinnacles Reef Tract) (Weaver et al. 2001), and the other looked at diel feeding periodicity (Ouzts and Szedlmayer 2003). Although Siegel (1983) collected seasonal data, he found no significant seasonal trends, possibly due to small sample size.

Some researchers suggest that reef associated fishes such as red snapper might not be feeding at the reef, but rather on mud/sand-associated organisms that surround the reef (Bohnsack 1989; Bohnsack et al. 1991; Sedberry and Cuellar 1993; Nelson and Bortone 1996; Bohnsack et al. 1997b). This behavior may create an important energetic link between artificial reefs and the surrounding habitat (Parrish 1989) implying that the fish biomass on artificial reefs is dependent upon trophic subsidies from the surrounding environment. The importance of the reef itself, versus the water column or adjacent sediments as feeding grounds, is still poorly understood (Sedberry and Cuellar 1993) and may vary by location and by species. If reef fishes are not feeding on reef-associated organisms, then they may only be attracted to artificial reefs as a result of a behavioral preference (Bohnsack 1989). If true, this may reveal important management implications concerning the relationship between artificial reefs and reef fishes, as well as for the use of artificial reefs to enhance fishing.

Additional information about red snapper diet on Alabama artificial reefs can provide insight into the role that artificial reefs play in red snapper feeding ecology. Off Alabama a quantitative estimate of the prey demand of the red snapper population living on artificial reefs is lacking. Moreover, the role of artificial reefs in the life history of the species is inconclusive. To this end, we examined the affects of artificial reefs on adult red snapper trophic dynamics, focusing on seasonal and size-specific changes in their diet over a year-long period. Diet data then were used, along with

data on abundance and size-distributions from Strelcheck et al. (2005) and Szedlmayer and Furman (2000), and an empirically-derived estimate of time-specific consumption rate (Palomares and Pauly 1989) to obtain first-order estimates of the annual and seasonal prey demand of the red snapper population on Alabama artificial reefs.

Methods

Monthly sampling.—Red snapper were collected with hook and line from artificial reefs in the northern Gulf of Mexico (Gulf) off the coast of Alabama between May 1999 and April 2000. Most fish were caught by recreational fishermen in the Hugh Swingle General Permit Area (see map of study area in Strelcheck et al. 2007, this volume). However, some larger red snapper were opportunistically collected from local spearfishing and angling fishing tournaments. Knowing that red snapper are prone to regurgitation (Adams and Kendall 1891; Camber 1955; Moseley 1966; Bradley and Bryan 1975; Parrish 1987), we collected 39–86 fish per month to ensure that we obtained a significant number of fish with prey in their stomachs.

At capture, all red snapper were weighed to the nearest 0.01 kg, their total length (TL) and fork length (FL) measured to the nearest mm, and their sex determined before the stomach was removed. Stomachs were severed at the esophagus and duodenum below the pyloric sphincter, slit to allow complete preservation, and then preserved in 10% formalin for at least 48 h. They then were transferred to 70% isopropyl alcohol until they could be sorted. Stomachs were dissected, prey items removed and identified to the lowest possible taxonomic level, and each taxon weighed to the nearest 0.01 g after being blotted dry. Empty stomachs were either labeled as 'genuinely empty' or 'distended' according to the description of Treasurer (1988).

Enumeration of Stomach Contents.—The relative contribution of each of several prey categories was determined by using four methods: (1) percent composition by weight (%W); (2) percent composition by number (%N); (3) percent frequency of occurrence (%FO); and, (4) percent index of relative importance (%IRI). Percent frequency of occurrence was calculated as in Bowen (1996): %FO = number of stomachs containing one particular prey category/number of stomachs with any prey (excluding bait). The index of relative importance was calculated as (Pinkas et al. 1971; modified by Hacunda 1981): IRI = (%N +%W) × %FO. Percent IRI was calculated by dividing the IRI value for each prey category by the sum of the IRI values and multiplying by 100. These descriptive indices were used to describe the overall diet, as well as to evaluate the diet by size-class of red snapper (size classes = 200–299 mm FL, 300–399, 400–499, 500–599, and >600) and on a seasonal basis (summer = June, July, and August; fall = September, October, November; winter = December, January, February; and spring = March, April, and May). However, %W was the primary index used to describe the diet, as Bowen (1996) suggested it to be the best descriptive index if the ultimate goal is to measure the contribution of the prey to the predator's nutrition (Bowen 1996).

The identifiable contents of all red snapper stomachs combined were divided into seven major prey categories (Table 1): fish; adult mantis shrimp, *Squilla empusa*; crabs; penaeid shrimp; squid, *Loligo* sp.; pelagic zooplankton; and miscellaneous benthic-associated species (hereafter, miscellaneous benthic species). Larval fish were not included in the pelagic zooplankton category; they were grouped with fish because it was often difficult to determine if they had flexed. In addition, not all demersal species were grouped in the miscellaneous benthic species category. This category contained only those taxa that did not fall within one of the other major categories. The diet also consisted of an unidentified material category, which was defined as that having no recog-

Table 1. Prey contained in all red snapper *Lutjanus campechanus* stomachs and the 300-499 mm FL subset of stomachs collected on Alabama artificial reefs based upon four descriptive indices for seven prey categories ranked in decreasing order of importance for each index. %W = percent weight, %N = percent number, %FO = percent frequency of occurrence, %IRI = percent index of relative importance, and Misc. benthic sp. = Miscellaneous benthic species.

Category	Prey Type	%W[a] (rank)	%W[b] (rank)	%N (rank)	%FO (rank)	%IRI (rank)
All stomachs	Unidentified material	35.91 (1)				
	Fish	19.48 (3)	28.70 (1)	25.88 (2)	38.81 (2)	31.14 (2)
	Adult *Squilla empusa*	12.59 (4)	16.08 (4)	14.02 (4)	21.27 (4)	9.41 (4)
	Crab	20.25 (2)	26.79 (2)	24.35 (3)	35.82 (3)	26.93 (3)
	Shrimp	1.70 (6)	2.19 (6)	2.04 (6)	3.73 (5.5)	0.23 (6)
	Loligo sp.	0.43 (8)	0.54 (7)	0.31 (7)	1.49 (7)	0.02 (7)
	Pelagic zooplankton	7.97 (5)	23.51 (3)	31.02 (1)	39.93 (1)	32.01 (1)
	Misc. benthic sp.	1.67 (7)	2.20 (5)	2.38 (5)	3.73 (5.5)	0.25 (5)
300-499	Unidentified material	37.82 (1)				
	Fish	18.37 (2)	27.33 (2)	24.78 (2)	36.63 (2)	28.54 (2)
	Adult *S. empusa*	13.78 (4)	17.69 (4)	15.95 (4)	21.51 (4)	10.82 (4)
	Crab	15.43 (3)	20.80 (3)	18.37 (3)	27.33 (3)	16.01 (3)
	Shrimp	2.49 (6)	3.20 (5)	2.88 (5)	4.65 (5)	0.42 (5)
	Loligo sp.	0.43 (8)	0.52 (7)	0.32 (7)	1.16 (7)	0.01 (7)
	Pelagic zooplankton	10.16 (5)	28.42 (1)	35.60 (1)	45.93 (1)	43.97 (1)
	Misc. benthic sp.	1.52 (7)	2.06 (6)	2.10 (6)	3.49 (6)	0.22 (6)

[a] Represents the % weight including the unidentified material category
[b] Represents the % weight excluding the unidentified material category

nizable bones or hard parts, thus preventing classification into any of the categories listed above. Unidentified material was not included in all of the analyses because %N, %FO, and IRI cannot be determined for this category.

Diet studies can introduce bias depending on how prey items identified with different taxonomic resolution are grouped together (Hansson 1998). To eliminate bias and to provide more detailed diet information, four of the seven major prey categories (fish, pelagic zooplankton, crabs, and miscellaneous benthic species) were further subdivided and combined with the other three prey types that consisted of a single species or genus, e.g., adult *S. empusa*, penaeid shrimp, and *Loligo* sp., for a total of 47 groups (see Table 2 for a complete listing). This more detailed breakdown of prey was also examined by season and size-class using the same descriptive indices listed above.

To further analyze the diet data, the PRIM-ER statistical package (Clarke and Warwick 1994) was used. Because this study possessed groups defined *a priori*, such as month, season, and size-class, the nonparametric permutation procedure ANOSIM (Analysis of Similarities, PRIMER) (Clarke and Warwick 1994) was used to test for significant differences among seasons and size classes. Prey categories that most contributed to the observed differences among season and size-class were elucidated with BVSTEP. SIMPER (Similarity Percentages, PRIMER), a multivariate multiple permutations test, was used to examine the contribution that a prey type made to the average within-group (season or size-class) similarity and between-group dissimilarity (Clarke 1993).

Caloric Density.—The caloric density (calories/g) of the major diet items either was estimated directly with bomb calorimetry (McCawley 2003) or was borrowed from

the literature. An index of caloric importance (ICI) was calculated for each prey type for the overall diet as well as by season and by size-class with the formula: ICI = (%W × C) × %FO, where C = calories/g wet weight. Percent ICI (% ICI) was calculated with the formula: %ICI = (ICI for each prey category/ sum of the ICI values) × 100. A prey importance index (PI) also was calculated for each prey category for the overall diet as well as by season and by size-class according to the equation from Pope et al. (2001):

$$PI_i = \frac{1}{P} \sum_{j=1}^{P} \left(\frac{W_{ij}X_i}{\sum_{i=1}^{Q} W_{ij}X_i} \right)$$

where i = prey type;

  j = fish with prey (here red snapper stomachs);

  P = number of fish with food in their stomachs;

  W_i = weight (g) of food category i;

  X_i = caloric value (cal/g wet weight) of food category i; and,

  Q = number of food categories.

Percent PI (% PI) was calculated by multiplying each PI value by 100. The %ICI and %PI indices were compared to %W and %IRI to determine which index best described the diet.

