

Abstract—We examined the diets and habitat shift of juvenile red snapper (*Lutjanus campechanus*) in the north-east Gulf of Mexico. Fish were collected from open sand-mud habitat (little to no relief), and artificial reef habitat (1-m³ concrete or PVC blocks), from June 1993 through December 1994. In 1994, fish settled over open habitat from June to September, as shown by trawl collections, then began shifting to reef habitat—a shift that was almost completed by December as observed by SCUBA visual surveys. Stomachs were examined from 1639 red snapper that ranged in size from 18.0 to 280.0 mm SL. Of these, 850 fish had empty stomachs, and 346 fish from open habitat and 443 fish from reef habitat contained prey. Prey were identified to the lowest possible taxon and quantified by volumetric measurement. Specific volume of particular prey taxa were calculated by dividing prey volume by individual fish weight. Red snapper shifted diets with increasing size. Small red snapper (<60 mm SL) fed mostly on chaetognaths, copepods, shrimp, and squid. Large red snapper (60–280 mm SL) shifted feeding to fish prey, greater amounts of squid and crabs, and continued feeding on shrimp. We compared red snapper diets for overlapping size classes (70–160 mm SL) of fish that were collected from both habitats (Bray-Curtis dissimilarity index and multidimensional scaling analysis). Red snapper diets separated by habitat type rather than fish size for the size ranges that overlapped habitats. These diet shifts were attributed to feeding more on reef prey than on open-water prey. Thus, the shift in habitat shown by juvenile red snapper was reflected in their diet and suggested differential habitat values based not just on predation refuge but food resources as well.

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Diet shifts of juvenile red snapper (*Lutjanus campechanus*) with changes in habitat and fish size

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Larval red snapper (*Lutjanus campechanus*) spend approximately 26 days in the plankton, prior to metamorphosis and first appearance on benthic substrate. For the most part the fish settle on open substrate, where peaks in recruitment are observed in August and September, after which they may move to more structured habitat sometime within the first year (Szedlmayer and Conti, 1999). The apparent advantage of this habitat shift would be increased food resources and protection from predators. To help clarify the value of increased food resources on reef habitats, comparisons of diets from the two habitats are necessary. Also, because many fish species shift diets with increasing size (Sedberry and Cuellar, 1993; Burke, 1995; Rooker, 1995; Lowe et al., 1996), we need to distinguish possible ontogenetic diet differences from shifts that are due to habitat.

Previous red snapper diet studies have focused on larger individuals and on small sample sizes for fish <250 mm SL (Camber, 1955; Moseley, 1966; Bradley and Bryan, 1975). Camber (1955) described the diets of 15 “small red snapper” from Campeche Banks, and reported that 14 of the 15 stomachs contained small penaeid shrimps. Moseley (1966) described the diets of 45 “juvenile red snapper” collected off the coasts of Texas, and 28 off Louisiana. Louisiana fish fed on fishes, shrimps,

detritus, and stomatopods, and Texas fish fed on shrimps, crabs, and mysid shrimps.

Perhaps the most comprehensive red snapper diet study to date has been that of Bradley and Bryan (1975) which described the diets, by season, of trawl-collected (open sand-mud habitat) and hook-and-line reef “rough bottom areas” fish off the Texas coast. They described the diets of 258 open-habitat and 190 reef red snapper and found that juvenile red snapper (25–325 mm FL) were dependent on shrimp, crabs, and other crustaceans and that adults (325–845 mm FL) were dependent on fish, crabs, and other crustaceans. They described a change in juvenile red snapper diet as fish size increased, “young red snapper depend almost exclusively upon invertebrates,” and showed a gradual increase in vertebrate prey with growth. However, they did not separate out the proportions of their “juvenile” red snapper that were collected from reef versus open habitat. Thus, the shift from open to reef habitat is still poorly understood. If and when this shift occurs and whether this shift is accompanied with a diet shift that is independent of fish-size effects needs to be defined.

The purpose of the present study is to describe the diet of red snapper off the coast of Alabama—from the juvenile stage (just after settlement) to one-year old fish. We examined overall

ontogenetic shifts in red snapper diet with increasing size and possible changes in diet with habitat shifts from open substrate to structured habitat (artificial reefs).

Materials and methods

Red snapper were collected from open-flat substrate (sand and mud) and reef habitats (artificial reefs; Fig. 1). The open habitat was located approximately 6 km south of Mobile Bay, Alabama (30°06'N, 88°03'W), and ranged in depth from 12 to 20 m. Previous studies showed very high concentrations of age-0 red snapper from these areas (Szedlmayer and Shipp, 1994; Szedlmayer and Conti, 1999). The artificial reef habitats were located in the Hugh Swingle artificial reef area, approximately 20 km south of Mobile Bay, AL, and ranged in depth from 18 to 23 m (Szedlmayer and Shipp, 1994; Szedlmayer, 1997).

We collected fish from open substrate by trawl (7.62-m head rope, 2.54-cm mesh, 2-mm codend mesh). Samples were taken every two weeks from June to December 1994; however, time between samples was longer in the winter because of poor weather. Each trawl was fished for 10 min, and all age-0 and age-1 red snapper collected were placed on ice, returned to the laboratory, and frozen for later analysis. Bottom dissolved oxygen, salinity, and temperature were sampled with a Hydrolab Surveyor II at each location (Szedlmayer and Conti, 1999).

