Feeding ecology of red snapper
Lutjanus campechanus in the northern Gulf of Mexico

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ABSTRACT: We used stable isotopes and stomach content analyses to describe diet of red snapper *Lutjanus campechanus* in the northern Gulf of Mexico (GOM). Approximately 1000 fish were collected over 2 yr to test possible effects of ontogeny, habitat, and a non-trawl artificial reef permit area on red snapper diets. Stable isotopes of carbon (δ^{13}C), nitrogen (δ^{15}N), and sulfur (δ^{34}S) were measured in both red snapper and potential primary producers. Ontogenetic shifts in diet occurred with increasing red snapper size-at-age, resulting in higher δ^{13}C and nitrogen δ^{15}N and lower δ^{34}S in larger fish. Stomach content results supported ontogenetic shifts in diet by showing a change in diet from zooplankton, mysid shrimp, and squid for juvenile red snapper (ages 0 to 1) to diets dominated by benthic crustaceans and fishes for adults (ages 2+). Habitat-specific differences in isotopes and stomach contents of similarly sized fish were identified; however, feeding differences appeared to reflect ontogeny more than habitat type. In addition, seasonal differences, both in δ^{13}C and in prey identified from stomach contents, were detected, but were minimal. Red snapper from areas outside a single non-trawl reef permit area had higher δ^{15}N and lower δ^{34}S values than for conspecifics collected inside the non-trawl reef permit area. This study highlights the use of stable isotopes in detecting red snapper feeding differences inside and outside of an artificial reef permit area in the northern GOM, but additional studies are needed to verify if similar trends are present in other areas.

KEY WORDS: Red snapper · Feeding · Stomach contents · Stable isotopes · Ontogeny · Habitat · Artificial reef permit area

INTRODUCTION

Red snapper *Lutjanus campechanus* are opportunistic feeders that consume a suite of different prey such as fishes, benthic crustaceans, squids, and pelagic zooplankton (McCawley et al. 2006). Juvenile diets are composed primarily of shrimp and other crustaceans; fishes, squid, pelagic zooplankton, and other benthic crustaceans are consumed by adults (Szedlmayer & Lee 2004, McCawley et al. 2006). Studies have suggested that adult red snapper feed adjacent to reefs over sand and mud bottoms (Bradley & Bryan 1975, McCawley et al. 2006). However, other studies focusing on red snapper from 70 to 399 mm standard length

(SL) have reported diets that consist of reef-associated prey (Ouzts & Szedlmayer 2003, Szedlmayer & Lee 2004). To date, no studies have attempted to evaluate red snapper feeding on low-relief natural reefs and shell-rubble features on the northern Gulf of Mexico (GOM) shelf.

The combination of stomach content and stable isotope analyses has been used successfully to interpret feeding studies in fishes (Cocheret de la Morinière et al. 2003). Stomach content analysis provides information about feeding based upon recently ingested prey, thereby serving as an indicator of short-term (hours to days) feeding habits (Bowen 1996). However, problems associated with prey identification,

regurgitation, and the large number of samples necessary to investigate feeding patterns means additional techniques are needed to understand trophic dynamics.

Naturally occurring stable isotopes have been widely used in feeding ecology studies (Peterson & Fry 1987, Litvin & Weinstein 2004). In contrast to stomach contents, stable isotopes in animal tissues are derived from assimilated food; thus, they are indicative of long-term (weeks to months) feeding patterns. Comparisons of isotope values of carbon, nitrogen, and sulfur between consumers and their prey provide information on nutrient sources and trophic relationships. Carbon isotope ($\delta^{13}C$) values of predators directly reflect those of their prey, changing only 0.5 to 1.5‰ per trophic level; thus, they are useful for providing information on organic source materials (Fry & Sherr 1984, Sweeting et al. 2007). Nitrogen isotope values ($\delta^{15}N$) increase approximately 3‰ per trophic level between the animal and its diet, and are used to infer trophic relationships (Peterson & Fry 1987, Rooker et al. 2006). Sulfur isotope values ($\delta^{34}S$) also are useful for clarifying feeding habits, because they change only slightly with increasing trophic level and are useful for identifying food sources (Peterson & Fry 1987). Thus, the combination of stomach content and stable isotope analyses can provide increased insight into dietary changes and feeding habits for red snapper.

The impacts of some fishing activities on ecosystems are known to be negative (NRC 2002), but few studies have addressed the impact on the feeding patterns of commercially and recreationally important species (Kaiser & Spencer 1994). Here, we use an artificial reef permit area to investigate if feeding differences exist in red snapper collected inside and outside of the area. Protected non-trawl areas are rare in the northern GOM, and it was not possible to include multiple non-trawl areas in this study. Our comparisons are limited to one habitat-specific location inside and outside the permit area, to provide an initial test of the use of stable isotopes as tools in detecting feeding differences that may be attributed to trawling activities. The goals of the present study were to investigate the relative roles of ontogeny, habitat, and the presence of a non-trawl artificial reef permit area on the feeding habits of red snapper. The specific research questions in the study were (1) Do feeding habits of red snapper change with respect to ontogeny and, if so, do the stable isotope values change abruptly or gradually with respect to the associated habitat shifts? (2) Can diets of red snapper be used to infer possible mechanisms of red snapper habitat shifts? (3) Can stable isotopes be used to detect feeding differences of red snapper in a trawl versus non-trawl area?

MATERIALS AND METHODS

Study site and sample collections. Red snapper *Lutjanus campechanus* were collected seasonally (winter, spring, summer, fall) during 2004 and 2005 over 4 distinct habitat types: sand, low relief shell-rubble (<1 m vertical relief, <40% $CaCO_3$,), high relief shell-rubble (1 to 3 m vertical relief, >40% $CaCO_3$), and natural reefs (>2 m vertical relief). Study sites were located on the northern GOM continental shelf off Alabama (Fig. 1). Random samples were obtained within each habitat type enclosed in an artificial reef permit area and outside of the reef permit area. Areas inside and outside the reef permit area were surveyed with digital sidescan sonar and boxcore sediment analysis to verify that similar habitat types existed within each area and to verify that no artificial reefs existed within our study areas to confound comparisons (Dufrene 2005, Patterson et al. 2005). Results indicated that similar habitat types inside and outside the reef permit area contained similar grain size, organic content, and calcium carbonate content, and no artificial reefs existed over our
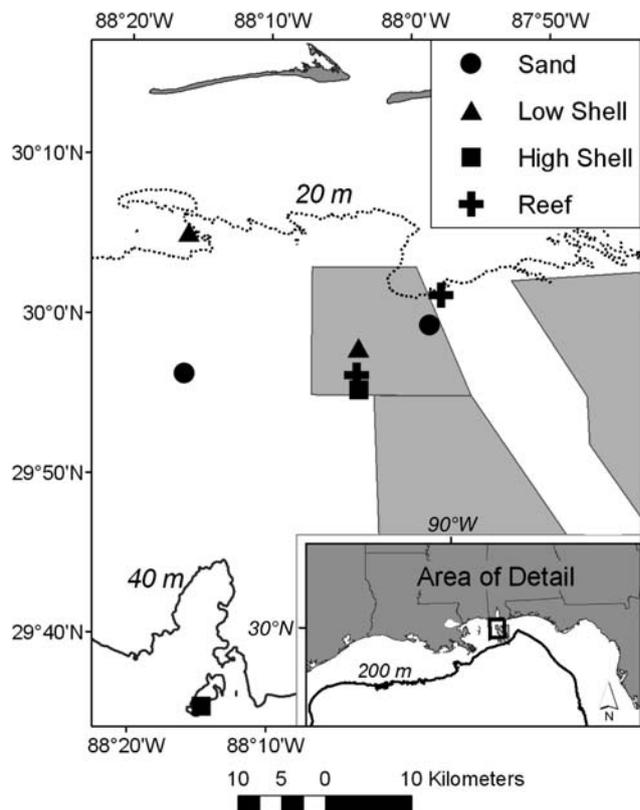
Fig. 1. Study site locations in the north central Gulf of Mexico off Alabama. The 20 and 40 m depth contours are shown, with the 200 m depth contour representing the shelf edge. Enclosed shaded regions indicate the artificial reef permit area used as the de facto non-trawl area