Prey Habitat Preference.—A habitat preference was specified from the literature for each of the 47 red snapper prey categories. Five major habitat types were identified: sargassum-associated (*SA*); sand/mud-associated (*SM*); reef- or structure-associated (*R*); water column associated (*WC*); and, those prey found on a variety of habitats (*V*). A *SA* organism was defined as that which lives among floating sargassum. Sand/mud-associated organisms were defined as those

organisms that live on the sand or mud bottom, as well as those that spend most of their time burrowed in the mud (such as a shrimp eel, Ophichthidae or mantis shrimp). A *R* organism (e.g., sea horses family Syngnathidae) was liberally defined as an organism that would not otherwise be found in a particular habitat unless a reef (artificial or natural) or some type of structure was present. Water column organisms were either mostly planktonic organisms or those swimming in the water column, such as *Loligo* sp. An organism that was not characteristic of any one habitat type was classified as being found on a variety of habitats. These habitat types were paired with each prey's %W contribution to the diet and then summed by habitat type to determine the cumulative contribution made to the diet by prey from each habitat. The cumulative habitat contribution was examined for the overall diet as well as by season and by size-class. The average caloric density for prey from each habitat type also was determined.

Annual Prey Demand.—To obtain an estimate of population consumption for red snapper on Alabama artificial reefs, an estimate of Q/B = 1.44% per day for *Lutjanus campechanus* was taken from Palomares and Pauly (1989). Q represents the amount of food consumed, B represents biomass, and thus Q/B is a time-specific ratio of the food consumed to the weight of the consumer. To estimate an annual weight-specific prey demand for red snapper, Q/B was multiplied by the number of days in a year (365) and then multiplied by the mean (±SE) biomass of red snapper on 14 experimental artificial reefs in the Hugh Swingle Permit Area determined by Strelcheck et al. (2005) from catch-per-unit-effort (CPUE) data. An annual prey demand estimate also was obtained in a similar manner with biomass data collected via visual census in Strelcheck et al. (2005). However, in this prey demand estimate, the mean (±SE)

Table 2. Most detailed taxonomic breakdown of stomach contents (47 prey categories) for all red snapper *Lutjanus campechanus* collected on Alabama artificial reefs based upon four descriptive indices. Prey categories are ranked for each index in decreasing order of importance. %W = percent weight, %N = percent number, %FO = percent frequency of occurrence, and %IRI = percent index of relative importance and Misc. benthic species = Miscellaneous benthic species.

Prey Type	%W[a] (rank)	%W[b] (rank)	%N (rank)	%FO (rank)	%IRI (rank)
Unidentified material	35.91 (1)				
Fish					
Unidentified fish	9.97 (3)	13.40 (2)	11.03 (3)	17.16 (4)	15.35 (3)
Family Ophichthidae	3.21 (7)	4.09 (8)	3.94 (8)	6.34 (8)	1.86 (8)
Family Triglidae	1.75 (9)	2.35 (10)	2.06 (10)	2.61 (12)	0.42 (11)
Family Haemulidae	0.35	0.46	0.56	0.75	0.03
Family Syngnathidae	0.07	0.12	0.15	0.75	0.01
Ophidion sp.	0.50	0.62	0.47	0.75	0.03
Decapterus sp.	0.25	0.30	0.30	0.37	0.01
Lagodon rhomboides	0.27	0.37	0.37	0.37	0.01
Anchoa hepsetus	0.19	0.23	0.07	0.37	<0.01
Fish larvae	2.93 (8)	6.75 (6)	6.92 (7)	11.94 (6)	5.97 (7)
Crabs					
Unidentified crabs	8.09 (4)	11.08 (4)	9.84 (5)	17.54 (3)	13.43 (4)
Family Portunidae	0.49	0.64	0.91	2.24	0.13
Portunus gibbesii	5.77 (5)	7.41 (5)	7.78 (6)	11.19 (7)	6.22 (6)
P. sayi	1.08	1.34	1.41	2.99 (11)	0.30 (12)
P. spinimantus	0.45	0.55	0.53	1.12	0.04
P. spinicarpus	0.13	0.16	0.29	0.37	0.01
P. ordiwayi	0.11	0.14	0.09	0.37	<0.01
P. sebae	<0.01	<0.01	0.05	0.37	<0.01
Callinectes sp.	0.25	0.31	0.19	0.37	0.01
C. sapidus	0.89	1.11	0.70	1.87	0.12
C. exasperatus	0.21	0.26	0.19	0.37	0.01
C. danae	0.01	0.01	0.05	0.37	<0.01
Ovalipes floridanus	1.20	1.65 (12)	0.77	2.61	0.23
Calappa flammea	0.60	0.75	0.50	0.75	0.03
C. agusta	0.28	0.35	0.19	0.37	0.01
Hepatus epheliticus	0.17	0.31	0.37	0.75	0.02
Parthenope granulata	0.52	0.73	0.50	0.75	0.03
Pelagic zooplankton					
Larval *Squilla empusa*	4.52 (6)	11.78 (3)	13.94 (2)	21.64 (1)	20.37 (2)
Unidentified mollusk larvae	0.84	1.44	1.20	1.87	0.18
Crab megalopa and zoea	0.31	0.50	0.77	1.87	0.09
Order Amphipoda	0.91	5.76 (7)	10.25 (4)	16.79 (5)	9.84 (5)
Order Euphausicaea	<0.01	0.75	0.75	0.75	0.04
Order Isopoda	0.01	0.38	0.50	0.75	0.02
Order Mysidacea	<0.01	0.03	0.20	0.75	0.01
Order Calanoida	<0.01	0.01	0.01	0.37	<0.01
Family Sergestidae	0.03	0.13	0.30	1.49	0.02
Family Palaemonidae	<0.01	0.05	0.06	0.37	<0.01
Cavolinia sp.	1.35	2.62 (9)	2.98 (9)	4.10 (9)	0.84 (9)
Sagita sp.	<0.01	0.06	0.06	0.75	<0.01

Table 2. (Continued)

Prey Type	%W[a] (rank)	%W[b] (rank)	%N (rank)	%FO (rank)	%IRI (rank)
Adult *Squilla empusa*	12.59 (2)	16.08 (1)	14.02 (1)	21.27 (2)	23.43 (1)
Penaeid shrimp	1.70 (10)	2.19 (11)	2.04 (11)	3.73 (10)	0.58 (10)
Squid	0.43	0.54	0.31	1.49	0.05
Miscellaneous Benthic species					
Phylum Arthropoda	<0.01	0.08	0.09	0.37	<0.01
Pagurus sp.	0.30	0.37	0.37	0.37	0.01
Sicyonia sp.	0.10	0.13	0.28	0.75	0.01
Glycera sp.	<0.01	0.05	0.01	0.37	<0.01
Albunea paretii	1.27	1.57	1.62 (12)	1.87	0.22

[a] Represents the % weight including the unidentified material category
[b] Represents the % weight excluding the unidentified material category

biomass of all reef fish was multiplied by the mean percent abundance of red snapper on all reefs (to determine the % biomass of red snapper) before being multiplied by the Q/B ratio. For visual census data from Strelcheck et al. (2005), mean biomass was calculated only from reefs where visibility was greater than or equal to 4 m. The resulting weight (kg) of food needed to support the snapper population on one artificial reef then was used to determine the amount of food needed to support a population of red snapper on 14; 8,000; and 20,000 artificial reefs. The latter two numbers were taken from Minton and Heath (1998) and Patterson (1999) and were used to bound the estimate of prey demand for the entire snapper population on artificial reefs off Alabama. This extrapolation was done assuming that red snapper biomass on all artificial reefs is similar to that found at the experimental reefs in Strelcheck et al. (2005). Estimates of consumption based upon CPUE and visual census data were further partitioned by percent weight (%W) among the seven major prey categories found in the diet.

To provide additional insight, annual prey demand also was estimated with visual census data from Szedlmayer and Furman (2000), who observed a mean size of red snapper of 279 ± 59 mm standard length (SL) and a mean abundance (±SD) of 86.3 ± 69.4 on 28 artificial reefs off Alabama. A distribution of SL of red snapper ($N = 5000$) was simulated with the Monte-Carlo method (Sokal and Rohlf 1981). A normal probability function was constructed based on mean length and standard deviation specified by Szedlmayer and Furman (2000). To estimate SL for an individual fish, a probability value ranging from 0.0001 to 0.9999 was randomly drawn (with replacement) and the corresponding SL was assigned to the fish; SL then was converted to fork length (FL) with the regression equation $FL = 1.669 \times SL + 5.911$ taken from measurements ($n = 50$) from red snapper collected off Alabama. The assigned FLs then were used to obtain an estimated weight for each red snapper with a length-weight regression: Log weight (kg) = $3.014(log$ FL$)$ $- 4.7799$ obtained from all snapper collected in this study. A mean weight (±SD) then was determined from the estimated weights. Biomass of red snapper at a reef was calculated by multiplying the mean abundance of red snapper observed in Szedlmayer and Furman (2000) by the mean weight (±SD) of red snapper estimated here from their data. Annual

prey demand of red snapper was determined from these data by multiplying annual Q/B estimates by the estimated biomass of red snapper on the reefs they observed. Assuming that red snapper biomass on all artificial reefs was similar to the reefs they studied, the prey demand of a red snapper population on one reef was used to determine the amount of food needed to support a red snapper population on 14; 8,000; and 20,000 artificial reefs and then partitioned into the seven major prey categories as described above. These annual prey demand estimates based on data from Szedlmayer and Furman (2000) were compared to annual estimates based on CPUE and visual census data from Strelcheck et al. (2005).

Results

Enumeration of Overall Diet

Stomach contents of 656 red snapper ranging from 207 to 913 mm FL were examined. Of these, 268 (40.9%) stomachs contained identifiable prey, 262 (39.9%) were empty, 63 (9.6%) contained only bait, and 63 (9.6%) contained only unidentified material. Of the 262 stomachs classified as empty, 169 (64.5%) were considered 'truly' empty and 93 (35.5%) were considered distended or empty due to regurgitation. The empty and bait only stomachs were excluded from further analyses. All red snapper containing prey were staged as adults (Jackson et al. 2007, this volume) and ranged in length from 240 to 913 mm FL with a mean of 463 mm, a median of 426 mm, and a mode of 410 mm FL.