Prior to diet analysis, red snapper were thawed, weighed to the nearest 0.1 g, and measured to the nearest 0.1 mm SL. The whole fish was preserved in 10% formalin if SL was <50 mm, whereas for larger fish, stomachs were removed and preserved. After 48 hours in formalin, stomach samples were transferred to 75% isopropyl alcohol.

Concrete block and PVC artificial reefs (1 m³) were placed in the Hugh Swingle reef area in August 1992 and July 1993 (Szedlmayer, 1997). "Reef" is used here for defining these artificial habitats. Reefs were not sampled for a minimum of 3 months after placement. Red snapper were collected from June 1993 through December 1994. Fish were collected from these reefs by SCUBA divers first placing a drop net (3.0 m radius, 1.3 cm square mesh) over the reef and then releasing rotenone into the enclosed area. Reef fish were placed on ice in the field and transported back to the laboratory. Approximately 12–18 h after collection all reef fish were weighed to the nearest 0.1 g and measured to the nearest 1.0 mm. Stomachs were fixed in 10% formalin, and after 24 h transferred to 75% isopropyl alcohol. Red snapper size classes were also estimated by SCUBA visual surveys in July and August 1994. On each visual survey, divers counted red snapper by 50-mm size intervals. Bottom dissolved oxygen, salinity, and temperature were sampled with a Hydrolab Surveyor II during each survey.

All stomachs were dissected and contents placed in petri dishes. All prey were counted and identified to the lowest possible taxon. Volume was calculated by using an adaptation of the method described by Hellawell and Able (1971). Each prey taxon from each stomach was placed into a glass well of a known depth. A cover slide was placed on the well,

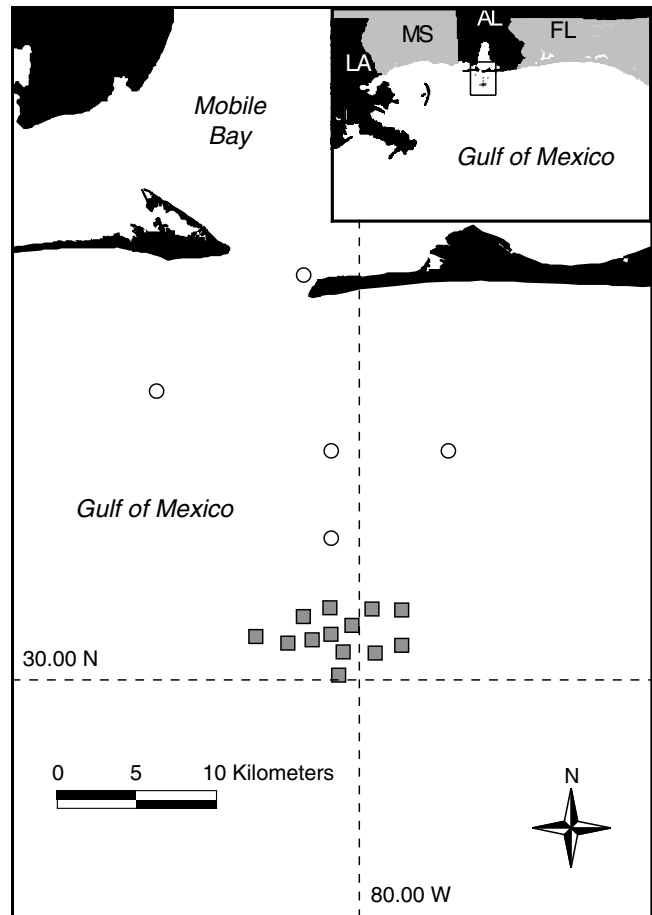
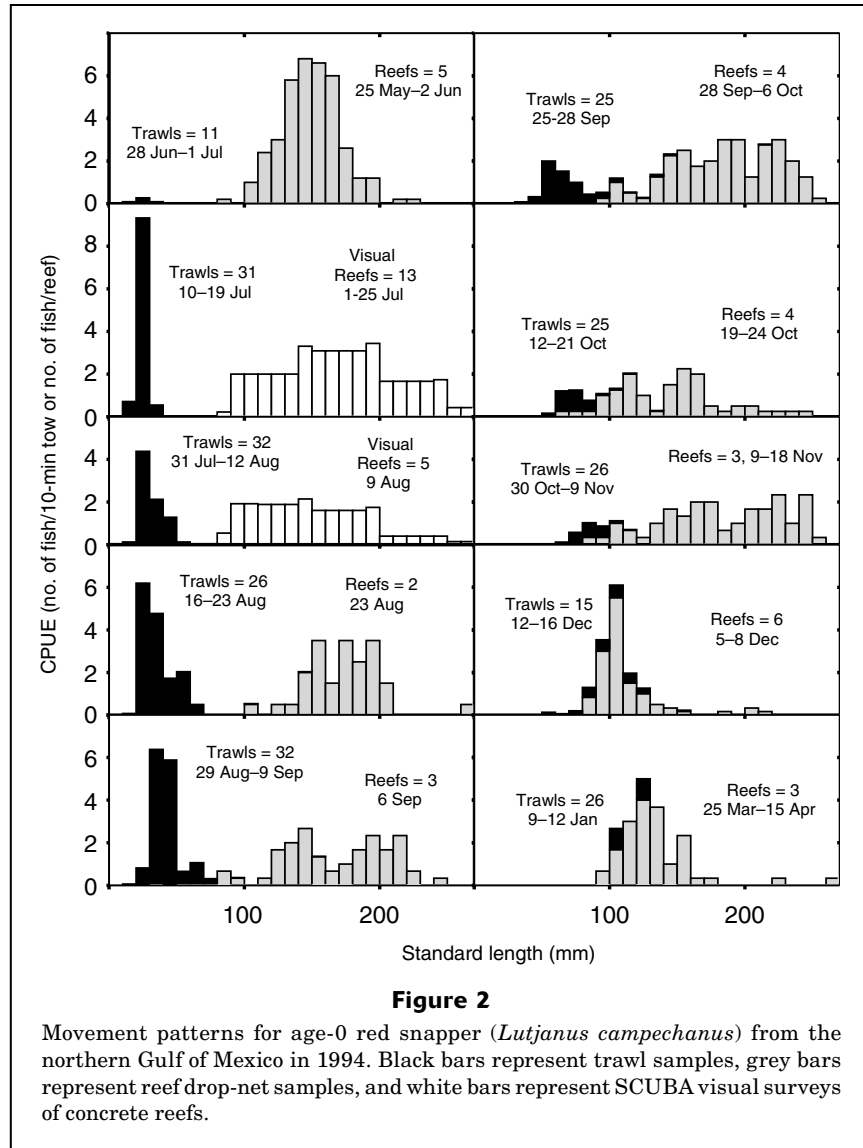