study areas (Dufrene 2005). The artificial reef permit area comparison was limited to only one of each habitat type inside and outside the permit area; however, each site was 8 km² in size. We used this area as an initial test to assess the impacts of trawling, as this artificial reef permit area has not been trawled since 1987 and therefore served as a de facto non-trawl area. Wells (2007) showed sufficient trawling effort occurred over the study area outside the permit area to sweep the seafloor at least once per year, and shrimp trawl effort data are concentrated outside of the reef permit area (NRC 2002). Link (1997) has suggested these reef permit areas have added a significant amount of untrawlable area to the northern GOM shelf.

Red snapper were collected with both otter trawls and fish traps over each habitat type. Trawl gear included a single 12.8 m wide net with 4 cm mesh size and a 0.7 cm cod end lining and was towed at approximately 4.6 km h^{-1} for 10 min. Three replicate trawl tows were performed at each site. Traps were deployed adjacent to the trawl locations and were used due to the difficulty in trawling directly over the natural reef structure and to collect larger red snapper that are relatively invulnerable to trawling. A chevron trap (dimensions: 150 cm width × 180 cm length × 60 cm height; opening: 10 cm × 5 cm; mesh: 3.8 cm plastic-coated wire) designed to capture large individuals and 2 small fish traps (dimensions: 64 cm width × 60 cm length × 43 cm height; mesh: 2.2 cm plastic-coated wire) that targeted juveniles were deployed at a fixed location for a 2 h period. Traps were baited with a single Atlantic menhaden *Brevoortia tyrannus* inside a non-accessible bait container; the bait was replaced after each deployment. All sampling was performed during daylight hours.

Red snapper larvae were collected in the study region during a 2002 plankton survey using a 1 × 1.5 m multiple opening/closing net and environmental sensing system (MOCNESS) or with a Tucker trawl with 335 µm mesh towed obliquely from near-bottom to surface in 5 min intervals. Particulate organic matter (POM) was used as a proxy for phytoplankton and was collected by filtering seawater from the sampling area with 47 mm GF/F filters (precombusted for 1 h at 450°C), with an effective pore size of 0.8 µm. In addition, benthic microalgae (BMA) (e.g. diatoms) were collected over the same time and area using a benthic grab sampler. BMA were isolated with a modification of the vertical migration technique (Eaton & Moss 1966), with lens tissue replaced by Nytex mesh, and identified to confirm that sufficient numbers were collected for isotopic analysis. Visual assessment showed benthic diatom species were successfully isolated and dominated the samples. Pennate diatoms, including species from the genera *Tryblionella*, *Pinnularia*, *Nit-*

zschia, and *Navicula*, were identified from the samples collected.

Stomach content and stable isotope procedures. All red snapper were immediately frozen before being transported to the laboratory for storage at –80°C. In the laboratory, fish were measured to the nearest millimeter total length (TL) and weighed to the nearest gram. Stomachs were dissected, weighed to the nearest gram, opened, and fixed in 10% formalin for 48 h. Stomachs were then preserved in 70% ethyl alcohol until analyzed for stomach contents. All items in the gut were identified to the lowest possible taxon, sorted, counted, dried at 60°C for 24 h, and weighed to the nearest 0.0001 g.

Red snapper epaxial muscle tissue was dissected from the left side and dried in a Yamato DX 600 drying oven at 60°C for 24 h or until the sample reached a constant weight, after which the tissue was homogenized with a ball-mill grinder (Dentsply International). Lipids were not removed from muscle tissue because C/N ratios for muscle sample were low (<4) across the size spectrum of fish, indicating little lipid content and little influence of lipids on muscle $\delta^{13}C$ values (Post et al. 2007). Then, 4 to 5 mg of ground tissue was placed in a tin boat with 10 mg of precombusted vanadium pentoxide (V_2O_5). Six small hole punches were made from each POM and BMA filter and were placed in a tin boat. The isotopic composition of carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$), and sulfur ($\delta^{34}S$) were determined from the tissue and plant materials with a Finnigan MAT Delta-Plus continuous-flow stable isotope mass spectrometer attached to a Carlo Erba elemental analyzer at the Louisiana State University (Fry 2007). Isotopic values are reported relative to Vienna PeeDee belemnite for carbon, atmospheric N_2 for nitrogen, and Vienna Canyon Diablo troilite for sulfur with the standard equation:

$$\delta^{13}C,\ \delta^{15}N,\ \text{or}\ \delta^{34}S\ (‰)\ =\ (R_{sample}/R_{standard} - 1) \times 1000$$

where R represents the ratio of the heavy to light isotope ($^{13}C/^{12}C$, $^{15}N/^{14}N$, $^{34}S/^{32}S$). Stable isotopes were analyzed for a subset of fish collected over all habitats in 2004 (n = 298), 18 red snapper larvae, and for POM (n = 3) and BMA (n = 2) samples.

Data analysis. Differences in red snapper feeding were investigated by age, habitat type, presence of reef permit area, and season. Red snapper were grouped into 5 age bins based upon a von Bertalanffy size-at-age model (Wells 2007). These included age 0 (≤100 mm TL), age 0.5+ (101 to 179 mm TL), age 1 (180 to 279 mm TL), age 2 (280 to 336 mm TL), and age 3+ (≥337 mm TL). Differences between years were investigated within size × habitat × presence of reef permit area × season; no significant year differences were detected; data were therefore combined to increase power.