Seven prey categories.—The unidentified material category contributed the largest proportion to red snapper diet by %W (35.9%), followed by crab (20.2%), fish (19.5%), adult *S. empusa* (12.6%) and pelagic zooplankton (8.0%) (Table 1). After exclusion of the unidentified material category (listed by descending %W), fish, pelagic zooplankton, crab, and adult *S. empusa* were the principal components of red snapper diet when all stomachs were combined (Table 1). However, no single group was largest by all indices. Pelagic zooplankton was the largest category by %N, %FO, and %IRI, whereas fish was the largest category by %W.

Forty-seven prey categories.—When the stomach contents for all the nonempty red snapper collected were divided into their highest taxonomic resolution (47 prey categories) unidentified material was again the largest category (Table 2). After excluding unidentified material, the ten most abundant taxa in the diet (contributing over 81%, listed by descending %W) were adult mantis shrimp *S. empusa*, unidentified fish, larval *S. empusa*, unidentified crabs, iridescent swimming crab *Portunus gibbesii*, larval fish, amphipods, family Ophichthidae, *Cavolinia* sp., and family Triglidae. Adult *S. empusa* was the largest category in all indices except %FO, wherein larval *S. empusa* was the largest contributor. In general, smaller prey (e.g., amphipods and larval *S. empusa*) were more important by %N than by %W. The ranking of prey by %FO and %IRI found amphipods, penaeid shrimp, and larval *S. empusa* to be more important than in %W. The largest categories by %W revealed that demersal crustaceans were important contributors to the diet in the form of adult *S. empusa*, unidentified crabs, and *P. gibbesii*. Demersal fishes (family Ophichthidae and family Triglidae), as well as unidentified fishes and larval fish, were also important contributors to the overall diet.

Enumeration of Seasonal Diet

All nonempty red snapper collected were divided into 5 size classes; however, not every size-class of red snapper was collected in every month. Before testing for seasonal

differences in red snapper diet, we chose to include only those size classes that were collected in all seasons. As such, red snapper in the 300–399 and 400–499 mm FL size classes ($N = 452$) were collected in every season. Fish within this size range are indicative of the predominant size classes of red snapper inhabiting several experimental reefs in the Hugh Swingle reef permit area (Strelcheck 2001) and represent the dominant sizes of recreationally harvested red snapper off Alabama and Louisiana (375–425 mm FL) (Fischer et al. 2004). Thus, these two size classes of red snapper were combined (300–499 mm) for the statistical evaluation of red snapper diet by season.

The descriptive indices for the 300–499 mm size-group were similar to results pooled over all sizes (Table 1). For this subset, the diet as a whole was composed primarily of pelagic zooplankton by all four indices. The next most important diet items were fish, then crabs, followed closely by adult *S. empusa*. Compared to all stomachs combined, pelagic zooplankton and adult *S. empusa* made up a larger portion of this subset diet, while fish and crab made up smaller portions. The contributions made by penaeid shrimp, *Loligo sp.,* and miscellaneous benthic species were largely unchanged.

Seven prey categories.—Gut content examination by %W by season for the 300–499 mm subset indicated that unidentified material was the largest contributor to the diet in every season (Table 3). After excluding the unidentified material from further analysis, examination of seasonal diet by %W (Table 3) revealed fish were present in red snapper diets in all seasons (comprising between 24.5 and 31.8% W), but they did not contribute the greatest amount by %W in any season. The diet in summer and winter was composed predominately of adult *S. empusa* (33.0% W and 34.4% W respectively), in fall of crabs (35.1% W), and spring of pelagic zooplank-

ton (46.5% W).

Demersal crustaceans (crabs and adult *S. empusa*) were present in all seasons, comprising between 41.9% and 54.4% by %W of the diet in summer, fall, and winter. During the spring, red snapper fed on high numbers of pelagic zooplankton. However, the amount of pelagic zooplankton consumed appeared to be inversely related to the amount of demersal crustaceans eaten by red snapper, a pattern that was especially evidenced by the shift in spring from consuming primarily demersal crustaceans to feeding on pelagic zooplankton. When the seasonal diet was examined by %N, %FO, and %IRI (Table 3), the same trends were present; however pelagic zooplankton comprised a larger portion of the diet in all seasons.

Percent weight data by season for the 300–499 mm red snapper for seven prey categories were included in the test for significance. ANOSIM found a highly significant difference among the %W data by season ($p = 0.001$) despite a low (0.089) R-value. Even though ANOSIM found an overall significant difference among seasons, low R-values (with significant P-values) from the ANOSIM pairwise comparisons between seasons indicate significance, but high overlap, revealing that red snapper were feeding on nearly the same kinds of organisms year-round.

BVSTEP results revealed that differences among season were attributable to four influential prey types: fish, crab, adult *S. empusa*, and pelagic zooplankton. There was a 99.5% correlation between these prey types and the overall pattern seen in the samples. The SIMPER results revealed that red snapper collected in winter had the largest number of prey types contributing to within-season similarity, with all four influential prey types contributing. Spring fish had the fewest prey types with only two prey types contributing. Demersal crustaceans were the largest contributors (45.0–48.0%) to every season's within-season similarity except

Table 3. Taxonomic breakdown of stomach contents from 300-499 mm FL red snapper *Lutjanus campechanus* collected on Alabama artificial reefs by season based upon four descriptive indices for seven prey categories ranked in decreasing order of importance for each index. %W = percent weight, %N = percent number, %FO = percent frequency of occurrence, and %IRI = percent index of relative importance, and Misc. benthic sp. = Miscellaneous benthic species.

Season	Prey Type	%W[a] (rank)	%W[b] (rank)	%N (rank)	%FO (rank)	%IRI (rank)
Summer	Unidentified material	37.84 (1)				
	Fish	15.47 (3)	24.48 (2)	21.39 (3)	38.10 (3)	24.20 (3)
	Adult *Squilla empusa*	21.85 (2)	32.96 (1)	26.55 (2)	40.48 (2)	33.36 (1)
	Crab	9.98 (4)	14.46 (4)	15.67 (4)	23.81 (4)	9.94 (4)
	Shrimp	3.59 (6)	5.64 (5)	4.64 (5)	9.52 (5)	1.36 (5)
	Loligo sp.	0.00 (8)	0.00 (7)	0.00 (7)	0.00 (7)	0.00 (7)
	Pelagic zooplankton	9.60 (5)	20.09 (3)	29.37 (1)	45.24 (1)	30.99 (2)
	Misc. benthic sp.	1.67 (7)	2.38 (6)	2.38 (6)	2.38 (6)	0.16 (6)
Fall	Unidentified material	32.05 (1)				
	Fish	16.11 (3)	24.84 (3)	23.37 (3)	29.55 (3)	23.37 (3)
	Adult *S. empusa*	5.66 (5)	6.82 (4)	7.95 (4)	9.09 (4.5)	2.20 (4)
	Crab	27.18 (2)	35.09 (1)	31.06 (1)	36.36 (1.5)	39.46 (1)
	Shrimp	1.89 (7)	2.27 (6)	2.27 (6)	2.27 (6)	0.17 (6)
	Loligo sp.	0.00 (8)	0.00 (7)	0.00 (7)	0.00 (7)	0.00 (7)
	Pelagic zooplankton	12.94 (4)	25.68 (2)	29.97 (2)	36.36 (1.5)	33.20 (2)
	Misc. benthic sp.	4.17 (6)	5.30 (5)	5.37 (5)	9.09 (4.5)	1.59 (5)
Winter	Unidentified material	27.41 (1)				
	Fish	18.80 (3)	27.55 (2)	26.80 (2)	35.14 (2)	29.74 (2)
	Adult *S. empusa*	29.62 (2)	34.43 (1)	34.23 (1)	40.54 (1)	43.35 (1)
	Crab	16.69 (4)	19.99 (3)	19.37 (3)	27.03 (3)	16.57 (3)
	Shrimp	0.31 (6)	0.36 (6)	1.35 (5)	2.70 (5.5)	0.07 (5)
	Loligo sp.	0.00 (8)	0.00 (7)	0.00 (7)	0.00 (7)	0.00 (7)
	Pelagic zooplankton	7.15 (5)	17.11 (4)	17.57 (4)	18.92 (4)	10.22 (4)
	Misc. benthic sp.	0.02 (7)	0.56 (5)	0.68 (6)	2.70 (5.5)	0.05 (6)
Spring	Unidentified material	51.26 (1)				
	Fish	23.28 (2)	31.84 (2)	27.43 (2)	42.86 (2)	22.87 (2)
	Adult *S. empusa*	0.67 (7)	1.71 (6)	0.26 (6)	2.04 (6)	0.04 (6)
	Crab	9.19 (4)	14.02 (3)	8.52 (3)	22.45 (3)	4.55 (3)
	Shrimp	3.57 (5)	4.08 (4)	3.06 (4)	4.08 (4.5)	0.26 (4)
	Loligo sp.	1.58 (6)	1.81 (5)	1.12 (5)	4.08 (4.5)	0.11 (5)
	Pelagic zooplankton	10.45 (3)	46.54 (1)	56.92 (1)	75.51 (1)	72.17 (1)
	Misc. benthic sp.	0.00 (8)	0.00 (7)	0.00 (7)	0.00 (7)	0.00 (7)

[a] Represents the % weight including the unidentified material category
[b] Represents the % weight excluding the unidentified material category

spring when pelagic zooplankton was the largest contributor. Fish also was characteristic of every season and was the second largest contributor (27.6–30.2% contribution) in all seasons except fall. However, low values of average similarly (<34.1) for each season indicate that within-season diet composition was variable and not dominated by the influence of a single prey type.

Forty-seven prey categories.—Unidentified material was the largest component of the diet in all seasons contributing between 27.4 and 51.3% W to the forty-seven prey category breakdown. After exclusion of this category, adult *S. empusa* were the largest contributors to the diet in summer and winter by %W. *P. gibbesii* was the largest contributor in the fall and amphipods were the largest contributor in the spring. On the whole,

the largest contributors by %W were larger organisms, such as unidentified fish, unidentified crabs, and fishes from the families Triglidae and Ophichthidae. In contrast, smaller organisms, were more important by %N, %FO, and %IRI, especially in spring and fall. Overall, red snapper diets in summer and winter were comprised mainly of demersal crustaceans and spring and fall had more pelagic zooplankton and larval fish.

