Red Snapper (*Lutjanus campechanus*) Diet in the North-Central Gulf of Mexico on Alabama Artificial Reefs

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ABSTRACT

Red Snapper, *Lutjanus campechanus*, is a highly exploited reef fish in the Gulf of Mexico (Gulf) that occupies both natural hard-bottom and artificial habitats. Despite its importance, little is known about its feeding habits. Toward this end, we examined the size-specific diet of red snapper collected for stomach content analysis from artificial reefs in the north-central Gulf off Alabama between May 1999 - April 2000. Thirty-nine to 86 stomachs per month were removed and prey items were identified to the lowest possible taxonomic level. The relative contribution of prey items was determined using percent composition by weight, percent composition by number, percent frequency of occurrence, and index of relative importance (IRI). Results suggest that snapper are feeding on organisms not associated with reefs, such as mantis shrimp and portunid crabs. Diet changes seasonally, with crabs being most important (38% and 43% by IRI) in summer and fall, while mantis shrimp dominate in winter (42% IRI). Pelagic zooplankton was the greatest by percent weight in the diet in spring (60% IRI). Fish also contribute to each season, but they are not the principal prey items in any season (28% - 30% IRI). These diet data ultimately will be used in combination with a bioenergetics model to estimate prey demand of snapper on Alabama artificial reefs.

KEY WORDS: Artificial reefs, diet analysis, *Lutjanus campechanus*

INTRODUCTION

Red snapper, *Lutjanus campechanus,* is a highly exploited finfish in the Gulf of Mexico (Gulf). It has been harvested both commercially and recreationally since the late 1800s (Moseley 1966, Goodyear 1995, Schirripa and Legault 1997). Thus, stocks declined throughout the Gulf until the early 1990s (Szedlmayer and Shipp 1994). Since then, regulations enacted by the National Marine Fisheries Service, including size and bag limits and total allowable catches, have led to some recovery of the stock (Schirripa and Legault 1997, Patterson 1999).

This recovery also has been attributed in part to an increase in structure in the form of artificial reefs and oil and gas platforms. The Alabama shelf has the largest artificial reef program in the nation with over 4000 km^2 of reef permit area (Shipp

1999). Perhaps as many as 20,000 artificial reefs have been deployed in the permitted areas off the Alabama coast (Patterson 1999); these structures support red snapper and other reef associated species. However, the role that artificial reefs play in trophic dynamics is largely unknown; some have suggested that they may actually be energy sinks (Bortone 1998).

In addition, there has been a growing recognition that interacting species, such as those found on artificial reefs, cannot be managed individually. This idea has led to the development of multispecies ecosystem models, which has generated the need for more information about the food consumed by the communities of reef fish (Munro 1987). This study examines the role that artificial reefs may play in red snapper trophic dynamics, focusing on seasonal changes in diet.

METHODS

Red snapper were collected by hook and line from artificial reefs in the northern 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. However, some were collected in July 1999 and 2000 from local fishing tournaments. Knowing that red snapper are prone to regurgitation (Parrish 1987), approximately 39 to 86 fish were collected per month to ensure a significant number of fish with full stomachs. All snapper were weighed to the nearest 0.01 kg, and their total length (TL) and fork length (FL) determined to the nearest mm before their stomachs were 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 hours. They then were transferred to 70% isopropyl alcohol until they could be sorted. Preserved stomachs were opened and contents removed and sorted to the lowest possible taxonomic level. Prey items were then weighed by taxon to the nearest 0.01g.

The relative contribution of each of several prey categories was determined using four methods:

i) Percent composition by weight,
ii) Percent composition by number,
iii) Percent frequency of occurrence, and
iv) Index of relative importance.