Ten prey categories were used to analyze stomach content data: amphipods, copepods, crabs, euphausiids, fish, mysids, polychaetes, shrimp, squid, and stomatopods (mantis shrimp). Prey was identified to genus and species if possible. Importance of prey type was analyzed by 3 methods: frequency of occurrence, percent composition by number, and percent composition by weight (Bowen 1996). The percent composition by weight was the primary method chosen to analyze stomach content data, because this metric is commonly used to assess the nutritional contribution of prey type (Rooker 1995, Bowen 1996). In addition, a percent index of relative importance (%IRI) was computed that incorporates both the numerical and weight-based metrics into the prey contribution to red snapper diet:

$$\text{IRI} = (\% \text{ number} + \% \text{ weight}) \times \% \text{ frequency of occurrence}$$

$$\%\text{IRI} = (\text{IRI}_{\text{prey item}} / \text{IRI}_{\text{total}}) \times 100$$

Percent composition by weight of each prey category was computed for each individual. Percent composition for all prey types then was square root transformed to reduce the importance of the most abundant prey. Differences among factors were investigated with the analysis of similarity (ANOSIM) procedure in Plymouth Routines in Multivariate Ecological Research (PRIMER; Clarke & Warwick 2001). The similarity percentages (SIMPER) procedure was used to assess which prey categories were the most important in discriminating among levels of age, habitat, presence of reef permit area, and seasonal feeding differences (Clarke & Warwick 2001).

Stable isotopes of red snapper were compared with multiple analysis of covariance (MANCOVA) in SAS (SAS Institute 2006), with carbon, nitrogen, and sulfur as the dependent variables (Litvin & Weinstein 2004). Independent variables included habitat type, presence of reef permit area, and season, with length as the covariate to control for size-related differences in stable isotope levels in red snapper tissue. Univariate analysis of covariance (ANCOVA) models were used to identify individual dependent variable responses.

The potential carbon contribution of planktonic sources (POM) versus benthic sources (BMA) to red snapper diets was estimated with the 2-source mixing model of Fredriksen (2003) and Rooker et al. (2006), using newly settled red snapper as the planktonic end member ($\delta^{15}N = 11.28$; $\delta^{13}C = -19.08$) and large adults as the benthic end member ($\delta^{15}N = 14.77$; $\delta^{13}C = -16.01$):

$$\%C_{\text{benthic}} = \frac{(\delta^{13}C_{\text{consumer}} - \delta^{13}C_{\text{planktonic}} - I)}{\delta^{13}C_{\text{benthic}} - \delta^{13}C_{\text{planktonic}}} \times 100$$

where I is the average fractionation value of $\delta^{13}C$ per trophic level. A carbon trophic enrichment factor of 1.0‰ was used; thus, I was equal to the estimated trophic level (Rooker et al. 2006). Red snapper trophic level was calculated following Hobson & Welch (1992):

$$\text{Trophic level} = 2.5 + (\delta^{15}N_{\text{consumer}} - 13.03) / 3$$

where 13.03 was the average $\delta^{15}N$ value of the end members and 3.0‰ was used as the $\delta^{15}N$ enrichment value per trophic level (Rooker et al. 2006).

Prey habitat selection. Habitat use by the most abundant prey (fish and crabs) found in sub-adult (age 1) and adult (age 2+) red snapper stomachs was characterized to investigate whether habitat-specific prey resources were unique to red snapper collected from that habitat. Included was only the percentage of prey identified to family or greater; thus, general fish or crab material was not included in calculations. Prey habitats were classified according to previous studies that have investigated red snapper–prey habitat associations (Szedlmayer & Lee 2004, McCawley et al. 2006). We acknowledge that prey are mobile and are not limited to one exclusive habitat; thus, our goal was to provide a general habitat affiliation of each prey type. Fish prey in the families Bothidae, Ogcocephalidae, Sparidae, Synodontidae, and Triglidae were classified as sand and mud associated. Open water prey fishes included only Engraulidae, and reef-associated prey fishes included both Haemulidae and Serranidae. Crab prey items in the families Calappidae and Portunidae were classified as sand and mud associated, while families Porcellanidae, Pseudorhombilidae, Raninidae, and Xanthidae were reef associated.

RESULTS

A total of 936 red snapper *Lutjanus campechanus* was analyzed for stomach contents; 795 red snapper (85%) contained prey items and were used for statistical comparisons. In addition, 316 red snapper were analyzed for stable isotope composition. A large size and age range was analyzed; post-settled red snapper sizes ranged from 23 to 435 mm TL, and ages ranged between 28 d and 5 yr. Pre-settled red snapper larvae were between 3 and 18 mm TL.

Ontogenetic effects

Red snapper displayed ontogenetic shifts in their diets from the planktonic larval stage, to settlement and into juvenile and adult stages. A general trend of increasing crab and fish consumption with a corresponding decrease in squid and mysid shrimp con-

Table 1. *Lutjanus campechanus.* Percent index of relative importance (%IRI) of the most important prey groups in red snapper diets, by age class

	Amphipod	Copepod	Euphausiid	Mysid	Crab	Shrimp	Mantis shrimp	Fish	Polychaete	Squid
Age 0	0.24	22.16	0.13	53.40	1.25	0.36	0.02	4.53	0.00	17.91
Age 0.5+	0.30	0.66	4.17	12.93	5.25	5.02	0.31	26.42	0.04	44.91
Age 1	0.01	0.00	0.37	0.46	6.60	3.90	0.77	72.18	0.05	15.65
Age 2	0.00	0.00	0.00	0.09	5.27	2.76	2.04	89.85	0.00	0.00
Age 3+	0.03	0.00	0.00	0.00	25.02	0.00	0.05	73.06	0.00	1.84

sumption was observed in red snapper stomachs with increasing age (Table 1, Fig. 2). Age 0 red snapper fed primarily upon mysid shrimp, squid, and copepods, and began consuming euphausiids by age 0.5+. Age 1 red snapper primarily ate fish, crabs, and squid, while age 2 fish consumed mantis shrimp, fish, crabs, and shrimp. Age 3+ red snapper primarily consumed fish and crabs.