When evaluating the 300–499 mm red snapper diet by 47 prey categories, using the %W data, ANOSIM again found that red snapper diet varied significantly by season ($p = 0.001$) despite high diet overlap ($R = 0.106$). BVSTEP results revealed that these differences were attributable to a combination of six prey categories having a 95.1% correlation with the overall pattern of the samples. The six prey categories consisted of unidentified fish, larval fish, unidentified crab, adult *S. empusa*, larval *S. empusa*, and amphipods. SIMPER results revealed that the prey categories that contributed to within-season similarity were generally some of the five largest categories by %W. Overall, average within-season similarity values decreased when compared to the SIMPER analysis using seven prey categories. Moreover, SIMPER again showed demersal crustaceans contributed to every season's within-season similarity, making the smallest contribution in spring and the largest contribution in summer. Likewise pelagic zooplankton, made a contribution to within-season similarity, and the largest contribution in spring.

Enumeration of Size-Specific Diet

Seven prey categories.—All nonempty stomachs were pooled for examination of size-class differences in red snapper diet. Red snapper were divided into five size classes: 200–299 mm, 300–399 mm, 400–499 mm, 500–599 mm, and over 600 mm. However, because all size classes were not collected

during all seasons, our data do not permit either a direct statistical comparison of diet by size-class or a size by season interaction, thus only descriptive results are given.

By %W, unidentified material was the largest diet component of every size-class except for red snapper over 600 mm, where crab was the largest category. However, after excluding unidentified material, fish were present in the diets of all size classes and were the largest contributor by %W to the diets of 200–299 mm and 500–599 mm red snapper (Figure 1). The diet of 300–399 mm fish was almost equally proportioned among the seven prey categories, however crab was the largest contributor. Crab also dominated the diet of >600 mm red snapper. The diet of the 400–499 mm red snapper was dominated by pelagic zooplankton. There was an apparent shift in diet by size-class. As red snapper got larger they ate more demersal crustaceans and less pelagic zooplankton. Demersal crustaceans made up 18.2% W of the diet in the 200–299 mm fish and contributed over 68.9% W to the diet of the >600 mm fish, whereas pelagic zooplankton made up 27.3%W in the 200–299 mm fish and only 6.5% W in the red snapper over 600 mm.

The trends in diet by size-class remain approximately the same for the other diet indices. However, smaller organisms made a larger contribution in the other indices; pelagic zooplankton became the largest category of the 300–399 mm snapper by %N, %FO, and %IRI. Similarly in the 500–599 mm red snapper, fish was the largest group by %W and %IRI, but pelagic zooplankton was the largest group by %N and %FO.

Because of data inadequacies a test for significance was not run; however, BVSTEP found that differences did exist among the diets of different red snapper size classes and these differences resulted from six influential prey types: fish, adult *S. empusa*, crab, penaeid shrimp, pelagic zooplankton, and miscellaneous benthic species. There
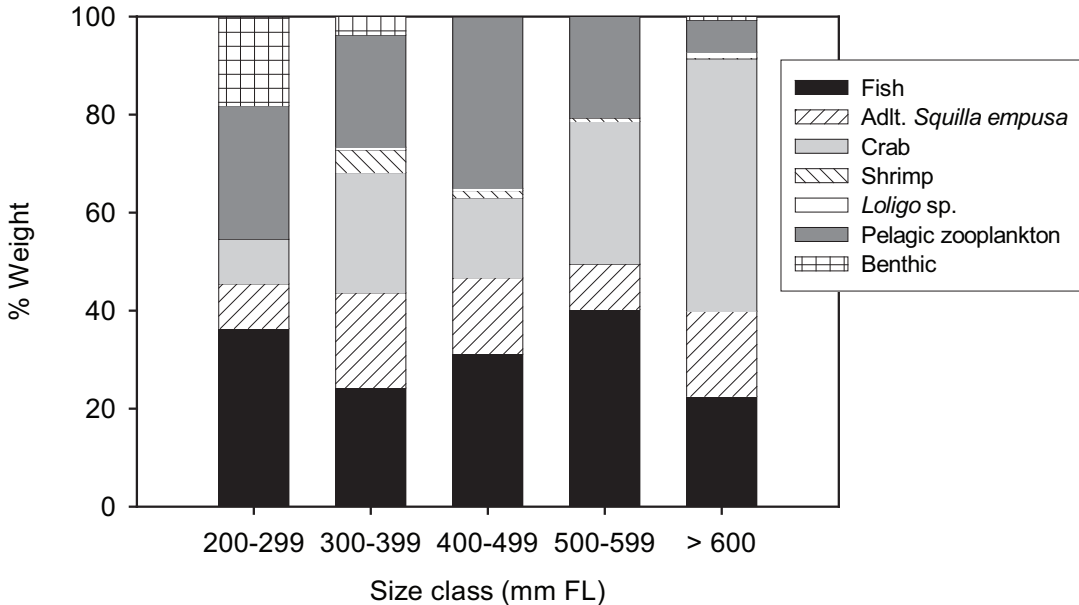
Figure 1. Prey contained in all red snapper *Lutjanus campechanus* stomachs collected on Alabama artificial reefs broken down by size class by % weight for seven prey categories. Benthic = Miscellaneous benthic species.

was an 82.2% correlation between these prey types and the overall pattern found in the samples. The SIMPER results revealed that the 300–399 mm size-class had the largest number of contributing prey types (fish, crab, pelagic zooplankton, and adult *S. empusa*) to within-size-class similarity. The 200–299 mm size-class had the smallest number of contributing species, with fish and pelagic zooplankton accounting for over 90% of the within-size-class similarity. Fish was the largest contributor to within-size-class similarity in the 200–299, 300–399, and 500–599 mm red snapper diets. Pelagic zooplankton was the largest contributor to within-size-class similarity of 400–499 mm red snapper and crab the largest contributor to within-size-class similarity of fish over 600 mm. Red snapper over 600 mm had the highest average similarity (37.3), meaning that stomach contents of red snapper in this

size-class were more similar to each other than they were in any other size-class. The aforementioned trend of larger red snapper eating more demersal crustaceans, and less pelagic zooplankton was again evident as the 200–299 mm red snapper did consume pelagic zooplankton, but did not have a demersal crustacean as a contributor to within-season similarity. Snapper over 600 mm had demersal crustaceans present in their diet, but no pelagic zooplankton.

Forty-seven prey categories.—Size-class differences also were examined when the diet was divided into the 47 different prey categories mentioned previously. Unidentified material was the largest contributing category to every size-class by %W ranging from 16.6% W in the 200–299 mm fish to 47.8% W in the fish over 600 mm. After excluding the unidentified material cat-

egory, the largest contributing prey category varied by size-class. The largest category for the 200–299 mm size-class was larval fish. For the 300–399 mm fish and fish over 600 mm, adult *S. empusa* was the largest prey category. Larval *S. empusa* was the largest category for the 400–499 mm red snapper, and unidentified crab was the largest category for the 500–599 mm red snapper.

Overall, larger organisms, such as *P. gibbesii*, ophichthid fishes, adult *S. empusa*, unidentified fish, and unidentified crabs, made a greater contribution by %W. By %N, %FO, and %IRI, some smaller organisms, such as larval fish, larval *S. empusa*, and amphipods, made a greater contribution to the diet. In general, as snapper got larger they ate more demersal crustaceans and less pelagic zooplankton; this trend was identified by all of the indices.

Descriptive calculations with BVSTEP indicated that differences among size classes were the result of seven influential prey types: unidentified fish, larval fish, unidentified crab, *P. gibbesii*, adult *S. empusa*, larval *S. empusa*, and amphipods. There was a 97.0% correlation among these prey types and the patterns detected in the samples.

Caloric Density

Caloric density (calories/g) was determined for each of the 47 major red snapper prey categories, either directly by bomb calorimetry or taken from literature values. These values were used with %W and %FO to determine the %ICI for each of the 47 prey types (Appendix 2). The results indicated that adult *S. empusa* was the most important prey category with a %ICI of 35.9%, followed by larval *S. empusa*, *P. gibbesii*, and larval fish. ICI could not be determined for unidentified fish and crabs because a caloric value cannot be assigned to these categories. Caloric density values were also used to determine the %PI

for each of the seven and 47 prey categories. A comparison was made among %W, %IRI, %ICI and %PI for the seven major prey categories (Figure 2). The %PI values were very similar to the %W values; however, the %ICI values were higher for some of the prey types with higher caloric densities, such as fish and crab. Thus, we believe %ICI to be more informative than %IRI or %PI because it better takes into account the effects of caloric density when describing diet contribution. When the diet was examined by season, %PI gave similar results to %W, but %ICI revealed a slightly different picture (Table 4). For example, in the fall %IRI ranked pelagic zooplankton as second in importance and %ICI ranked fish second, the difference due to the caloric differences between these prey items. Similar results occurred when the data were examined by size-class.

Prey Habitat Preference

After assigning a habitat type to each of the 47 prey categories, the %W values were summed for each habitat type (Appendix 3). Sand- or mud-associated organisms made up the largest portion of the overall diet, followed by water column organisms. Reef-associated organisms only made a 1.3%W contribution to the diet of red snapper off Alabama. When the habitat preference of the prey was examined by season (Table 5), sand- or mud-associated organisms not associated with reefs dominated every season except spring, when water column organisms made up half of the diet. Prey derived from the water column was the second most important category by %W in other seasons. Reef-associated fauna were not present in summer and winter diets and contributed less than 1% in fall and spring.

When prey item habitat preference was examined by red snapper size-class (Table

5), water column species were the largest contributors by %W to the diet of the 200–299 and 400–499 mm size classes. Sand- or mud-associated organisms were the largest contributors to the 300–399, 500–599, and >600 mm size classes. Reef-associated prey species made up less than 1%W in the 200–299, 300–399, and 400–499 mm size classes, and only 2.5%–4.8% in the 500–599 and over 600 mm size classes. There does not appear to be a size related trend in the habitat over which red snapper feed based upon these results. Red snapper of all sizes appear to be feeding either in the water column or in the sand/mud areas surrounding the reef. Despite the fact that few reef-associated species were consumed, reef-associated prey had the highest average caloric density of all the prey types, with water column and sand/mud-associated prey being the next highest.