Figure 1

Collection sites for red snapper (*Lutjanus campechanus*) in the northern Gulf of Mexico. Open circles are open habitat trawl sites, and gray squares are 1-m³ concrete or PVC artificial reefs.

depressing the prey taxon to a known depth (e.g., 1 mm). The prey were video taped with a high-8 Sony camera and images were digitized with Image Pro 2.0 software (Media Cybernetics, Silver Spring, MD). Image size was calibrated to 0.01 mm by a stage micrometer. The surface area of each preparation was measured by using Image Pro software. Volume was calculated by multiplying the surface area by the known depth. Specific volumes for particular prey taxa were calculated by dividing prey volume by individual fish weight (mm³/fish wt g). Comparisons of diet shift by increasing fish size were made by grouping prey taxa into ten prey groups and by calculating specific volume for 10-mm-size intervals of red snapper.

A dissimilarity index (Bray-Curtis) was calculated from specific volumes of individual prey taxa, for overlapping size classes of red snapper both within and between habitats: $Bray-Curtis = \frac{\sum |Y_{ij} - Y_{ik}|}{\sum (Y_{ij} + Y_{ik})}$, where Y = specific volume of i^{th} species, and j and k are the samples being compared (Field et al., 1982). The dissimilarities were then used in a multidimensional scaling analysis (MDS; Schiffman et al., 1981). The MDS provided a two-dimensional "map" of the distances between samples (fish



size and habitat type) in Euclidian space based on the Bray-Curtis index. Thus, comparisons of red snapper diets were based on all prey taxa, yet independent of capture habitat and fish size.

Results

In the sampling areas during the summer and fall of 1994, salinity ranged from 30 to 35 ppt. Dissolved oxygen was 7 ppm in the early summer, decreased to 3 ppm in July and August, and increased to 7 ppm in the fall. Temperature was 22°C in June, increased to 28°C in late August, then dropped to just below 20°C by December. No significant differences were detected between trawl and reef sites for these environmental measures (t -test, $P \leq 0.05$).

Red snapper showed a clear shift in habitat during their first few months of life (Fig. 2). Fish first recruited to open

habitat at the end of June, at sizes <40 mm SL. Fish continued to recruit to open habitat until early September, at which time they were larger (30 to 100 mm SL) and began shifting to more structured habitat. By mid-October most age-0 fish had moved to reef habitat. During the initial settlement no new recruits were collected or visually observed on the artificial habitats (Fig. 2). Overall, only red snapper <160 mm SL were collected from open habitat, whereas only red snapper >70 mm SL were collected from reef habitat. Size overlapped from 70.0 to 160 mm SL between habitats (Fig. 3).