Red snapper stomach contents and %IRI corresponded well with stable isotope trends and also showed an ontogenetic dietary shift. Red snapper had higher $\delta^{13}C$ and $\delta^{15}N$ values, while $\delta^{34}S$ values decreased with increasing age (Fig. 3). In addition, stable isotope values changed abruptly between larval and early juvenile stages (Fig. 4), with a gradual change during later juvenile and adult stages (Fig. 3). Pre-settled red snapper initially decreased in $\delta^{15}N$, but then began to increase in $\delta^{15}N$ by 10 mm TL (Fig. 4b). Red snapper $\delta^{15}N$ increased by 6.6‰ from a low of 8.2‰ as larvae, to 11.3‰ at the early juvenile stage (age 0), and to 14.8‰ at sub-adult (age 1) and adult
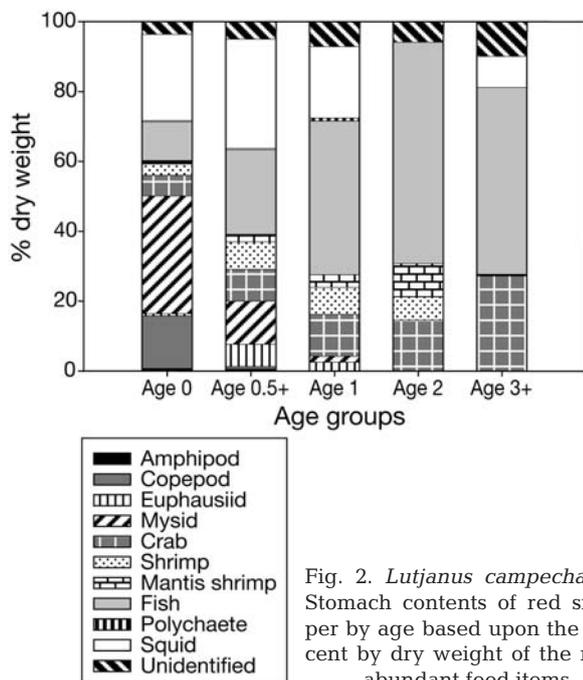
Fig. 2. *Lutjanus campechanus.* Stomach contents of red snapper by age based upon the percent by dry weight of the most abundant food items
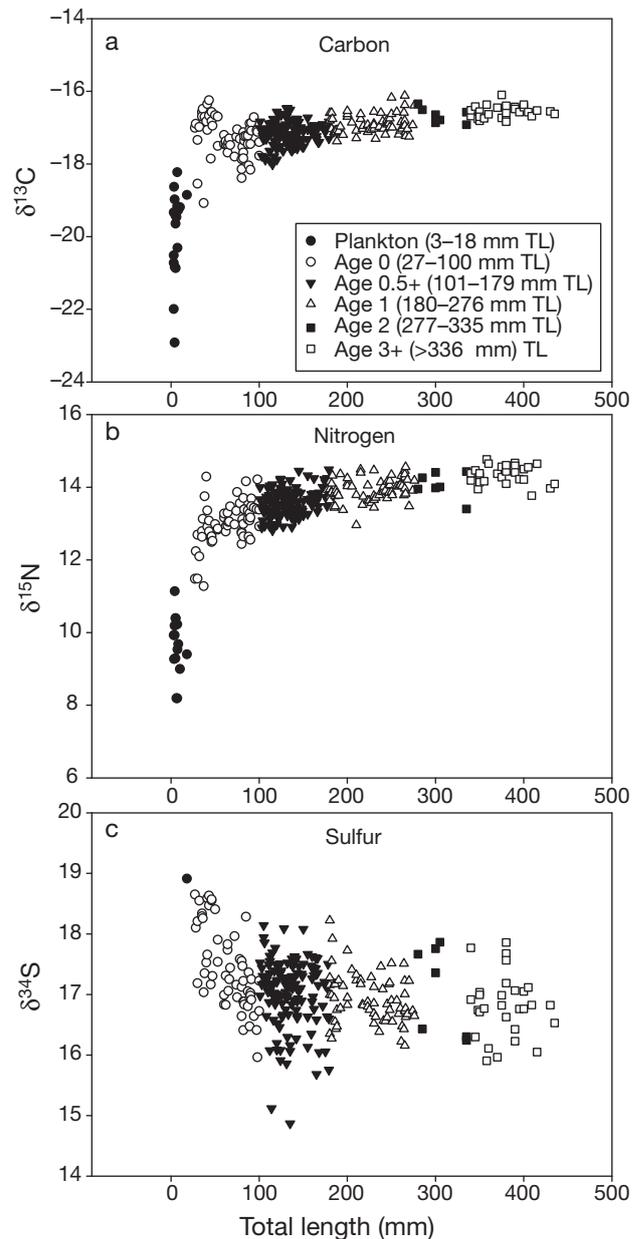
Fig. 3. *Lutjanus campechanus.* (a) Carbon ($\delta^{13}C$), (b) nitrogen ($\delta^{15}N$), and (c) sulfur ($\delta^{34}S$) as a function of red snapper total length (TL). Specific age groups of red snapper are shown based upon a von Bertalanffy size-at-age model
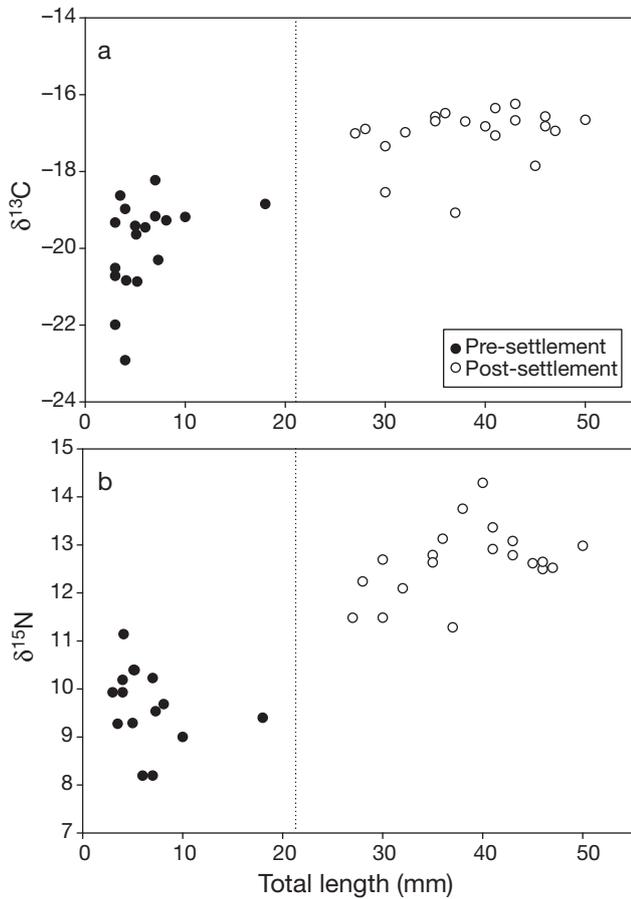
Fig. 4. *Lutjanus campechanus.* (a) Carbon ($\delta^{13}C$) and (b) nitrogen ($\delta^{15}N$) as a function of both pre- and post-settled red snapper total length (TL), with vertical dotted line showing the size-at-settlement (~21 mm TL)

stages (age 2+) (Fig. 3b). Red snapper increased in $\delta^{13}C$ by approximately 4‰ from the small larvae (–22.9‰) to recently settled fish (–19.1‰) (Fig. 4a), and further by 3‰ from recently settled to ages 2+ (–16.1‰)

(Fig. 3a). Sulfur isotope values were more variable, but decreased by almost 3‰ from recent settlement (18.7‰) to ages 2+ (16.0‰) (Fig. 3c). Sulfur isotope values were not determined for red snapper <18 mm TL, due to the limited amount of tissue that was available for analysis.