Annual Prey Demand

The estimates of annual mean prey demand of the red snapper population on artificial reefs off Alabama indicate that, depending on the data source and collection method, between 6.4×10^5 and 31.1×10^6 kg of food are required annually to support the red snapper population found on Alabama artificial reefs (Table 6A). Estimates based on Szedlmayer and Furman (2000) biomass data resulted in the highest prey demand and Strelcheck et al. (2005) visual census data gave the lowest. When these estimates were partitioned into the seven major red snapper diet categories, red snapper off Alabama could require up to 5.6×10^6 kg of fish, 8.4×10^6 kg of demersal crustaceans (crabs and adult *Squilla empusa*) and 4.6×10^6 kg of pelagic zooplankton annually (Table 6B).
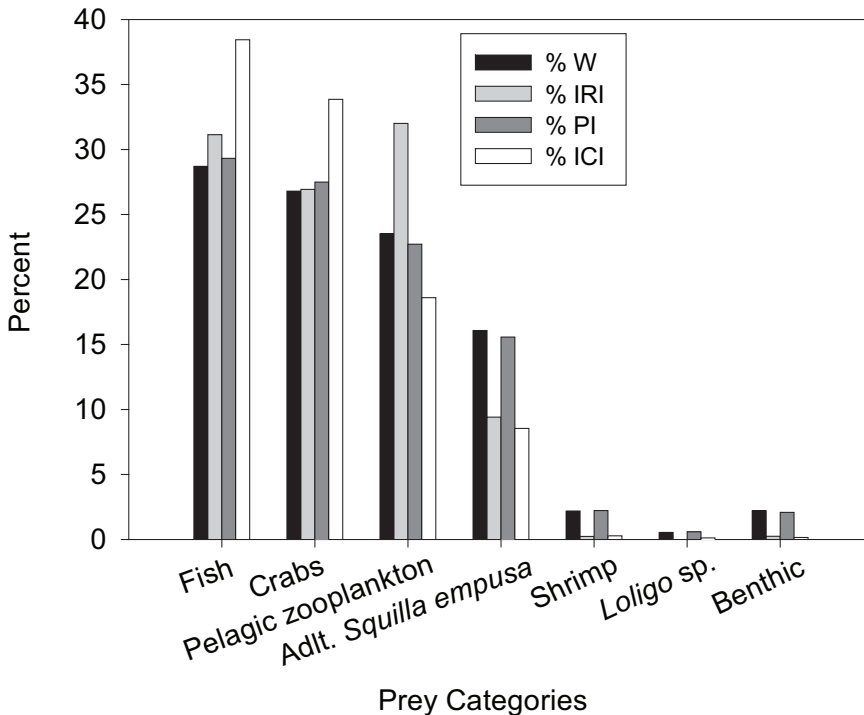

Figure 2. Comparison of prey importance in red snapper *Lutjanus campechanus* diet on Alabama artificial reefs by four indices of prey importance for seven prey types. %W = percent weight, %IRI = percent index of relative importance, %PI = percent prey importance index, %ICI = percent index of caloric importance, and Benthic = Miscellaneous benthic species.

Table 4. Comparison of four prey importance indices by season for all red snapper *Lutjanus campechanus* collected on Alabama artificial reefs based upon seven prey categories. Prey categories are ranked for each index in decreasing order of importance. %W = percent weight, %IRI = percent index of relative importance, %ICI = percent index of caloric importance, %PI = percent prey importance index, and Misc. benthic sp. = Miscellaneous benthic species.

Season	Prey Type	%W (rank)	%IRI (rank)	%ICI (rank)	%PI (rank)
Summer	Fish	28.08 (2)	29.72 (2)	33.70 (2)	28.63 (2)
	Adult *Squilla empusa*	23.23 (3)	18.12 (3)	16.05 (3)	22.25 (3)
	Crab	31.48 (1)	38.01 (1)	43.02 (1)	32.57 (1)
	Shrimp	2.26 (5)	0.26 (5)	0.30 (5)	2.33 (5)
	Loligo sp.	0.50 (7)	0.02 (7)	0.03 (7)	0.50 (7)
	Pelagic zooplankton	13.23 (4)	13.77 (4)	6.84 (4)	12.60 (4)
	Misc. benthic sp.	1.22 (6)	0.11 (6)	0.06 (6)	1.11 (6)
Fall	Fish	24.85 (3)	23.80 (3)	28.20 (2)	25.44 (2)
	Adult *S. empusa*	6.25 (5)	1.90 (5)	1.47 (5)	6.25 (5)
	Crab	34.25 (1)	38.72 (1)	48.26 (1)	34.51 (1)
	Shrimp	2.08 (6)	0.15 (6)	0.16 (6)	2.08 (6)
	Loligo sp.	0.00 (7)	0.00 (7)	0.00 (7)	0.00 (7)
	Pelagic zooplankton	25.62 (2)	32.98 (2)	20.27 (3)	24.99 (3)
	Misc. benthic sp.	6.94 (4)	2.45 (4)	1.64 (4)	6.71 (4)
Winter	Fish	25.48 (2)	25.93 (2)	31.70 (2)	25.90 (2)
	Adult *S. empusa*	33.35 (1)	42.06 (1)	36.96 (1)	32.90 (1)
	Crab	19.49 (4)	16.87 (3)	20.98 (3)	19.87 (4)
	Shrimp	0.33 (6)	0.06 (5)	0.03 (5.5)	0.33 (6)
	Loligo sp.	0.00 (7)	0.00 (7)	0.00 (7)	0.00 (7)
	Pelagic zooplankton	20.83 (3)	15.02 (4)	10.30 (4)	20.61 (3)
	Misc. benthic sp.	0.51 (5)	0.05 (6)	0.03 (5.5)	0.39 (5)
Spring	Fish	34.16 (2)	28.40 (2)	43.47 (1)	35.02 (2)
	Adult *S. empusa*	1.81 (5)	0.08 (5)	0.10 (5.5)	1.64 (5)
	Crab	18.53 (3)	8.29 (3)	13.88 (3)	19.13 (3)
	Shrimp	3.22 (4)	0.24 (4)	0.36 (4)	3.21 (4)
	Loligo sp.	1.27 (7)	0.06 (6)	0.10 (5.5)	1.47 (6)
	Pelagic zooplankton	39.58 (1)	62.90 (1)	42.05 (2)	38.10 (1)
	Misc. benthic sp.	1.43 (6)	0.04 (7)	0.03 (7)	1.43 (7)

Discussion

Diet Comparison with Other Studies.— This is the most comprehensive study of adult red snapper diet on Alabama artificial reefs to date. As in other studies (see Appendix 1 for review), red snapper in this study were found to feed opportunistically on a variety of organisms, the proportions of which changed seasonally and with size. Red snapper off Alabama ate primarily demersal crustaceans (crabs and adult *S. empusa*), fish, and pelagic zooplankton. Parrish (1987), in a literature review of lutjanids, reported that the principal food groups in most studies are fish and decapod crustaceans, and that anguilliform fishes, like the ophichthids we found, were common in the snapper diets he reviewed. Parrish (1987) also found that crabs, specifically portunid and calappid crabs, and shrimps and other crustaceans (especially stomatopods) were frequently consumed.

The proportions of the major red snapper diet categories changed significantly with season; the diet in summer and winter was dominated by adult *S. empusa*, crabs were the largest category in the fall, and pelagic zooplankton the largest category in the spring. These findings also are relatively similar to other studies of red snapper diet (Appendix 1). However, we recognize that the short, one year duration of our study, and likely changes in local prey availability necessitates that conclusions based upon seasonal data from

Table 5. Habitat association of prey consumed by red snapper *Lutjanus campechanus* given as percent weight by season for 300–499 mm FL snapper and by size class (mm FL). SM = sand-and/or mud-associated; R = reef-associated; WC = water-column-associated; SA = sargassum-associated; and V = a variety of habitats.

Summary of Prey Affiliation by Season for 300–499 mm FL Red Snapper

Habitat Type	Percent Weight Contribution by Season			
	summer	fall	winter	spring
SM	47.3	47.9	55.3	13.2
R	0	0.55	0	0.31
WC	25.9	31.8	21.1	60.4
SA	0	0	0	0
V	0	0	5.3	0

Summary of Prey Affiliation by Size Class (mm FL)

Habitat Type	Percent Weight Contribution by Size Class				
	200-299	300-399	400-499	500-599	>600
SM	27.3	46.4	31.1	30.3	59.8
R	0	0.3	0.2	4.8	2.5
WC	54.6	28.1	45.9	29.1	7.7
SA	0	0	0	0	7.8
V	0	1.0	1.3	0	0

this and several of the other studies (Appendix 1) should be interpreted with caution.

Our research provided a size-class (200 to >600 mm) comparison of adult red snapper diet off Alabama, which has been lacking in other studies. A shift in diet with size was indicated: as red snapper grew, the amount of pelagic zooplankton in their diet decreased and the amount of demersal crustaceans increased, with fish remaining a component in the diet of all size classes. However, unlike most of the other studies summarized in Appendix 1, we observed patterns with size that are somewhat atypical. Surprisingly, we observed a small decrease in the amount of fish in the diet of the largest red snapper we examined. However, our data should be interpreted with caution because not all size classes of red snapper were collected at all times of the year. Most red snapper diet studies have found that as individuals grow, there is a shift in their diet from invertebrates and zooplankton to a dependency on fish (Moseley 1966; Bradley and Bryan 1975; Szedlmayer

and Lee 2004). Few studies (e.g., Camber 1955) have reported that large red snapper continue to eat demersal crustaceans. Also, pelagic zooplankton contributed to the diet of all size classes in our study, decreasing in importance only for snapper larger than 500 mm FL. Moseley (1966) found a decline in the occurrence of zooplankton in red snapper diets after 170 mm SL. Moseley (1966) concluded that it is inefficient for red snapper larger than 110 mm SL to exist on zooplankton. However, Siegel (1983) found that adult red snapper up to 550 mm SL off Alabama continued to consume significant amounts of pelagic zooplankton, especially larval decapods and stomatopods.