The index of relative importance (IRI) was calculated as: IRI = (%N +%W) x %FO, where N = number, V = volume, and FO = frequency of occurrence (Pinkas 1971, modified by Hacunda 1981). Percent IRI (% IRI) also was calculated by dividing the IRI value for each prey category by the sum of the IRI values and multiplying by 100. These indices were used to describe overall diet, as well as to evaluate diet on a seasonal basis (summer = June, July, and August; fall = September, October, November; winter = December, January, February; and spring = March, April, and May). The identifiable contents of all stomachs combined were divided into six major prey categories: fish; crabs; adult mantis shrimp; penaeid shrimp; squid; and, 'others'. The 'other' category was further subdivided into pelagic zooplankton and demersal/benthic associated species, with the exception of larval fish, which were included in the fish category and crab megalopae and zoea, which were included in the crab category. The diet also consisted of an 'unidentified' category, however it was not included in all of the analyses because IRI cannot be determined for this category.

To further analyze the diet data, the PRIMER statistical package (Clarke and Gorley 2001) was used to calculate Bray-Curtis similarity coefficents, which then were used to assess the extent of similarity between the weight proportions of the prey items for each red snapper stomach with prey. The non-parametric permutation procedure ANOSIM (Analysis of Similarities, PRIMER) (Clarke and Warwick 1994) was used to test for significant differences between seasons. Which prey categories that most contributed to the observed differences between season were elucidated with BVSTEP, a stepwise procedure that attempts to determine influential species "whose among sample relationships capture nearly the same multivariate pattern as the full species set" (Clarke and Gorley 2001). SIMPER (Similarity Percentages, PRIMER), a multivariate multiple permutations test was used to examine the contribution a prey group made to the average within group similarity and between group dissimilarity. Descriptive indices then were used to further examine the SIMPER results by breaking down three of the major categories (i.e. fish, crab, and pelagic zooplankton) further, to examine the specific species that contributed to the observed trends (Table 1).

RESULTS

Stomach contents of 656 red snapper ranging from 207 to 913mm FL were examined. Of these, 268 stomachs contained identifiable prey (40.8%), 262 were empty (39.9%), 63 contained only bait (9.6%), and 63 contained only unidentifiable prey (9.6%).

The 'unidentified' prey category made up the largest proportion of the diet by %W. After exclusion of the unidentified category, fish, pelagic zooplankton, and crab were the principal components of red snapper diet when all stomachs were combined (Figure 1). However, no single group was largest by all indices. Pelagic zooplankton dominated by % FO (39.3%) and % N (30.2%), whereas fish dominated by % IRI (30.9%) and % W (28.7%). Unidentified fish, larval fish, fish of the families Ophicthidae (shrimp eels), and Triglidae (sea robins) contributed largely to the fish portion of the diet, whereas crabs of the family Portunidae and unidentified crabs were important in the crab category. Pelagic zooplankton consisted primarily of larval mantis shrimp, amphipods, and pteropods (*Cavolinia* sp.).

Table 1. Three major diet categories broken down into their component species for each season using percent weight for 300 - 499mm FL fish only.

Prey Type	Percent by Weight in Season Encountered			
	Summer	**Fall**	**Winter**	**Spring**
Fish				
Unidentified fish	50.0	30.8	53.8	44.5
Ophicthids	12.5	0	23.1	4.8
Syngnathids	0	0	0	4.8
Pinfish	0	0	0	0
Anchovy	6.2	0	0	0
Sea robin	0	30.8	0	0
Scad	0	0	0	0
Cusk eel	0	0	7.7	3.0
Haemulids	0	7.6	0	0
Fish larvae	31.3	30.8	15.4	42.9
Pelagic zooplankton				
Larval mantis shrmp	67.6	45.7	85.6	29.5
Amphipods	6.1	25.1	0.1	55.4
Pteropods	21.1	0	0	13.7
Isopods	5.2	0	0	0
Sergestid shrmp	0	1.0	0	0.6
Mollusk larvae	0	25.7	0	0
Chaetognath	0	2.4	0	0.1
Copeopods	0	0.1	0	0
Euphausids	0	0	14.3	0
Mysids	0	0	0	0.3
Palaemonidae	0	0	0	0.4
Crabs				
Unidentified crabs	80.0	29.4	30.5	64.3
Portunids	20.0	58.8	49.3	14.3
Calappids	0	5.9	0.7	0
Parthenopids	0	0	19.5	0
Crab mega. and zoea	0	5.9	0	21.4