Habitat effects

Habitat-specific feeding differences were less pronounced than ontogenetic feeding differences of red snapper (Table 2, Fig. 5). Overall, 71.4% of all pairwise differences were significantly different when analyzing red snapper stomach contents of different age groups collected over similar habitats (Table 2). In contrast, only 44.6% of all pairwise differences were significantly different for similar aged red snapper collected over different habitats (Table 2). Stomach contents of red snapper residing on different habitats showed increasingly similar diets with age, and significant differences were observed only in age 0, age 0.5+, and age 1 fish ($p < 0.01$) (Fig. 5). Dominance of both fish and crab material in the stomachs of age 2 and age 3+ red snapper indicated similar diets for these larger fish, with no statistical differences (age 2: $p = 0.051$, age 3+: $p = 0.457$). Results of the SIMPER analysis indicated mysid shrimp, fish, and squid were the most important prey items differentiating habitat-specific diets of age 0, age 0.5+, and age 1 red snapper, but no consistent habitat-specific preferences for prey were observed across ages (Fig. 5).

Red snapper $\delta^{13}C$ and $\delta^{15}N$ stable isotope values varied significantly across habitats (Table 3). The most distinct separation among stable isotope values was found at the youngest age analyzed (Table 4). Among age 0 red snapper, those collected over sand had the most enriched $\delta^{13}C$ and $\delta^{34}S$, along with depleted $\delta^{15}N$ (Table 4). In contrast, age 0 red snapper collected over

Table 2. *Lutjanus campechanus.* Percent of pairwise comparisons of red snapper stomach contents that were significantly different ($p < 0.05$), based upon ontogeny and habitat. IR: inside artificial reef permit area; OR: outside artificial reef permit area. Ontogenetic comparisons were made among age 0, age 0.5+, and age 1 groups over the same habitat. Habitat comparisons were made among different habitats over similar age groups. Age 2 and 3+ groups were not included due to lack of differences. NA: not applicable due to low sample size

| | | Sand | | Low shell | | High shell | | Reef | | Total |
		OR	IR	OR	IR	OR	IR	OR	IR	average
Age 0	Ontogeny	100	100	100	50	NA	50	100	100	85.7
	Habitat	50	33	100	33	NA	33	50	0	42.7
Age 0.5+	Ontogeny	50	100	50	0	NA	50	100	100	64.3
	Habitat	50	100	50	67	NA	67	0	100	62.0
Age 1	Ontogeny	50	100	50	50	NA	0	100	100	64.3
	Habitat	0	67	33	33	0	33	33	0	24.9
Total	Ontogeny	66.7	100	66.7	33.3	NA	33.3	100	100	71.4
Average	Habitat	33.3	66.7	61.0	44.3	NA	44.3	29.3	33.3	44.6
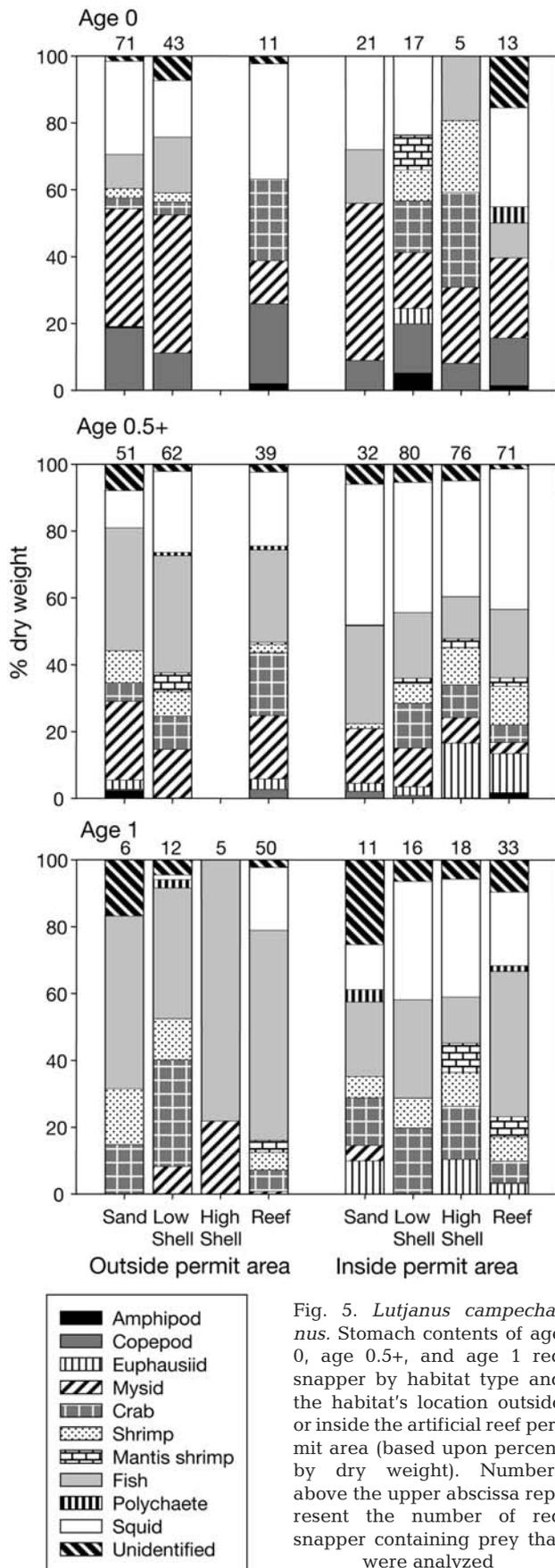
Fig. 5. *Lutjanus campechanus.* Stomach contents of age 0, age 0.5+, and age 1 red snapper by habitat type and the habitat's location outside or inside the artificial reef permit area (based upon percent by dry weight). Numbers above the upper abscissa represent the number of red snapper containing prey that were analyzed

Table 3. Multiple analysis of covariance and univariate analyses of covariance models for each factor adjusted for length (covariate: length). Pillai's trace statistic represents calculated p-values

Factor	df	*F*-value	p-value
Multiple analysis of covariance (C, N, & S)			
Habitat	9, 798	3.25	0.0007
Trawl	3, 264	5.96	0.0006
Season	9, 798	11.45	0.0001
Analysis of covariance: habitat			
$\delta^{13}C$	3, 266	3.95	0.0089
$\delta^{15}N$	3, 266	3.64	0.0134
$\delta^{34}S$	3, 266	0.31	0.8161
Analysis of covariance: artificial reef permit area			
$\delta^{13}C$	1, 266	11.94	0.0006
$\delta^{15}N$	1, 266	12.14	0.0007
$\delta^{34}S$	1, 266	6.97	0.0088
Analysis of covariance: season			
$\delta^{13}C$	3, 266	4.93	0.0024
$\delta^{15}N$	3, 266	2.47	0.0621
$\delta^{34}S$	3, 266	2.26	0.0821

reef had the most depleted $\delta^{13}C$ and $\delta^{34}S$, while $\delta^{15}N$ was highest for age 0 red snapper on low shell-rubble (Table 4). Red snapper collected on low shell-rubble continued to exhibit the most enriched $\delta^{15}N$ for both age 0.5+ and age 1 fish compared to similar-sized fish collected over different habitats. Three of the 4 age groups (age 0, age 1, age 2, age 3+) collected over the reef exhibited depleted $\delta^{13}C$. Lastly, a general trend of increasing uniformity of stable isotope values was observed with increasing red snapper age (Fig. 3, Table 4).