Foraging in the water column on zooplankton has been reported previously for red snapper and other lutjanids. Parrish (1987) found numerous studies of lutjanid diets that reported large zooplankton as an important part of the diet. Haight et al. (1993), in a study of deepwater lutjanids at Penguin Bank, Hawaii, found a diet of primarily zooplankton.

Likewise, Weaver and Sulak (2001) estimated that 1.5 million zooplankters would be available to the reef fish in a meter wide swath in the water column above the deep reef community of the Pinnacles Reef Tract off Alabama. Zooplankton is the primary source of prey for that deep-water reef fish community. Results of our study, combined with results of previous work, strongly support the conclusion that red snapper are opportunistic feeders, and apparently do not consume

significant amounts of prey derived directly from reef habitat.

Prey Preference.—Red snapper in this study fed opportunistically on nonreef-associated benthic fauna and pelagic zooplankton; however, it is unclear whether their feeding habits vary due to preference for certain prey, or due to the differences in the availability of food in the environment (Cailliet 1976). Bradley and Bryan (1975) believed

Table 6. A = Estimates of annual mean prey demand of a red snapper *Lutjanus campechanus* population on artificial reefs off Alabama. B= Estimates of annual mean prey demand of a red snapper *Lutjanus campechanus* population on artificial reefs off Alabama broken down by seven prey categories. Misc. benthic sp. = Miscellaneous benthic species.

A.

Biomass Data Source	Number of Reefs	Minimum Prey Demand (kg)	Mean Prey Demand (kg)	Maximum Prey Demand (kg)
Strelcheck	1	76	82	88
2001	14[a]	1,069	1,154	1,239
CPUE	8,000[b]	611,021	659,346	707,751
	20,000[c]	1,527,553	1,648,365	1,769,377
Strelcheck	1	32	38	43
2001	14	450	525	600
Visual census	8,000	257,386	300,270	342,754
	20,000	643,464	750,675	856,886
Szedlmayer	1	395	975	1556
and Furman	14	5,532	13,655	21,777
2000	8,000	3,161,036	7,802,780	12,444,124
Visual census	20,000	7,902,590	19,506,951	31,110,311

B.

Biomass Data Source	Prey Type	Mean Prey Demand (kg) Per Number of Reefs			
		1	14[a]	8,000[b]	20,000[c]
Strelcheck	Fish	24	331	189,213	473,033
2001	Adult *Squilla empusa*	13	186	106,012	265,031
CPUE	Crabs	22	309	176,621	441,553
	Penaeid shrimp	2	25	14,438	36,096
	Loligo sp.	0	6	3560	8900
	Pelagic zooplankton	19	271	154,997	387,492
	Misc. benthic sp.	2	25	14,504	36,260
Strelcheck	Fish	11	151	86,169	215,422
2001	Adult *Squilla empusa*	6	84	48,279	120,696
Visual census	Crabs	10	141	80,434	201,086
	Penaeid shrimp	1	12	6575	16,438
	Loligo sp.	0	3	1621	4053
	Pelagic zooplankton	9	124	70,586	176,466
	Misc. benthic sp.	1	12	6605	16,513
Szedlmayer	Fish	280	3919	2,239,174	5,597,935
and Furman	Adult *Squilla empusa*	157	2195	1,254,562	3,136,404
2000	Crabs	261	3658	2,090,156	5,225,390
Visual census	Penaeid shrimp	21	299	170,864	427,160
	Loligo sp.	5	74	42,131	105,327
	Pelagic zooplankton	229	3210	1,834,250	4,585,626
	Misc. benthic sp.	21	300	171,644	429,110

[a] 14 = Number of experimental reefs from Strelcheck et al. (2005)
[b] 8,000 = Estimated minimum number of artificial reefs off Alabama from Minton and Heath (1998)
[c] 20,000 = Estimated maximum number of artificial reefs off Alabama

that young red snapper were eating a wider variety of prey items (such as more zooplankton) in winter due to the scarcity of more preferred prey. Thus, red snapper could be eating whatever is available around the reef, which may not be the most preferred items with respect to caloric content. Results of our study combined with our review of the available literature (Appendix 1) also suggest the need to compare in more detail the diets of red snapper collected on natural versus artificial habitats, as almost all of the recent studies, including ours, are based upon fishes collected at artificial reefs.

Assuming that fish is a preferred prey because of its caloric content, our results may have been biased by differential digestion rates of organisms, causing less fish to be found in the stomachs than the amount that was actually eaten. Longley and Hildebrand (1941) studied the rate of digestion of lutjanids in the Dry Tortugas and found that after 3.5 h, prey fish in the stomachs were almost completely disintegrated, while digestion of crabs had barely occurred. However, Popova and Sierra (1985) report that the digestion rate of lane snapper, *Lutjanus synagris*, and gray snapper, *Lutjanus griseus*, to be about 40 h in winter and about 20 h in summer since digestion is temperature dependent. Thus, depending on the digestion rate of red snapper, some fish prey could have been underrepresented in the diet. In contrast, when examining gastric evacuation in Atlantic horse mackerel *Trachurus trachurus*, Temming and Herrmann (2001) concluded that the greater the energy density of an organism, the slower it is evacuated. As such, we found numerous organisms of varying caloric content in the stomachs of red snapper including fish having a high caloric content. Thus, we are unsure if fish was underrepresented in the diet.

Prey Demand.—To date, no other estimates of red snapper prey demand on artificial reefs exist. We found that over 31 million kg of prey could be required annually to sustain the red snapper population on artificial reefs off Alabama. However, whether or not these prey demands are being met remains to be answered. The distribution and abundance of red snapper off Alabama over mud bottom, which once supported much lower densities than at present, has been altered (Cowan et al. 1999; Shipp 1999). The permit areas that were once habitat for juvenile reef fish are now home to as many as 20,000 artificial reefs (Cowan et al. 1999; Shipp 1999), where large numbers of red snapper may now be overexploiting their prey resources. However, to quantitatively address this issue, prey production and turnover rates need to be measured and then compared with prey demand estimates.

Differences in annual prey demand estimates based on data from Szedlmayer and Furman (2000) and Strelcheck et al. (2005) are due to the differences in the size of the red snapper on the reefs each sampled, as well as the size of the experimental reefs each examined. The red snapper on the reefs sampled by Strelcheck et al. (2005) were smaller than the red snapper found on the reefs examined by Szedlmayer and Furman (2000), and the artificial reefs that Strelcheck et al. (2005) sampled were smaller than those examined by Szedlmayer and Furman (2000). Moreover, the estimate of annual prey demand based on data from Strelcheck et al. (2005) assumed all artificial reefs off Alabama were of the size he studied, whereas the estimate based on data from Szedlmayer and Furman (2000) assumed all artificial reefs off Alabama were larger. Because artificial reefs off Alabama vary in size, thus causing variability in the number and size of the fish they hold, the annual prey demand for the red snapper population on Alabama artificial reefs probably lies somewhere between these two estimates. Our result may be conservative because we did not take into account the red snapper population over natural hard-bottoms off Alabama.

Contribution of Reef versus Off-Reef Prey.—Foraging by red snapper off Alabama does not appear to be associated with the reef structure *per se*, and thus they may be gaining little nutritional support from reef-associated fauna. Red snapper diet was composed primarily of benthic organisms, such as portunid crabs, adult *S. empusa*, ophichthid fishes, triglid fishes, and *Ophidion* sp.; these organisms typically are associated with mud or sand substrates. Several other studies of red snapper diet describe foraging habits that support this contention (Moseley 1966; Beaumariage and Bullock 1976; Futch and Bruger 1976; Siegel 1983, Parrish 1989). Bohnsack et al. (1991 and 1997b) suggest that feeding on encrusting organisms is not a major attractant for fishes to artificial reefs because most reef fishes depend on pelagic prey and surrounding benthos for food. Similarly, studies of a variety of reef fishes also indicate that snappers, groupers, grunts and other species often eat benthic organisms not associated with artificial or natural reefs (lane snapper, Duarte and Garcia 1999; gray snapper, Croker 1962; Nassau grouper, *Epinephelus striatus*, Eggleston et al. 1998; pigfish, *Orthopristis chrysoptera*, Howe 2001). In a review of lutjanid feeding ecology, Parrish (1987) reports that most snapper probably remain within a few meters of the bottom because most of their prey must be captured from the substrate. He classifies red snapper as an intermediate depth feeder, which means they forage anywhere from relatively shallow water up to 100 m depth. He contends that such feeders either forage widely from shelter over soft bottom to gain food or forage by "patrolling up to several meters off the bottom for nektonic prey" as well as "periodically foraging on substrate for fully benthic forms." Our study found that red snapper consumed some organisms, such as larval *S. empusa*, fish larvae, amphipods, and *Cavolinia* sp., which reside higher in the water column, and other assorted pelagic zooplankton as well as mud-associated species.

Red snapper foraging primarily on benthic invertebrates and pelagic zooplankton suggests that they may be a vital link between the reef community and surrounding habitats if they are translocating energy from the water column and the adjacent sand or mud bottom to the reef through defecation (Parrish 1989). Sedberry and Cuellar (1993) suggested that vermilion snapper off South Carolina and Georgia are important in transferring energy from benthic sand habitats and the water column to the reef because they feed on crustaceans that are not reef-associated. Lindquist et al. (1994), in a study off North Carolina, determined that the sand-associated organisms around the reefs are an important source of energy for artificial reef fish. Davis and Birdsong (1973) describe coral reefs and other habitat interfaces as rich in diversity, suggesting they "represent 'cross roads' between foraging and refuge areas." Artificial reefs can be seen in much the same context, as red snapper seem to fill their energetic demands from habitats other than reefs. It is still unclear if red snapper are simply leaving reefs to forage on nearby mud bottoms or if they are feeding during their transit between reefs, or both. In contrast, Szedlmayer and Lee (2004) found that small red snapper over artificial reefs ate reef-associated prey, such as fish (*Halichoeres* sp., *Serranus* sp. and *Centropristis* sp.) and shrimp (*Lysmata* sp. and *Synalpheus* sp.), although they examined primarily juvenile red snapper which were smaller (10 mm–230 mm SL) than those in our study. Perhaps smaller red snapper are more reef dependent than their larger counterparts or less likely to forage away from structure.