An examination of gut contents by season for all stomachs (%W) indicates that while fish was present in red snapper diet in all seasons (comprising between 25 - 34%W), it did not contribute the greatest amount by weight in any season (Figure 2). The diet in summer and fall was comprised predominately of crabs (31.4%W in summer and 36.3%W in fall). Winter diet was comprised predominately of adult mantis shrimp (33.3%W) and spring of pelagic zooplankton (39.1% W). Demersal crustaceans (crabs and adult mantis shrimp) were present in all seasons, comprising approximately 50% by weight of the diet in summer, fall, and winter. During the spring, red snapper fed on high numbers of pelagic zooplankton, which were present at some level in all seasons. However, the numbers of pelagic zooplankton consumed appeared to be inversely related to numbers of demersal crustaceans eaten by red snapper.

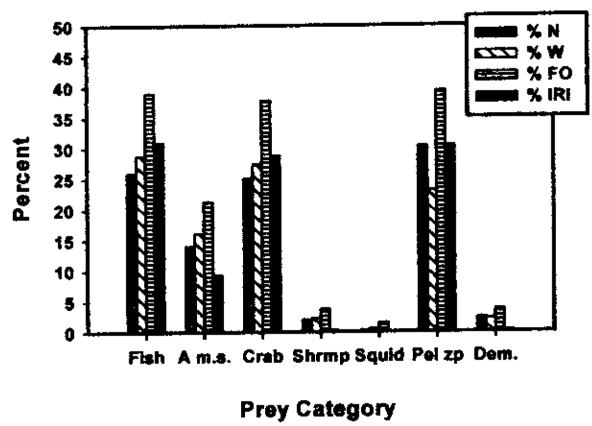

Figure 1. Indices of diet composition for all stomachs (N=268). (A.m.s. = adult mantis shrimp, Pel. zp. = pelagic zooplankton, and Dem. = demersal species)

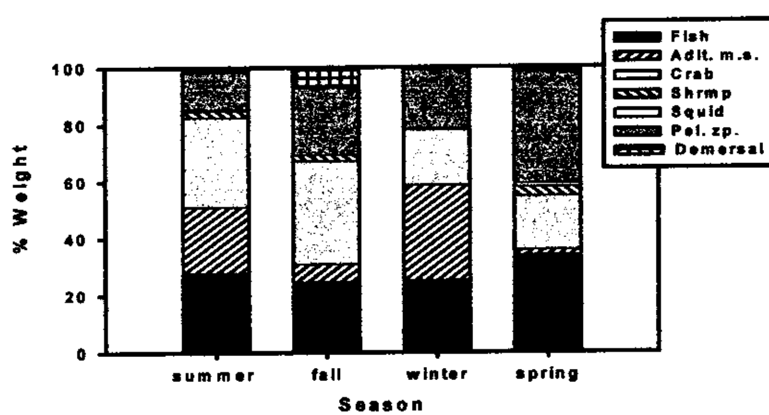

Figure 2. All stomachs (includes fish of all sizes) broken down by season by % weight (N = 268). (Adlt. m.s. = adult mantis shrimp and pel. zp. = pelagic zooplankton)