Artificial reef permit area effects

Stomach contents of red snapper collected from inside and outside the artificial reef permit area were both age and habitat specific. Age 0 red snapper collected over low shell-rubble within the permit area had different diets than individuals collected over low shell-rubble outside the permit area (p = 0.043). More amphipods, euphausiids, crabs, and mantis shrimp were found in the diets of fish collected within the permit area (Fig. 5). Older red snapper (age 2 and age 3+) showed no difference in stomach contents; in addition, red snapper had similar diets over sand habitats inside and outside the reef permit area, regardless of age.

Significant effects for $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ were found in red snapper collected between similar habitats inside and outside the reef permit area (Table 3). Several comparisons showed significant differences in average isotopic values. Specifically, red snapper $\delta^{13}C$ was higher outside the reef permit area (–17.0 ±

Table 4. *Lutjanus campechanus*. Habitat-specific stable isotope values (least square means ± 1 SE) of red snapper by age class. NA: not applicable due to no red snapper for the habitat-specific age class

Age group	Sand	Low shell	High shell	Reef
δ¹³C				
0	−17.12 (0.09)	−17.20 (0.11)	NA	−17.63 (0.13)
0.5+	−17.08 (0.04)	−17.01 (0.04)	−17.32 (0.10)	−17.23 (0.04)
1	−16.88 (0.10)	−16.79 (0.11)	−16.74 (0.10)	−16.98 (0.03)
2	NA	−16.64 (0.00)	−16.67 (0.16)	−16.68 (0.13)
3+	NA	NA	−16.23 (0.13)	−16.59 (0.03)
δ¹⁵N				
0	12.92 (0.11)	13.44 (0.13)	NA	12.93 (0.14)
0.5+	13.60 (0.08)	13.78 (0.05)	13.38 (0.07)	13.54 (0.05)
1	13.88 (0.19)	14.15 (0.12)	14.08 (0.09)	13.89 (0.04)
2	NA	13.98 (0.00)	14.12 (0.14)	14.03 (0.32)
3+	NA	NA	14.66 (0.10)	14.33 (0.05)
δ³⁴S				
0	17.67 (0.14)	17.19 (0.14)	NA	17.12 (0.09)
0.5+	17.02 (0.09)	16.83 (0.11)	17.24 (0.11)	17.07 (0.07)
1	17.07 (0.09)	17.33 (0.45)	17.24 (0.12)	16.79 (0.05)
2	NA	17.76 (0.00)	17.63 (0.15)	16.33 (0.06)
3+	NA	NA	16.36 (0.46)	16.85 (0.10)

0.05‰ SE) versus inside (−17.2 ± 0.03‰ SE) the area; however, habitat-specific differences were not significant (p > 0.05) (Fig. 6a). Red snapper $\delta^{15}N$ values were enriched over all habitats outside the reef permit area (13.9 ± 0.06‰ SE) when compared to similar habitats inside the permit area (13.6 ± 0.04‰ SE) (Fig. 6b). Red snapper occupying sand outside the reef permit area had significantly higher values for $\delta^{15}N$ (14.3‰) than conspecifics on sand inside the reef permit area (13.6‰) (p = 0.0122). Lastly, $\delta^{34}S$ values were depleted in fish collected over habitats outside (16.6 ± 0.07‰ SE) relative to inside (17.2 ± 0.05‰ SE) the reef permit area. Specifically, $\delta^{34}S$ values in red snapper collected over sand (15.9‰) and low shell-rubble (16.6‰) outside the reef permit area were lower than those collected over similar sand (17.1‰) and low shell-rubble (17.5‰) habitats within the non-trawl reef permit area (sand: p < 0.0001, shell: p = 0.0005) (Fig. 6c).

Seasonal effects

Seasonal differences in stomach contents were most common among the youngest age groups, and no differences were detected for older red snapper (age 2 and age 3+). Age 0 red snapper showed differences among all seasons (p < 0.01), except between winter and fall (p = 0.270), when mysid shrimp, fish, squid, and copepods (in descending order of importance) were the most important prey items in red snapper

winter diets. Squid and copepods were the most important prey items in age 0 red snapper diets during the spring and summer, and both mysid shrimp and squid contributed most to the red snapper diets in fall. Age 0.5+ red snapper showed differences among all seasons (p < 0.05), but squid was the most important by percent weight during the winter, spring, and fall, while fish material dominated diets in the summer. Winter diets of age 1 red snapper were different when compared to all other seasons, due to the abundance of crab in stomachs (p < 0.01).

Seasonal differences in red snapper $\delta^{15}N$ and $\delta^{34}S$ were negligible; however, $\delta^{13}C$ of red snapper showed a significant difference among seasons (Table 3). Results indicate that red snapper had lowest $\delta^{13}C$ (−17.3‰) in winter, slightly increased values in spring (−17.2‰), and highest $\delta^{13}C$ values in summer (−16.9‰) and fall (−17.0‰).

Prey habitat selection

The majority of fish and crab prey items (percent dry weight) found in adult red snapper were sand- and mud-associated organisms (Table 5). The most abundant sand- and mud-associated fish prey item was the largescale lizardfish *Saurida brasiliensis*, accounting for 37, 32, and 39% of the total dry weight of age 1, age 2, and age 3+ red snapper stomach contents, respectively. The striped anchovy *Anchoa hepsetus* was the lone open water fish species, and sand perch *Diplectrum formosum* and tomtate *Haemulon aurolineatum* represented reef-associated fish prey identified to species. The dominant crab prey items associated with sand and mud were *Callinectes* spp., accounting for 23, 97, and 100% of the total dry weight of age 1, age 2, and age 3+ red snapper stomach contents, respectively.