A total of 1639 red snapper stomachs were analyzed: 570 from open substrate and 1069 from reef habitat. Prey were found in 789 (48%) of the total stomachs examined, 346 (61%) from the open habitat and 443 (41%) from the reef habitat (Fig. 3). Trawl-collected red snapper were mostly collected from site one, but sample sizes were also large (>30 with prey) at two other sites (Table 1). Total red

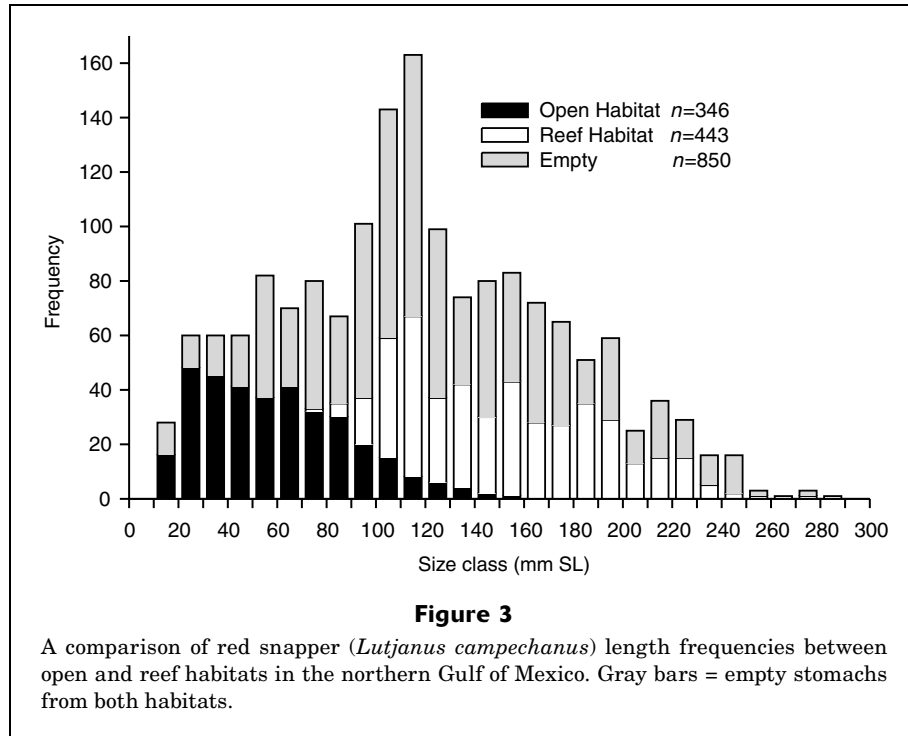


Table 1
Number of red snapper (*Lutjanus campechanus*) stomachs sampled (*n*), and number of stomachs containing prey from open and reef habitat in the northeast Gulf of Mexico.

Open trawl sites		Reef habitats	
<i>n</i>	<i>n</i> with prey	<i>n</i>	<i>n</i> with prey
356	223	108	53
45	21	17	5
75	58	198	115
57	33	55	31
37	11	249	71
		50	23
		14	1
		89	45
		11	5
		209	74
		35	10
		22	4
		12	6

Table 2
Number of red snapper (*Lutjanus campechanus*) stomachs sampled (*n*), and number containing prey, by month and year, from open and reef habitat in the northeast Gulf of Mexico.

Open habitat			Reef habitat		
Month and year	<i>n</i>	<i>n</i> with prey	Month and year	<i>n</i>	<i>n</i> with prey
Jul 1994	56	43	Jun 1993	94	50
Aug 1994	169	109	Oct 1993	370	169
Sep 1994	187	98	May 1994	141	37
Oct 1994	97	52	Jun 1994	46	37
Nov 1994	16	12	Aug 1994	41	8
Dec 1994	45	32	Sep 1994	155	86
			Oct 1994	76	28
			Nov 1994	65	12
			Dec 1994	81	16

snapper collected from the reefs varied by site (from 11 to 249 fish), but large samples were collected from at least 6 different reefs (Table 1). Large sample sizes were collected during most months over open habitat, with the exception of November 1994 (*n*=12), and for most months (6 out

of 9) from reef sites (Table 2). Only red snapper stomachs containing prey were used in our analyses.

Red snapper diets showed 55 different prey identified to the lowest possible taxon. In general, red snapper diets were dominated by fish (43%), squid (29.5%), shrimp (16.4%), and crabs (4.4%; Table 3). Specifically, the “shrimp” group included Mysidacea (mysid shrimps), Stomatopoda (mantis shrimps), Penaeidea (penaeid