Because red snapper > 600mm FL were collected almost exclusively in summer and fish 200 - 299mm FL were primarily collected in fall and winter, we were concerned that the results described above may be confounded by red snapper size effects. To eliminate this concern, we reanalyzed the seasonal data using fish only between 300 - 499mm FL, as sufficient numbers of fish in this size range (N = 452) were collected in all seasons. Results based upon the descriptive indices for the 300 - 499mm size group were similar to results pooled over all sizes. For this sub-set, diet was comprised primarily of pelagic zooplankton according to all 4 indices (%N, %W, %FO, % IRI). The next most important diet item was fish, then crabs, followed closely by adult mantis shrimp. Compared to the larger data set pelagic zooplankton (27% W) and adult mantis shrimp (18% W) made up a larger portion of the diet. Fish again were present in all seasons, comprising between 24.5 - 31.8% by weight of red snapper diet (Figure 3). Demersal crustaceans, such as crabs and adult mantis shrimp comprised between 44% and 54% of the diet of 300 - 499 mm FL red snapper in summer, fall, and winter and, as previously noted, when demersal species decreased, they were replaced by pelagic zooplankton. However, in the data subset, adult mantis shrimp contributed the most by weight in summer (33% W) and winter (34.4%), while crabs still contributed the most in fall (37% W) and pelagic zooplankton in spring (39% W).

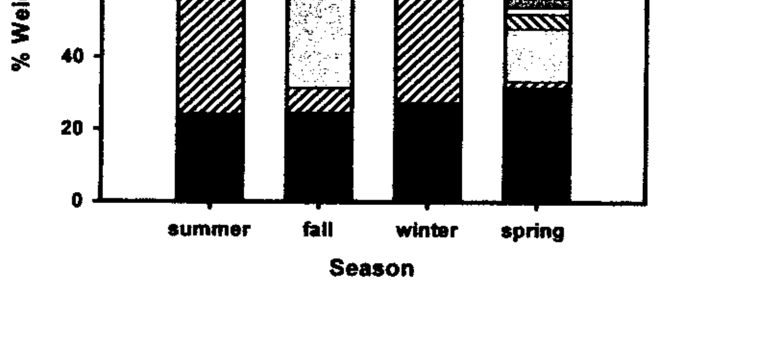

Figure 3. The 300-499mm FL fish broken down by season by % weight (N=172) (Adlt. m.s. = adult mantis shrimp and Pel. zp. = pelagic zooplankton

With seven prey categories (fish, adult mantis shrimp, crab, shrimp, squid, pelagic zooplankton, and demersal/benthic associated species) included in the test for significance for the 300 - 499mm snapper, ANOSIM found a significant difference between the weight proportion data for season (P = 0.001). Examination of the BVSTEP results reveal that these differences appear to be attributable to four influential prey types: fish, crab, adult mantis shrimp, and pelagic zooplankton. There was a 99.5% correlation between these four variables and the overall pattern in the samples. SIMPER results reveal the degree to which these four prey types contributed in different seasons (Table 2). All four categories contributed to within winter similarity, however only two or three of the prey types contributed within the other seasons. In winter, adult mantis shrimp contributed the most (45.6%) to within group similarity, followed by fish, crab, and pelagic zooplankton. In summer, adult mantis shrimp also contributed significantly (46.9%) to within season similarity, followed by fish and pelagic zooplankton. In fall, crab contributed the most to within season similarity (54.0%) followed by fish and pelagic zooplankton. Spring was typified by pelagic zooplankton and fish, with pelagic zooplankton contributing over 63% to within season similarity.

Table 2. SIMPER results of species contributions to within season similarity

Season	Species	Avg. Similarity	% Contribution	% Cum. Contribution
Summer		24.70		
	Adult mantis shrimp	10.43	46.91	46.91
	Fish	5.91	25.59	73.50
	Pelagic zooplnkton	3.76	16.91	90.41
Fall		24.94		
	Crab	13.47	54.02	54.02
	Fish	5.83	23.36	77.38
	Pelagic zooplnkton	5.13	20.58	97.97
Winter		24.70		
	Adult mantis shrimp	11.26	45.59	45.59
	Fish	7.25	29.34	74.93
	Crab	3.64	14.75	89.68
	Pelagic zooplnkton	2.55	10.32	100.0
Spring		33.17		
	Pelagic zooplnkton	20.97	63.21	63.21
	Fish	9.95	29.98	93.20

A pairwise comparison between each season revealed about the same amount of dissimilarity between each (75 - 81%), but with summer and fall diets being the most dissimilar, and winter and summer diets being the most similar (Table 3). Results further indicate that over 73% of the dissimilarity between summer and fall was contributed by crab and fish, thus they are good discriminating species for these two seasons. Winter and summer are the most similar seasons (least dissimilar) with adult mantis shrimp and fish contributing the most (81.7%) to their dissimilarity.