Similar patterns of prey habitat use were seen when investigating stomach contents of all red snapper age groups combined. The total percentage of all fish prey taxa that was classified as reef associated represented 2% of total fish prey by dry weight. *Saurida brasiliensis* represented 40% of total dry weight of fish material in red snapper stomachs, followed by *Anchoa hepsetus*, with 37%. The total dry weight percentage of all reef-associated crab material in red snapper stomachs was 8%, while 89% was represented by the family Portunidae, of which 55% was *Callinectes* spp.
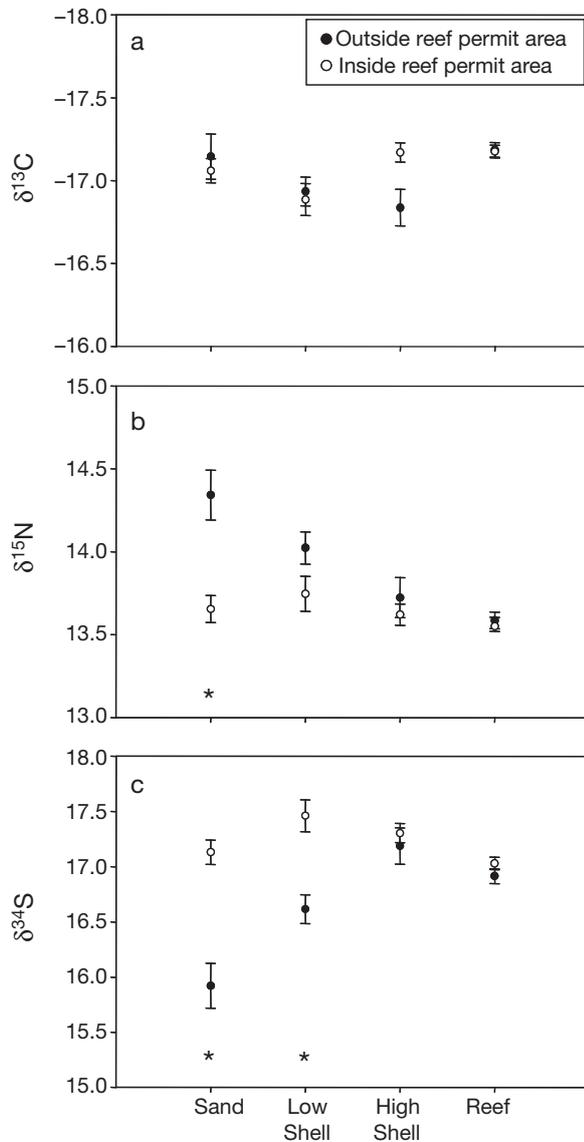
Fig. 6. *Lutjanus campechanus.* Stable isotope plots of red snapper (a) carbon ($\delta^{13}C$), (b) nitrogen ($\delta^{15}N$), and (c) sulfur ($\delta^{34}S$) collected over sand, low-shell, high-shell, and reef habitats both outside and inside the artificial reef permit area. Asterisks indicate significant differences (p < 0.05)

Table 5. *Lutjanus campechanus.* Percentages of crab and fish prey items (percent dry weight) collected in age 1+ red snapper stomachs according to prey habitat preference. Percentages are calculated for prey items identified to family or greater. The percent of red snapper collected on the reef by age group is also included

| Habitat | ——— Crab ——— | | ———————Fish——————— | | | Red snapper collected on reef (%) |
	Sand/ mud	Reef	Sand/ mud	Open water	Reef	
Age 1	96.2	3.8	40.9	58.5	0.6	56.1
Age 2	100.0	0.0	100.0	0.0	0.0	85.0
Age 3+	100.0	0.0	99.1	0.9	0.0	90.6

Planktonic versus benthic carbon contribution

The average $\delta^{13}C$ value of POM, which served as a proxy for the planktonic organic contribution to red snapper, was −22.7‰ (±1.0 SE). In contrast, the average $\delta^{13}C$ value of BMA, which served as the benthic contribution to red snapper, was −19.9‰ (±0.7 SE). Average $\delta^{15}N$ values of POM and BMA were 5.9‰ (±0.1 SE) and 7.2‰ (±0.4 SE), respectively.

Results of the 2-source mixing model indicate that benthic carbon contributions were potentially important to the food web of red snapper. Initially, planktonic sources were important for newly settled red snapper, accounting for 95% of the total carbon contribution. After several months, the planktonic contribution decreased to 78, 69, and 61% of age 0 red snapper occupying reef, shell, and sand, respectively. Age 0 red snapper collected over sand had the most enriched $\delta^{13}C$ values, which is consistent with benthic feeding; these fish were consuming benthic copepods (Fig. 3). Benthic source production continued to increase with increasing red snapper age, from 30% at 6 mo of age, to 34, 42, and 50% at ages 1, 2, and 3+, respectively.

DISCUSSION

The combination of both stomach contents and stable isotopes proved useful in determining the importance of ontogeny, habitat type, and the presence of an artificial reef permit area on red snapper *Lutjanus campechanus* diet. Our results indicate that red snapper exhibit distinct ontogenetic feeding shifts; however, the sand and mud habitats appear to provide the prey resources, while more structured habitats (i.e. shell-rubble, natural reefs) may act as a refuge from predators. In addition, a significant benthic contribution to red snapper diet was identified, while seasonal feeding differences were minimal. Lastly, stable isotopes of $\delta^{15}N$ and $\delta^{34}S$ appear useful as tools to identify feeding differences of red snapper collected inside and outside an artificial reef permit area, although more replication is needed to verify if these trends are consistent on a larger spatial scale.

The rapid isotopic changes in early life stages were likely attributed to a diet shift accompanied by fast tissue turnover time, which is common during the early life stages of fishes (Herzka & Holt 2000). The initial decrease in $\delta^{15}N$ of pre-settled red snapper followed by a rapid increase in $\delta^{15}N$ likely resulted from the transition from endogenous to exogenous feeding. Vander Zanden et al. (1998) found the same pattern for age 0

smallmouth bass *Micropterus dolomieu* and attributed the change to the transition from a parental nitrogen source to one dominated by exogenous nitrogen sources. A settlement signal was also observed between pre- and post-settled red snapper stable isotope values as the post-settled fish had enriched $\delta^{13}C$ (+1.5‰) and $\delta^{15}N$ (+3.0‰) values relative to pre-settled conspecifics.

The enrichment of $\delta^{13}C$ and $\delta^{15}N$ values in red snapper tissues with increasing size and age is consistent with other studies that have investigated ontogenetic diet shifts from juveniles to adults (Fry et al. 1999, Cocheret de la Moriniere et al. 2003). The large $\delta^{15}N$ difference of 3.5‰, combined with a major change in stomach contents from juvenile to adult red snapper, indicates a trophic level difference. The decrease in $\delta^{34}S$ values of red snapper reflects the changing sulfur source of the food web, from water column sulfates at small sizes, to an increasing importance of sediment sulfides from the benthos (Moncreiff & Sullivan 2001). Stomach contents corroborated stable isotope results by showing the transition of red snapper feeding on low trophic level prey items commonly occupying the water column (i.e. zooplankton) to one dominated by benthic feeding at higher trophic levels (i.e. benthic crustaceans and fishes).

Ontogenetic feeding shifts in red snapper appeared to be more important than the habitat-specific feeding patterns observed in the present study. Cocheret de la Moriniere et al. (2003) reported spatial separation of stable isotopes for adult and juvenile fishes are based upon the nursery and adult habitats from which the fishes were collected. Adult fishes collected over coral reefs retained isotopic values characteristic of a reef diet, while juveniles collected in seagrass and mangroves had diets corresponding to those habitats. We found decreasing separation of stomach contents and stable isotopes with increasing age, suggesting considerable movement for feeding over soft-sediment habitats by adults. The shell-rubble features in this study are approximately 100 to 200 m in width (Dufrene 2005), and the nearby reefs are relatively small, covering no more than several square kilometers (Schroeder et al. 1988); thus, red snapper would not need to move long distances to encounter all the habitats considered in this study. Alternatively, the larger prey consumed by adults may be moving among habitats.