Patterns of Foraging.—It is also possible that red snapper diet may change with distance from shore. Weaver et al. (2001) found red snapper on deep, natural reefs off Alabama (Pinnacles Reef Tract) to be eating similar organisms to red snapper found on the shallow artificial reefs where our red snapper were collected, however the red snapper they

examined ate considerably more fish (56% N) (in the form of planktivores, such as red barbier, *Hemanthias vivanus*; striped codlet, *Bregmaceros cantori*; and pike-conger eels, *Hoplunnis sp*.). Weaver and Sulak (2001) found that 90–99% of the fish on the Pinnacles Reef Tract on the Mississippi-Alabama shelf (50–110 m) were small planktivores. These fish served as prey for larger reef fish, and were found in the stomachs of the red snapper they sampled.

In contrast, similarly sized red snapper on inshore artificial reefs ate fewer fish (26%N), but more demersal crustaceans and pelagic zooplankton. As such, red snapper appear to be occupying a different trophic position than similar sized red snapper on deeper reefs further offshore. This suggests that there is a potential for density-dependant food limitation in inshore waters due to elevated adult red snapper densities that are atypical of the inshore habitat, calling into question the role of artificial reefs with respect to the production of new fish biomass.

Succession of Artificial Reefs.—Hueckel and Buckley (1987) discussed the succession of colonization of artificial reef communities in Puget Sound. They believed that in the first stage of development, predators that are aggregated at a reef feed primarily on organisms from the surrounding benthic community. In the second stage, piscivores colonize the reef and feed on fishes that are feeding on the benthic community. In the latter stages of succession, the reef itself can produce an adequate amount of prey to support fish that feed on reef-attached organisms. In their study, 70% of reef fish were feeding on reef-attached organisms. According to their theory of reef colonization, the prey that we found red snapper eating suggests that the artificial reefs off Alabama are indicative of immature communities with low amounts of reef-associated prey. Thus, something may be occurring to keep these reefs "young." Perhaps the

passage of tropical storms, which redistribute red snapper (Watterson et al. 1998; Patterson et al. 2001) and reset the benthic community via scouring from wave activity, never allow the artificial reefs to accumulate a mature community of these encrusting organisms, thus producing reef ecosystems that never fully mature.

Attraction versus Production.—Examining a theoretical idea about the attraction versus production debate, we can draw conclusions about the role of artificial reefs in the life history of red snapper. Bohnsack (1989) stated that attraction and production are not mutually exclusive, but rather opposite extremes along a gradient. He stated that five criteria are important for determining whether attraction or production was occurring within a reef system: reef availability, fishing intensity, population controls, reef dependency, and behavior of the target species. Increased production would be likely at locations where reef availability was low, fishing intensity was low, the population of interest was habitat limited, the species of interest was more obligately reef dependent, and the behavior of that species was demersal or territorial. Increased attraction would be likely at locations where reef availability was high, fishing intensity was high, the population of interest was recruitment limited, the species of interest was only partially or opportunistically reef dependent, and the behavior of that species was migratory (Bohnsack 1989). A broad look at the Alabama system using the criteria developed by Bohnsack (1989) provides insight about where the reefs off Alabama fall within the attraction versus production continuum for red snapper. From the current study, we know that red snapper rarely feed on reef dependent prey species. We also know that reef availability is high off Alabama, and that the area is known to have large amounts of low-relief natural hard bottom habitat (Strelcheck et al. 2005). Fishing intensity on these reefs is high as indicated by the large fraction

of the total recreational catch that is landed off Alabama (37% of the total recreational catch in the northern Gulf of Mexico, MRFSS 1993–2003); this is corroborated by high estimates of fishing mortality in Watterson (1998) and Schirripa and Legault (1999). There is no evidence that the availability of natural or artificial habitat limits the current population size of red snapper (Cowan et al. 1999), especially given the high mortality of prerecruits attributable to bycatch in the shrimp fishery. Many studies incorrectly conclude that higher densities of organisms around artificial reefs is evidence for increased production (Bohnsack et al. 1997a) by assuming that the amount of hard-bottom habitat is limiting reef fish populations (Bohnsack 1989; Bohnsack et al. 1991; Polovina 1991; Bohnsack et al. 1997a; Bohnsack et al. 1997b; Lindberg 1997). Finally, Patterson et al. (2001) and Patterson and Cowan (2003), showed that red snapper move more frequently and travel greater distances than previously thought, indicating only moderate site fidelity. When all of the above information is interpreted in light of Bohnsack's (1989) criteria, it seems likely that artificial reefs off Alabama are functioning more to attract red snapper than to produce them.

We conclude that red snapper are attracted to artificial reefs off Alabama as a result of a behavioral preference rather than for increased foraging opportunities. Instinctual behavioral responses may explain why red snapper congregate around artificial structures, even when by doing so they may decrease success in foraging (Strelcheck et al. 2005). Shipley and Cowan (University of South Alabama, unpublished data) used Ecopath with Ecosim and Ecospace, based upon a synthesis of much of the data reported here and elsewhere from studies off Alabama, to show that red snapper are capable of creating foraging halos of depleted prey resources around individual reefs. In these simulations, reefs spaced too closely together caused the halos to overlap, negatively affecting the fitness of red snapper occupying the reefs. Bohnsack (1989) suggests that evolutionary experience of fishes elicits responses that are not necessarily adaptive. If red snapper are attracted to Alabama reefs from other areas in the Gulf (Patterson et al. 2001), then limited or over-exploited prey resources coupled with high fishing mortality could make Alabama's artificial reefs a net sink for red snapper production in the northern Gulf. Strelcheck et al. (this volume) concludes this explicitly based upon G/Z ratios (Houde 1989) calculated for this region.

Acknowledgments

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Appendix 1. Literature review of *Lutjanus campechanus* diet studies in the northern Gulf of Mexico. FO = frequency of occurrence.

Source	Location of study	Fish size	# stomachs examined (# w/ food)	Description of Results
Stearns 1884	Northern Gulf of Mexico	?	450 (1)	[a] "fine sand worms and sponge like stuff" were reported. (Camber 1955 stated that find sand worms were probably *Cavolinia longirostris*)
Collins 1885	Gulf of Mexico	?	?	[a][b] Fish were the principal prey items and some pelagic plankton (urochordates)
Adams and Kendall 1891	Florida	?	Small #	[a] Flying fish, eels, crabs (*Calappa* sp.), and mantis shrimp (*Squilla* sp.)
Camber 1955	Campeche Banks	Juvenile	15 (14)	Penaeid shrimp
		Adult	100 (24)	Penaeid shrimp, crabs, octopus, conch, *Sicyonia* sp. and fish associated with coral reefs
Moseley 1966			712 (187)	
	Louisiana	Juvenile	(28)	39%FO of crustaceans in one sample, another sample had 60% *Squilla* sp. and 27% unidentified fish
		Adult	(46)	80% fish and 20% crustaceans in one sample, another sample had 44% fish and 8% crustaceans
	Texas	Juvenile	(45)	41% crustaceans in one sample and 89% crustaceans in another
		Adult	(68)	Fish dominated the diets in all samples (40-59%) and crustaceans made up 32% in one sample
Bradley and Bryan 1975	Texas	Juvenile and sub-adult	575 (258)	* Mostly dependent on shrimp throughout the year, but crabs and mantis shrimp also were important. Primary food items by season: summer-squid and fish; fall- octopods; winter and spring-shrimp and other crustaceans. Winter had the most varied diet. Zooplankton were not present in the diet after 150 mm FL.
		Adult	1139 (190)	* Primarily ate fish throughout the year, but in summer ate more crustaceans. Primary food items by season: summer-unid. fish, *Callinectes danae* and *Sicyonia dorsalis*; fall-fish, *S. dorsalis* and *C. danae*; winter-unid. fish and eels; spring-unid. fish, eels, mantis shrimp, and *Sicyonia* sp. Summer had the largest variety of organisms and winter the smallest variety.
Beaumariage and Bullock 1976	Florida	Juvenile	?	Invertebrates (shrimps, crabs, squids, and mud burrowing shrimp) made up a considerable portion of the diet
Futch and Bruger 1976	Florida, west of Clearwater	?	213 (56)	Invertebrates were represented more than fish. The inverts were associated with sand-shell bottom, such as Stomatopods and Decapods. Some larvae found in the stomachs also suggested some water column feeding.
Gallaway 1980	Buccaneer oil and gas platform in NW Gulf	70-450 mm FL	?	* *Squilla* sp. a major contributor in summer and spring; fish also important in summer; fall comprised of fish, shrimp and swimming crabs; winter most of diet was bait and a few fish
Siegel 1983	Primarily Alabama but also some samples from Louisiana and Florida	1-250 mm SL (Juveniles)	582 (289)	* Fish were most prominent throughout the year, followed by crabs (mostly portunids and albunids) and shrimp (Sicyonidae, Sergestidae, Penaeidae). Less frequent occurrence of zooplankton (such as amphipods). High occurrence of decapod and stomatopod larvae in June. Overall lack of significant seasonal trends. Consumed many different prey types.
		251-550 mm SL (Adults)	? (34)	* Fish and crabs (portunids and albunids) were the largest part of the diet. All sizes of adults consumed crabs, sicyonid and penaeid shrimp, and decapod and stomatopod larvae. Squid had minimal importance. Diversity of prey was highest in summer and lowest in winter. Summer and winter had larval *S. empusa* in abundance. Overall lack of significant seasonal trends. Consumed few different types of prey.
Bailey 1995	Alabama	330-691 mm TL	98 (45)	Principal prey items in summer were rock shrimp and crabs, also ate some eels and unidentified fish
Weaver et al. 2001	Alabama (Pinnacles Reef Tract)	192-465 mm SL	26 (?)	Characterized red snapper as a generalized carnivore. Found them eating 56% fish (all of which were deep water species) and 25.7% pelagic zooplankton. Also found 5% crab, 5% mantis shrimp, and 2.6% squid.
Ouzts and Szedlmayer 2003	Alabama Hugh Swingle Permit Area	185-590 mm SL	432 (164)	Fish prey dominated red snapper diet for entire diel cycle. Sand prey dominated dusk and dawn and reef prey dominated day and night. Pelagic prey were unimportant for all periods.
Szedlmayer and Lee 2004	Alabama	10-280 mm SL	1639 (789)	Red snapper on open habitat (most <70 mm SL) ate non-reef-associated species such as mysid shrimp, chaetognaths, squid, and copepods. Reef-associated red snapper (70-280 mm SL) ate reef associated species such as fish (*Halichoeres* sp., Blenniidae, and Serranidae), squid, portunid crabs, and shrimp (*Sicyonia* sp. and Squillidae).
McCawley et al. 2006	Alabama Hugh Swingle Permit Area	267-590 mm FL	268 (166)	Red snapper fed continuously throughout the day and night. Fed above the reef on water-column associated organisms during the day and away from the reef on sand/mud associated organisms at night.
This study	Alabama Hugh Swingle Permit Area	207-913 mm FL (Adult)	656 (331)	* Overall ate primarily demersal crustaceans (crab and adult *Squilla empusa*), fish, and pelagic zooplankton. Summer and winter dominated by adult *Squilla empusa*, fall dominated by crabs, and spring dominated by pelagic zooplankton. Diversity of prey was highest in summer and lowest in winter. As snapper got larger pelagic zooplankton decreased and demersal crustaceans increased, while fish remained a constant component. Primarily ate species not associated with reefs.