Table 3. SIMPER results of species contributions to between season dissimilarity (sm = summer, f = fall, w = winter, sp = spring)

Season	Species	Avg. Dis-similarity	% Contribution	% Cum. Contribution
w vs sm		75.13		
	Adlt mantis shrmp	22.31	26.69	26.69
	Fish	19.02	25.31	55.01
	Pelagic zooplktn	15.13	20.14	75.14
	Crab	14.26	18.97	94.12
sp vs f		75.30		
	Pelagic zooplktn	23.75	31.54	31.54
	Crab	20.48	27.19	58.73
	Fish	20.29	26.94	85.68
	Adlt mantis shrmp	4.15	5.51	91.19
w vs f		79.08		
	Crab	21.16	26.76	26.76
	Fish	19.22	24.31	51.07
	Adlt mantis shrmp	18.28	23.11	74.18
	Pelagic zooplktn	16.23	20.52	94.70
w vs sp		79.42		
	Pelagic zooplktn	23.58	29.69	29.69
	Fish	20.71	26.07	55.76
	Adlt mantis shrmp	17.47	21.99	77.76
	Crab	14.28	17.98	95.74
sp vs sm		79.44		
	Pelagic zooplktn	23.57	29.67	29.67
	Fish	20.09	25.29	54.96
	Adlt mantis shrmp	16.76	21.09	76.05
	Crab	12.31	15.49	91.54
sm vs f		81.04		
	Crab	20.47	25.26	25.26
	Fish	18.42	22.73	47.99
	Adlt mantis shrmp	17.64	21.77	69.76
	Pelagic zooplktn	16.97	20.93	90.69

Descriptive indices were used to further examine the SIMPER results for season, by first breaking down three of the major prey types, fish, pelagic zooplankton, and crab, into more specific prey types (Table 1). Thus, when these categories contributed to within season similarity, the specific species that contributed to the larger category can be ascertained. Fish contributed to every season's within season similarity, however the types of fish that made up this category changed seasonally. Unidentified fish was the largest category in every season (between 44.5-53.8% W), except fall where unidentified fish tied with larval fish and sea robins (all 30.7% W). Larval fish also were present in every season making up between 15.4-42.8% W. In winter, Ophicthids and cusk eels also were present. Ophicthids also contributed 12.5% by W to summer and 4.5% by W to the spring diet. Spring diet also included Syngnathids (4.7% W) and cusk eels (3.1% W).

Similarly, pelagic zooplankton also contributed to every season's within season similarity. In winter pelagic zooplankton was comprised of larval mantis shrimp (85.6% W) and euphausids (14.2% W). Larval mantis shrimp were prevalent in all seasons except spring (contributing between 45.7% - 85.6% W), which was comprised primarily of amphipods (55.4% W). Besides larval mantis shrimp, fall diet also consisted of mollusk larvae (25.6% W) and amphipods (25.1% W). In summer, pteropods, amphipods, and isopods also were observed in the diet. Crabs contributed to the within season similarity of winter and fall. In winter Portunids (49.3% W), unidentified crabs (30.5% W), and *Parthenope granulata* (19.5%) made up the crab category. Likewise in fall, the crab category was varied and was composed of Portunids (58.8% W), unidentified crabs (29.4% W), crab zooplankton (megalopae and zoea) (5.8% W), and Calappids (5.8% W).