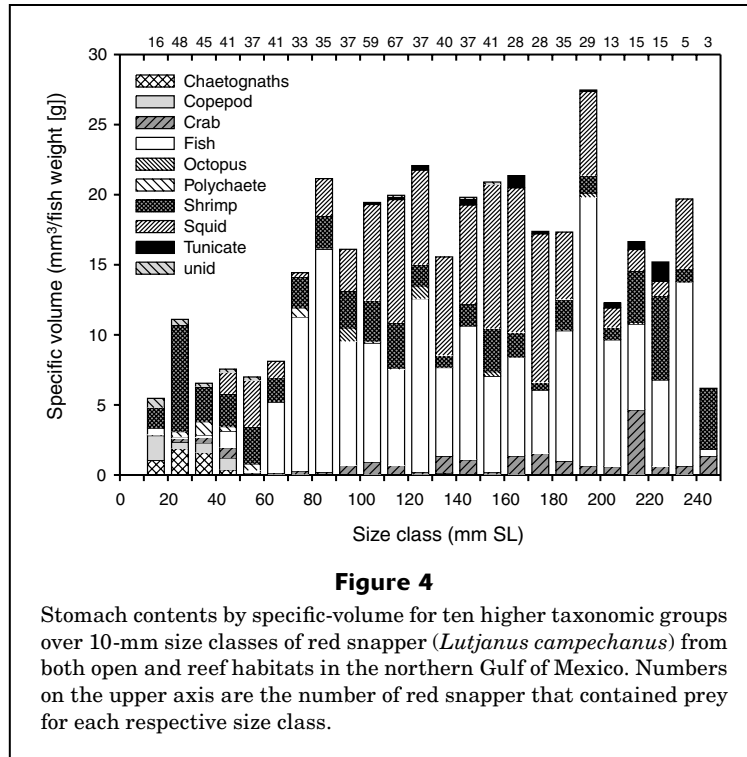
Table 3

Specific volume (mm³/fish weight g) for prey taxa from red snapper (*Lutjanus campechanus*). % = percent specific-volume of total volume, Habitat = prey habitat. General prey groups are noted in quotation marks. unid. = unidentified.

Prey taxa	Total volume	Percent	Lowest taxon	Specific volume	Percent	Habitat			
Osteichthyes "fish"	5408.2	43.5	unid. fish	3465.9	27.9				
			<i>Halichoeres</i> spp.	650.4	5.2	reef			
			Blenniidae	279.2	2.2	reef			
			Serranidae	278.1	2.2	reef			
			<i>Serranus subligarius</i>	240.8	1.9	reef			
			<i>Centropristis ocyurus</i>	207.3	1.7	reef			
			Engraulidae	117.9	0.9	open			
			Ophichthidae	100.6	0.8	open			
			Cynoglossidae	35.2	0.3	open			
			Triglidae	20.8	0.2	open			
			<i>Ophichthus</i> sp.	10.8	0.1	open			
			Cephalopoda "squid"	3665.6	29.5	Loliginidae	3665.6	29.5	open
			Natantia "shrimp"	2033.7	16.4	unid. shrimp	544.6	4.4	
Sicyoninae	359.6	2.9				reef			
Hippolytidae	345.7	2.8				reef			
Penaeidae	264.5	2.1				open			
Alpheidae	131.1	1.1				reef			
Sergestidae	24.2	0.2				open			
Luciferinae	22.6	0.2				open			
Ogyrididae	8.8	0.1				open			
Squillidae	221.8	1.8				open			
Mysidacea "shrimp"						Mysidacea	109.8	0.9	open
Reptantia "crabs"	550.8	4.4	Portunidae	302.0	2.4	mixed			
			unid. crab	143.0	1.2				
			Diogeninae	51.6	0.4	open			
			Leucosiidae	20.7	0.2	reef			
			Xanthidae	16.7	0.1	reef			
			Porcellanidae	7.3	0.1	reef			
			Chaetognatha	199.6	1.6	<i>Sagitta</i> spp.	199.6	1.6	open
			Polychaeta	130.1	1.0	Polycheata	75.4	0.6	mixed
Onuphidae	34.0	0.3				open			
Polychaeta			Maldanidae	19.9	0.2	open			
			Ascidiacea "tunicate"	121.0	1.0	Ascidiacea	121.0	1.0	reef
Calanoida "copepod"	118.2	1.0	Calanoida	113.3	0.9	open			
Octopodidae	93.6	0.8	<i>Octopus</i> sp.	93.6	0.8	reef			
unid.	79.5	0.6	unid.	79.5	0.6				
Amphipoda	13.8	0.1	Amphipoda	9.4	0.1	mixed			
Ostracoda	6.1	0.0	Ostracoda	6.1	0.0	open			

shrimps), and Caridea (caridean shrimps). In addition, all Squillidae were probably *Squilla empusa*, according to Hopkins et al., (1987). Among fish, many were unidentified due to digestion, but if proportions of unidentified fish are similar to identified fish, then dominant fish prey included *Halichoeres* spp., (5.2%), Blenniidae (2.2%), and Serranidae (2.2%). Two prey fish were identified to species: *Serranus subligarius* (1.9%), and *Centropristis ocyurus* (1.7%).

Among the squid taxon, one genus dominated: *Loliguncula* spp., (29.5%), but all squid were either *L. brevis* or *Loligo pealeii* (Hopkins et al., 1987). Among shrimp, dominant taxa included Sicyoninae (2.9%), Hippolytidae (2.8%), Penaeidae (2.1%), Squillidae (1.8%), and Alpheidae (1.1%). Among crabs, dominant taxa were mostly Portunidae (2.4%). Other groups showing greater than 1.0% included Chaetognatha (*Sagitta* sp. 1.6%), and Ascidiacea or tunicates (1.0%; Table 3).



Red snapper shifted diets with increasing size. For red snapper <60.0 mm SL, diets were dominated by shrimp, chaetognaths, squid, and copepods. Large red snapper (60–280 mm SL) shifted to feeding on fish prey, greater amounts of squid and crabs, and continued feeding on shrimp (Fig. 4).

The diets of juvenile red snapper changed as they moved from open to reef habitats. Fish collected had overlapping sizes of 70.0 to 160.0 mm SL from both open and reef habitats, and the MDS analysis for this size range showed a clear separation of diets between the two habitats (Fig. 5). Two points that were outliers (R75, T155) were biased because they represented only one fish each, and the third outlier (R85) was difficult to explain.