The ability to discriminate habitat shifts attributable primarily to feeding opportunities provided by habitat-specific resources was minimal. In addition, seasonal feeding differences were minimal in this study. Diet shifts, along with associated habitat shifts, have been noted in other studies (Rooker 1995, Cocheret de la Moriniere et al. 2003). Szedlmayer & Lee (2004) found unique habitat-specific prey resources in red snapper diets over sand and artificial reef habitats, and attrib-

uted the associated habitat shift to available prey resources. Our study showed habitat-specific differences, but indicated red snapper were primarily eating prey associated with sand and mud substrates, despite a sand–shell–reef habitat preference continuum by red snapper with increasing age. Differences may be attributed to the function of natural reefs in this study versus the artificial reefs studied by Szedlmayer & Lee (2004). However, Szedlmayer & Lee (2004) found no red snapper <70 mm SL on artificial reefs and no red snapper >160 mm SL on open sand habitat. They attributed these distinct habitat shifts to the availability of prey resources. Trawl and trap collections provided red snapper of all age groups at each habitat in this study, thus enabling us to determine whether feeding differences may be due to ontogeny, habitat, or a combination of both. Our study has demonstrated red snapper rely on sand- and mud-associated prey regardless of the habitat from which red snapper were collected, suggesting the structural importance of shell and natural reef habitats may be more important for red snapper survival than additional prey resources. Additionally, McCawley et al. (2006) performed a diet study on adult red snapper collected on artificial reefs and found stomach contents contained only 1.3% of reef-associated prey, by dry weight.

Habitat selection has been shown to be a function of predation pressure and prey availability (Auster et al. 1997). Small-scale biogenic and physical habitat features (e.g. shells, cobbles, sand waves) have been shown to be important for demersal fishes and have been suggested to increase juvenile survivorship (Lindholm et al. 1999, Thrush et al. 2002). An assumption in our approach is that natural mortality is growth rate-dependent and faster growing juveniles have lower mortality rates due to reduced exposure time to predators (Cowan et al. 1996). Therefore, it is advantageous to utilize high-quality habitats that convey greater foraging and growth opportunities, resulting in an enhanced probability of survival. Growth rates of age 0 red snapper were higher over sand habitats (Wells et al. in press), but it was difficult to identify any consistent feeding patterns among similar-sized red snapper over different habitats. However, the low shell-rubble provided the most enriched $\delta^{15}N$ values for all age groups that showed feeding differences (age 0, 0.5+, and 1), and the most important prey items for these red snapper age groups typically included fish material. Thus, juvenile red snapper occupying sand and mud may recruit to structured habitats, such as shell rubble, at a size refuge from predators, while obtaining prey items, such as fish, from the adjacent sand and mud areas.

Results of the artificial reef permit area comparison should be interpreted with caution given the limited

spatial replication in this study. Consequently, statistical power is weakened due to the presence of only one artificial reef comparison. Based on this initial study, feeding differences identified inside and outside the reef permit area suggest stable isotopes may be useful tools for future studies attempting to understand impacts of fishing activities on the feeding ecology of marine species. The presence of an artificial reef permit area was associated with changes in red snapper stable isotopes regardless of habitat type, but had little effect on the prey items identified in stomach content analysis. Consistent responses were observed with higher $\delta^{34}S$ and lower $\delta^{15}N$ values in red snapper collected from all habitats inside the reef permit area. Depleted $\delta^{34}S$ values found over the sand and low shell-rubble outside the reef permit area may be a result of sediment re-suspension events following trawl disturbances. Habitat disturbance by trawling has been shown to influence the dynamics of trace and heavy metals, nutrient fluxes, and chemistry in marine sediments (Warnken et al. 2003, Eggleton & Thomas 2004). The enriched $\delta^{15}N$ values observed in red snapper collected over areas outside the reef permit area may be attributed to an increase in the opportunity for red snapper to prey upon benthic organisms that have been injured or killed by trawling. Kenchington et al. (2005) found changes in the diets of demersal fishes were caused by changes in the prey availability brought about by trawling disturbances. An increase in foraging opportunities for large fish predators has been demonstrated in recently trawled areas where the fish predators rapidly moved to the trawled areas to feed (Wassenberg & Hill 1987, Kaiser & Spencer 1994). Similar processes have been observed in the GOM by bottlenose dolphin *Tursiops truncates* responding to the trawls and preying on fishes exiting trawl openings (University of Georgia Marine Extension Service and National Marine Fisheries Service Harvesting Branch 2003).

Our study was limited to one artificial reef permit area, which may affect overall conclusions. We acknowledge this form of pseudoreplication in this initial study and suggest future studies should aim at greater replication over a larger area of the shelf to test for the effect of fishing activities on benthic ecosystem processes. In addition, we assumed the presence of artificial reefs did not affect the feeding ecology of red snapper. Results of our study suggest red snapper do not feed on prey associated with natural reefs, while McCawley et al. (2006) found red snapper collected over artificial reefs rarely prey upon reef-associated organisms. Furthermore, we found no evidence of artificial reefs from sidescan surveys used to characterize habitat types in this study. Nevertheless, we acknowledge the presence of artificial reefs in the artificial reef permit area could alter behavior of red snapper in our study.

Isotope values for both POM and BMA, proxies for planktonic and benthic contributors, respectively, were similar to those found in other studies. Sauriau & Kang (2000) found average POM $\delta^{13}C$ values of $-22.2‰$ and $\delta^{15}N$ of $5.0‰$. Litvin & Weinstein (2004) found that BMA $\delta^{13}C$ values ranged between -21 and $-14‰$, and $\delta^{15}N$ ranged from 7 to 11‰. In addition, Nadon & Himmelman (2006) found $\delta^{13}C$ values of POM ranging from -25 to $-22‰$ and BMA averaging $-19.4‰$, quite similar to the values of -22.7 and $-19.9‰$ for POM and BMA in this study, respectively. Benthic $\delta^{13}C$ values were also similar to sediment organic matter collected by Kang et al. (2003) that averaged $-19.5‰$ in 3 different bay systems in Korea. Thus, our benthic collections may contain a mixture of pennate diatoms, bacteria, sediment, or POM that settled on the bottom. A recent review of $\delta^{13}C$ enrichment in benthic consumers with increasing depth found that factors other than the ingestion of enriched primary producers may account for the $\delta^{13}C$ enrichment in the consumers (Nadon & Himmelman 2006). Thus, we cannot completely eliminate other factors such as seasonal pulses of heavy ^{13}C enriched POM (Fry & Wainright 1991) or enrichment of POM as particles sink in the water column and become degraded by bacteria and consumers.

The importance of benthic primary production has been demonstrated in other studies of coastal food webs (Sauriau & Kang 2000, Kang et al. 2003). Benthic consumers have been shown to derive most organic material from benthic contributions, such as BMA, while pelagic consumers rely more on planktonic contributions (Kang et al. 2003). Sauriau & Kang (2000) estimated >70% of the total cockle production in a European Atlantic coastal bay system was produced from microphytobenthos. While a more detailed isotopic construction of the food web needs to be performed, this study suggests the importance of a benthic contribution to red snapper on the shallow (<30 m depth) northern GOM shelf.

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