DISCUSSION

The combined results show seasonal shifts in red snapper diet on Alabama artificial reefs. These findings are similar to most other studies of red snapper diet including another off Alabama (Bailey 1995) (Table 4). However, Bradley and Bryan (1974) found fish to be the largest category in fall, winter, and spring, but crabs contributed the most to the summer diet. In this study, fish were found in all seasons, but they were never the largest category by percent weight. Parrish (1987), in his literature review of snapper and grouper diet's stated that the principal food groups of snapper in most studies are fish and decapod crustaceans, which was consistent with the current study. Anguilliform fishes, like the Ophicthids that were found, were common and fairly abundant in the snapper diets he examined. Parrish found crabs were the second most abundant prey category, specifically with Portunid and Calappid crabs mentioned in several reports, and shrimps and other crustaceans (especially stomatopods) were the next largest diet category. He also stated that snappers often ate large plankton, which were an important part of the diet for some Lutjanid species he reviewed, specifically pteropods, which were found in our study to make up 13 - 21% W of the diet in spring and summer. Larval mantis shrimp, which were also found in the current study in large amounts in all seasons (highest in summer and winter) are thought to form large swarms in tropical waters (Morgan and Provenzano 1979). Randall (1967) found that they made up a considerable portion of the diet of reef fishes in the West Indies.

Many of the crustaceans we found in the diet are sand/mud inhabitants of the shelf. The Portunid crabs (swimming crabs such as *Portunus gibbesii*) as well as the mantis shrimp (*Squilla empusa*) inhabit mud or sand substrates (Williams 1984, Wenner and Wenner 1989, Manning and Heard 1997). Hildebrand (1954 cited in Williams 1984) found *S. empusa* to be the third most abundant crustacean in the Gulf of Mexico offshore trawl fishery only following *Penaeus* sp and *Callinectes* sp. On the Alabama shelf, *S. empusa* can be collected year-round from mud bottom areas, and are the most abundant stomatopod on the Alabama shelf (Aronson, pers. comm.). Rouse (1970) (cited in Williams 1984) stated that *P. gibbesii* was the most often collected Portunid in the Gulf. Other of the Portunids found in the stomachs, such as *P. spinicarpus*, *P. ordwayii*, and *C. sapidus* were also cited by Williams (1984) as being found either on mud bottoms or a variety of bottoms, but not on reefs. Most of the crustaceans we found in the stomachs are associated with mud bottom and are abundant in the Gulf.

Table 4. Literature review of red snapper diet studies relevant to the present study.

Source	Location of study	Fish size	# stomachs examined (# w/ food)	Description of Results
Moseley 1966			712 (187)	
	Louisiana	juvenile	(28)	30% FO of crustaceans, another sample had 60% *Squilla* (night sample), unidentified fish made up 27% of this sample
		adult	(46)	44% fish in one sample, 80% fish and rest crustaceans in another
	Texas	juvenile	(45)	41% crustaceans in one sample, 89% crustaceans in another
		adult	(68)	Fish dominated the diet in all samples (40-69%), crustaceans were present in small numbers
Bradley and Bryan 1974	Texas	juvenile and sub-adult	575 (258)	Summer ate shrimp and crabs, spring and winter ate squid. Mantis shrimp made up portion of diet in summer, winter had most varied diet
		adult	1139 (190)	Primarily ate fish, but in fall and winter ate more crustaceans. In spring 13% of diet was tunicates. Summer had largest variety and winter the smallest variety
Bailey 1995	Alabama	330-691 mm TL	98	Principal prey items in summer were rock shrimp and crabs, also ate some eels and unid. fish
Lee 1998	Alabama	10-280mm SL	1652 (792)	Reef associated red snapper fed on reef assoc. species; fish (*Halichoeres* sp., *Serranus* sp. and *Centropristis* sp.) and shrimp (*Lysmata* sp. and *Synalpheus* sp.) and squid

The seasonal trends we observed differed slightly in the reduced (300 - 499mm FL) data set. Differences such as predominance by crabs in summer in the complete data set compared to more mantis shrimp in the smaller data set, were probably due to size differences of red snapper. For example, many of the red snapper > 600 mm FL collected in summer contained crabs, thus influencing the summer results. Otherwise results derived from the data sub-set were similar to all size-classes combined.