The clear separation of red snapper diets shown by the MDS analysis can be attributed to several prey shifts that accompanied habitat shifts. For prey crabs, open-habitat red snapper diets were dominated by Xanthidae, and smaller amounts of Paguridae, Portunidae, Diogeninae, and Pinnotheridae (Fig. 6), whereas diets of red snapper from reef habitats shifted to a dominance by Portunidae and Diogeninae (Fig. 7). For prey shrimp, open habitat red snapper diets were dominated by Penaeidae and Mysidacea (Fig. 8), whereas diets from reef habitats shifted to a dominance of Sicyoninae, Hippolytidae, Alpheidae, and Squillidae (Fig. 9). For prey fish, open-habitat red snapper diets were dominated by Engraulidae (although most were unidentified; Fig. 10), whereas diets from reef habitat clearly reflected prey fish from reef habitats and included Blenniidae, Serranidae, and three prey fish identified to genera, *Centropristis* spp, *Halichoeres* spp., and *Serranus* spp. (Fig. 11).

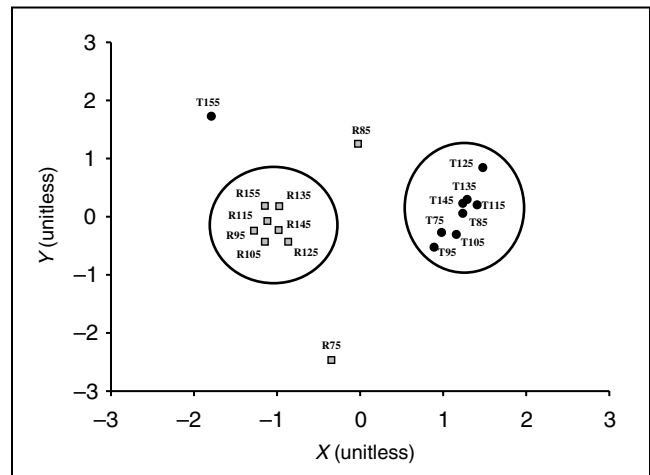
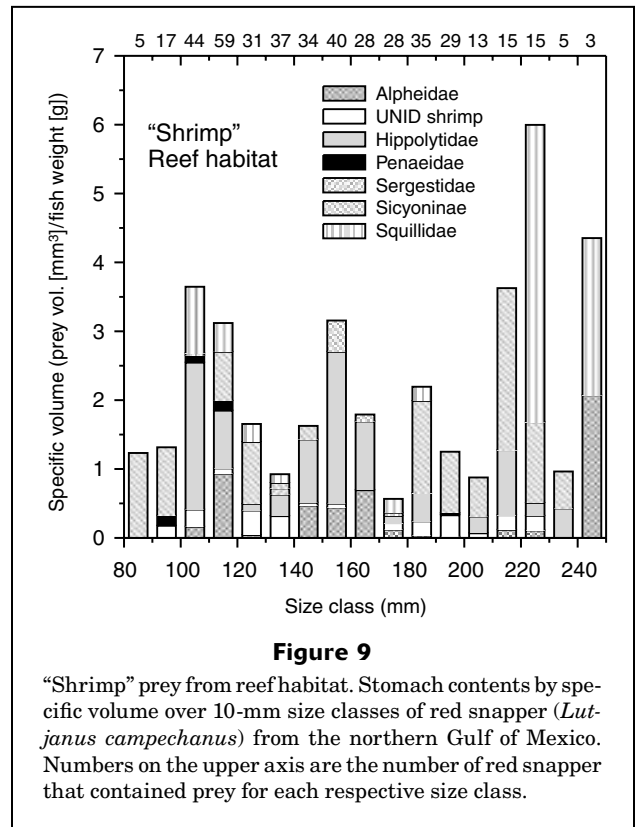
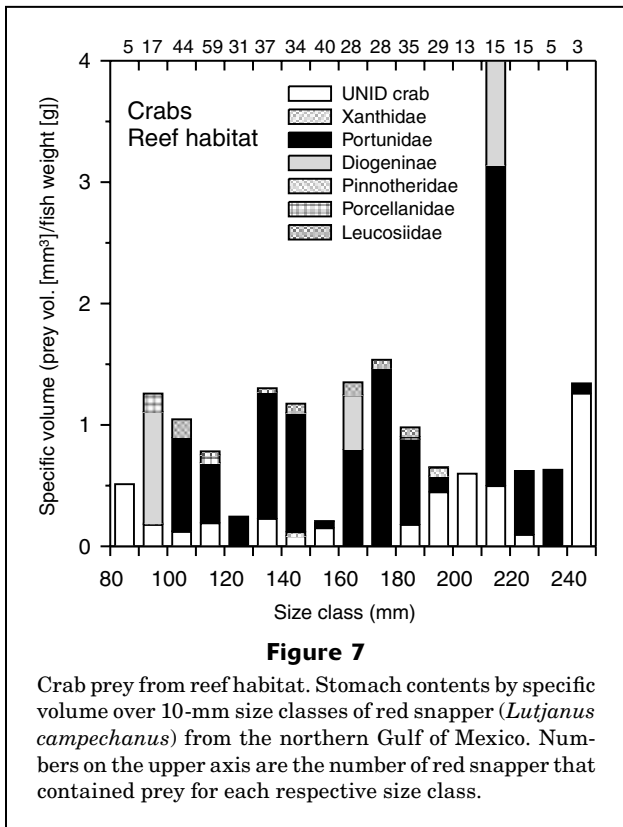
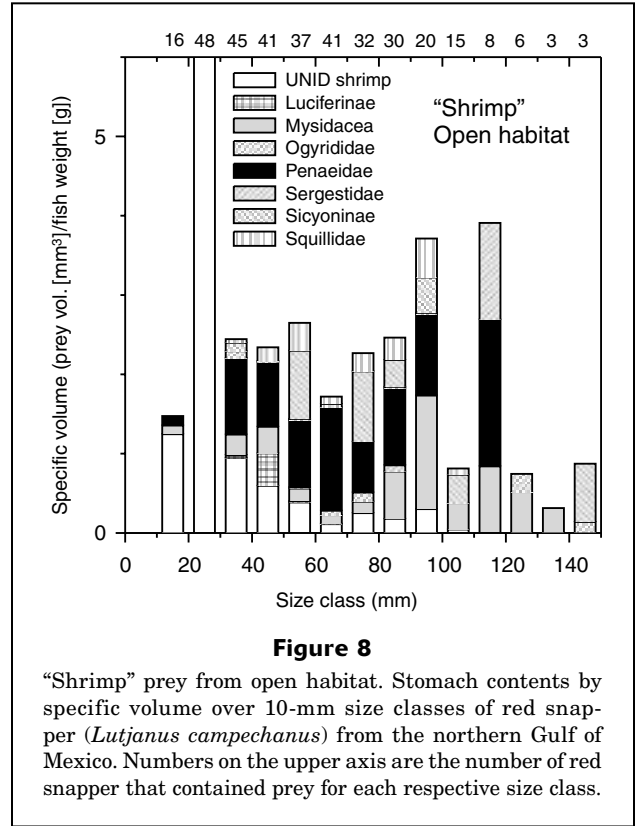
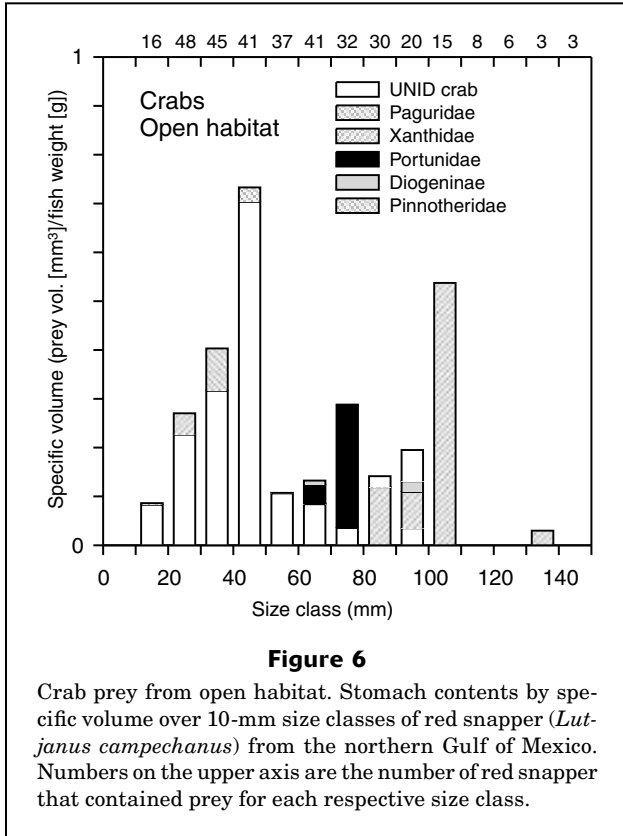
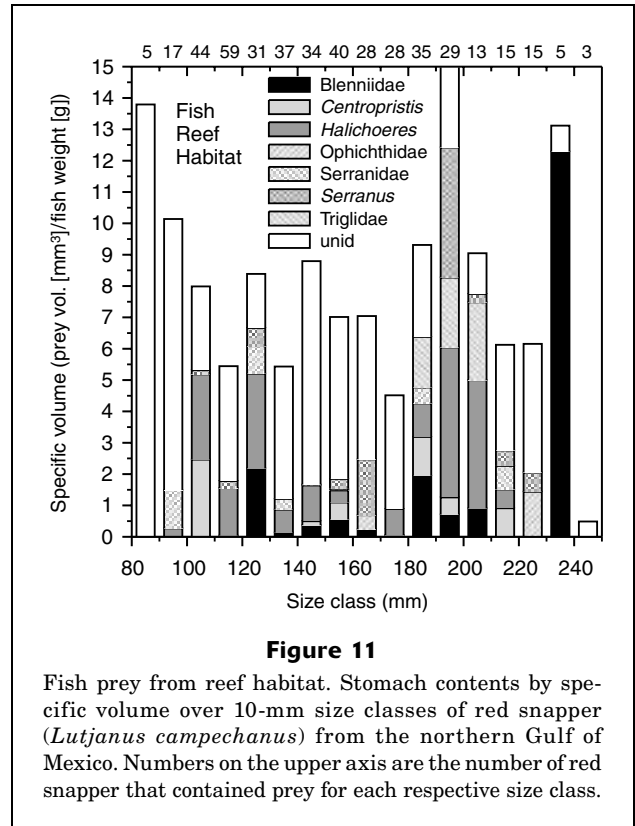
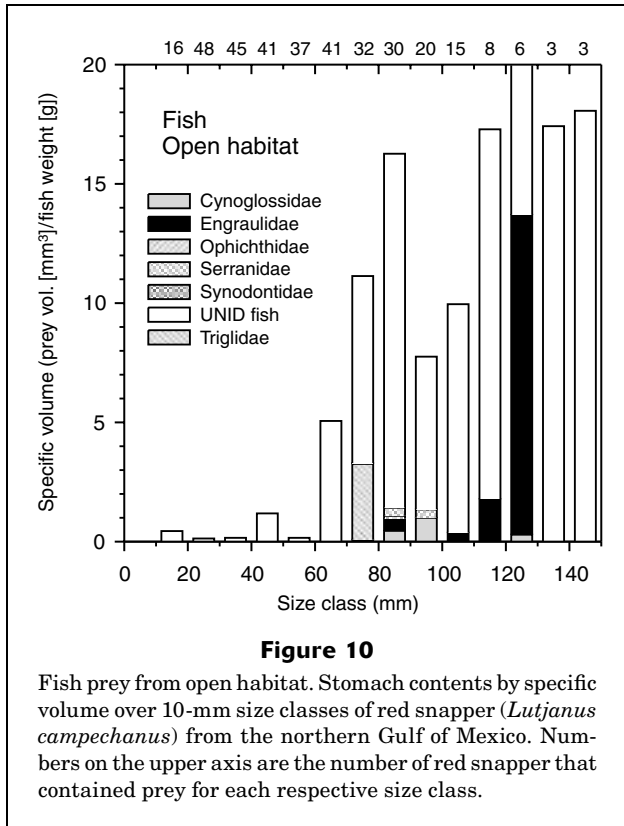