* Seasonal study
[a] Cited in Camber (1955)
[b] Cited in Parrish (1987)

Appendix 2. Percent index of caloric importance (%ICI) of red snapper *Lutjanus campechanus* diet items and the three values that compromise the index for 47 prey categories. Prey items are ranked in decreasing order of importance by the %ICI index. %W = percent weight, Cal/g wet wt = Calories/gram wet weight, %FO = percent frequency of occurrence, and %ICI = percent index of caloric importance.

Prey Type	%W	Cal/g wet wt	Source	%FO	%ICI (rank)
Fish					
Unidentified fish	13.40			17.16	
Family Ophichthidae	4.09	1278.67	McCawley 2003	6.34	4.03 (6)
Family Triglidae	2.35	882.25	McCawley 2003	2.61	0.66
Family Haemulidae	0.46	1234.13	McCawley 2003	0.75	0.05
Family Syngnathidae	0.12	1009.22	McCawley 2003	0.75	0.01
Ophidion sp.	0.62	1011.11	McCawley 2003	0.75	0.06
Decapterus sp.	0.30	1235.95	McCawley 2003	0.37	0.02
Lagodon rhomboides	0.37	1846.77	McCawley 2003	0.37	0.03
Anchoa hepsetus	0.23	1073.70	McCawley 2003	0.37	0.01
Fish larvae	6.75	1190.25	Harris et al. 1986	11.94	11.65 (4)
Crabs					
Unidentified crabs	11.08			17.54	
Family Portunidae	0.64	1146.58	McCawley 2003	2.24	0.20
Portunus gibbesii	7.41	1331.04	McCawley 2003	11.19	13.40 (3)
P. sayi	1.34	1146.58	McCawley 2003	2.99	0.56
P. spinimantus	0.55	939.02	McCawley 2003	1.12	0.07
P. spinicarpus	0.16	1146.58	McCawley 2003	0.37	0.01
P. ordwayii	0.14	1146.58	McCawley 2003	0.37	0.01
P. sebae	<0.01	1146.58	McCawley 2003	0.37	0.00
Callinectes sp.	0.31	1519.65	McCawley 2003	0.37	0.02
C. sapidus	1.11	1483.58	McCawley 2003	1.87	0.37
C. exasperatus	0.26	1519.65	McCawley 2003	0.37	0.02
C. danae	0.01	1519.65	McCawley 2003	0.37	0.00
Ovalipes floridanus	1.65	1059.01	McCawley 2003	2.61	0.55
Calappa flammea	0.75	1053.39	McCawley 2003	0.75	0.07
C. augusta	0.35	1053.39	McCawley 2003	0.37	0.02
Hepatus epheliticus	0.31	1053.39	McCawley 2003	0.75	0.03
Parthenope granulata	0.73	1295.81	McCawley 2003	0.75	0.09
Pelagic zooplankton					
Larval *Squilla empusa*	11.78	686.40[a]	Wissing et al. 1973	21.64	21.25 (2)
Unidentified mollusk larvae	1.44	686.40[a]	[a]	1.87	0.22
Crab megalopa and zoea	0.50	686.40[a]	[a]	1.87	0.08
Order Amphipoda	5.76	686.40[a]	Wissing et al. 1973	16.79	8.05 (5)
Order Euphausicaea	0.75	708.70	Morris and Hopkins 1983	0.75	0.05
				0.75	0.02
Order Isopoda	0.38	686.40[a]	Wissing et al. 1973	0.75	0.00
Order Mysidacea	0.03	714.00	Morris and Hopkins 1983	0.37	0.00
Order Calanoida	0.01	663.90	Morris and Hopkins 1983	1.49	0.02
Family Sergestidae	0.13	659.00	Morris and Hopkins 1983	0.37	0.00
Family Palaemonidae	0.05	686.40[a]	[a]	4.10	0.89
Cavolinia sp.	2.62	686.40[a]	[a]	0.75	0.00
Sagita sp.	0.06	686.40[a]	[a]		
Adult *Squilla empusa*	16.08	865.41	McCawley 2003	21.27	35.93 (1)
Penaeid shrimp	2.19	1166.86	McCawley 2003	3.73	1.16 (7)
Squid	0.54	1222.06	McCawley 2003	1.49	0.12
Miscellaneous Benthic species					
Phyllum Arthropoda	0.08	792.00	Cummins and Wuycheck 1971	0.37	0.00
Pagurus sp.	0.37	695.30[b]	[b]	0.37	0.01
Sicyonia sp.	0.13	654.89	McCawley 2003	0.75	0.01
Glycera sp.	0.05	639.00	Cummins and Wuycheck 1971	0.37	0.00
Albunea paretii	1.57	695.30[b]	[b]	1.87	0.25

[a] Estimated from other pelagic zooplankton values in this study.
[b] Estimated from other miscellaneous demersal species in this study.

Appendix 3. Percent weight (%W) of stomach contents and habitat association of prey consumed by red snapper *Lutjanus campechanus* for all stomachs collected from Alabama artificial reefs. SM = sand- and/or mud-associated; R = reef-associated; WC = water-column-associated; SA = sargassum-associated; and V = a variety of habitats.

Prey Type	%W	Habitat	Source
Fish			
Unidentified fish	13.40		
Family Ophichthidae	4.09	SM	Hoese and Moore 1998
Family Triglidae	2.35	SM	Hoese and Moore 1998
Family Haemulidae	0.46	R	Hoese and Moore 1998
Family Syngnathidae	0.12	R	Starck 1968
Ophidion sp.	0.62	SM	Hoese and Moore 1998
Decapterus sp.	0.30	R	Starck 1968
Lagodon rhomboides	0.37	R	Hoese and Moore 1998
Anchoa hepsetus	0.23	WC	Hoese and Moore 1998
Fish larvae	6.75	WC	Matsuura and Olivar 1999
Crabs			
Unidentified crabs	11.08		
Family Portunidae	0.64	SM	Britton and Morton 1989
Portunus gibbesii	7.41	SM	Britton and Morton 1989
P. sayi	1.34	SA	Williams 1984
P. spinimantus	0.55	SM	Williams 1984
P. spinicarpus	0.16	SM	Williams 1984
P. ordwayii	0.14	SM	Britton and Morton 1989
P. sebae	<0.01	SM	Kaplan 1988
Callinectes sp.	0.31	SM	Britton and Morton 1989
C. sapidus	1.11	SM	Britton and Morton 1989
C. exasperatus	0.26	SM	Britton and Morton 1989
C. danae	0.01	SM	Williams 1984
Ovalipes floridanus	1.65	SM	Kaplan 1988
Calappa flammea	0.75	SM	Williams 1984
C. augusta	0.35	SM	Britton and Morton 1989
Hepatus epheliticus	0.31	SM	Williams 1984
Parthenope granulata	0.73	V	Williams 1984
Pelagic zooplankton			
Larval *Squilla empusa*	11.78	WC	Morgan and Provenzano 1979
Unidentified mollusk larvae	1.44	WC	Todd et al. 1996
Crab megalopa and zoea	0.50	WC	Pohle et al. 1999
Order Amphipoda	5.76	WC	Stuck 1978
Order Euphausicaea	0.75	WC	Gibbons et al. 1999
Order Isopoda	0.38	WC	Smith and Johnson 1996
Order Mysidacea	0.03	WC	Murano 1999
Order Calanoida	0.01	WC	Pechenik 1996
Family Sergestidae	0.13	WC	Williams 1984
Family Palaemonidae	0.05	WC	Pechenik 1996
Cavolinia sp.	2.62	WC	Van der Spoel and Dadon 1999
Sagita sp.	0.06	WC	Casanova 1999
Adult *Squilla empusa*	16.08	SM	Britton and Morton 1989
Penaeid shrimp	2.19	SM	Britton and Morton 1989
Squid	0.54	WC	Britton and Morton 1989
Miscellaneous Benthic species			
Phyllum Arthropoda	0.08	SM	Pechenik 1996
Pagurus sp.	0.37	SM	Britton and Morton 1989
Sicyonia sp.	0.13	SM	Williams 1984
Glycera sp.	0.05	SM	Fauchald 1977
Albunea paretii	1.57	SM	Williams 1984

Summary of Habitat Types	
Habitat Type	% Weight
SM	41.2
R	1.3
WC	31.0
SA	1.3
V	0.7