Red snapper foraging does not appear to be associated with the reef structure, and they may be gaining little nutritional support from the reef. Rather, red snapper diet was focused primarily on benthic organisms, such as Portunid crabs, adult mantis shrimp, Ophicthid fishes, sea robins, and cusk eels. These organisms are associated with mud or sand substrates, thus foraging is probably occurring more over the nearby bottom than over the reef itself. The prey species that are abundant on Alabama artificial reefs, such as tomtates, sea basses, and grunts (Andy Strelcheck, pers. comm.), were not found in the diets of red snapper in this study, although they did eat in smaller numbers some organisms that are associated with structure such as Syngnathids (pipe fish and sea horses) and pinfish. Starck (1968) also lists species that have an affinity to reefs, such as lizardfish, gobies, and wrasses, which would be expected in the diet, but these fish were not found in the stomachs of the red snapper we sampled. Thus, we infer that red snapper are selectively or preferentially feeding on non-reef habitat.

Other studies of red snapper diet describe foraging habits that support this claim. Moseley (1966), in a red snapper diet study off of Texas and Louisiana, found that red snapper do not always feed on reef associated species. He stated that "Based on food habits, there seems to be no particular reason why red snappers should congregate on reefs or rocky areas…". Parrish (1987) states that snapper probably remain within a few meters of the bottom because most of their prey needs to be captured from the substrate. He classifies *L. campechanus* as an intermediate depth feeder, which means they forage anywhere from relatively shallow water up to 100 meters. He states that such feeders probably forage widely from shelter over soft bottom to gain food, or either forage by "patrolling up to several meters off the bottom for nektonic prey as well as periodically foraging on substrate for fully benthic prey." Supporting this idea, this study found that snapper consumed some organisms that reside higher in the water column, such as larval mantis shrimp, fish larvae, amphipods, and pteropods, and other assorted pelagic zooplankton as well as mud associated species. Davis and Birdsong (1973) describe coral reefs and other "habitat interfaces" as rich in diversity saying they "represent 'cross roads' between foraging and refuge areas". Artificial reefs can be seen in much the same context, as snapper seem to supply their energetic demands from habitats other than reefs. It is still unclear if red snapper are simply leaving a reef to forage on nearby mud bottom, or if they are feeding during their transit between reefs, or both. In contrast, Lee (1998) found 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 he examined snapper smaller (100 – 230 mm standard length) than what we studied). Perhaps smaller red snapper, such as the ones Lee examined, are more reef dependent than their larger counterparts.

There has been debate about how to analyze diet data. Indices alone are inadequate for making statistical comparisons (Ferry and Cailliet 1996). The fact that diet data is usually proportional and is dominated by zero values has presented problems. Multivariate techniques have been recommended, but the data often does not meet the heterogeneity of variance assumption (Ferry and Cailliet 1996). In the recent past, nonparametric techniques have become the norm in diet studies. However, some of these techniques still fall short of adequate quantitative analyses. The PRIMER statistical package (Clarke and Gorley 2001) allows multivariate analyses with very few assumptions about the data (ANOSIM), as well as determination of which prey categories or which species are responsible for groupings in the data found *a posteriori* or identified *a priori* (MDS, SIMPER, BIOENV, and BVSTEP). Thus, we support that it is widely applicable for many different types of diet analysis, such as comparing diets of numerous species found in concert (for example see Deudero 2001) or analyzing the diet of a single species, such as in the present study. PRIMER allows for hypothesis testing of the entire community at one time, a technique often impossible in diet studies in the past.

The data from this diet study will be used along with information on red snapper diel feeding patterns, and the caloric content of the prey species to present a complete picture of the foraging habits of red snapper off of Alabama. That data will then be used along with information on growth rates of snapper on artificial reefs as well as metabolism values in a bioenergetics model to obtain a first order estimate of the prey demand of a red snapper population on a reef.

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