Figure 5
 Multidimensional scaling of diets for red snapper (*Lutjanus campechanus*) based on the Bray-Curtis dissimilarity index computed for specific volume of prey taxa both within and between habitats for overlapping size classes (70.0 to 159.9 mm SL). The letter and number accompanying each point indicates the habitat and size class that each point represents (e.g., T = trawl, R = reef, 75 = 75 mm SL size class). Circles were drawn by hand. Axes are unitless.

Discussion

The present study provides a substantial sample size (n=1639) for red snapper diet analysis and a relatively





high percentage of stomachs with food (48%) compared to past studies. Rooker (1995) also showed a high percentage (69%; 312 out of 449 stomachs) of schoolmaster snapper (*Lutjanus apodus*) contained prey, when fish were collected from depths similar to those of the our study (1 to 27 m). The higher percentage of stomachs with prey found in our study compared to past studies of red snapper (Stearns, 1884; Camber, 1955; Moseley, 1966) may be due to the shallower depths sampled (18 m; DeMartini et al., 1996).

Juvenile red snapper showed feeding patterns similar to many other marine fishes. After settlement, from approximately 20 to 60 mm SL, they showed a wide-ranging diet that included shrimp, copepods, chaetognaths, and squid. Prey fish were also found in the stomachs of the smallest red snapper collected (15–20 mm SL) but were not a dominant component. Sweatman (1993) reported similar results for the snapper *Lutjanus quinquelineatus*, ranging from 24 to 29 mm SL, i.e., piscivorous in the first few days after settlement. Above 60 mm SL, fish prey tended to dominate specific volume, but not by feeding less on shrimp because shrimp continued to be an important prey. Squid became another dominant component of red snapper diet at about 100 mm SL and also continued as an important prey up to 240 mm SL. Unfortunately, sample size was reduced above 230 mm SL, and it was difficult to estimate if squid and fish continued as dominant prey components above these size classes. Sedberry and Cuellar (1993) reported a similar shift in diets of reef-associated vermilion snapper (*Rhombopites aurorubens*). This spe-

cies shifted from small crustaceans to fishes and cephalopods over a size range similar to that of red snapper in the present study. Moseley (1966) reported a “slow transition from zooplankton to macro animals for red snapper sizes between 40 and 90 mm” — a transition that probably included fish prey that he did not specifically identify. Bradley and Bryan (1975), showed a shift in juvenile red snapper diets with size (25–325 mm FL). Their smallest red snapper keyed on invertebrates, then showed a sharp increase in dependency upon prey fish above 175 mm FL, when Batrachoididae (toadfish) became a dominant component. These shifts in diet are important in helping to identify fish habitat and are potentially key aspects of early survival.

Red snapper showed two major habitat shifts in their first year. Juvenile red snapper first settled from the plankton to benthic substrate near 20 mm SL (Szedlmayer and Conti, 1999). The present study showed a second shift from open habitat to reef habitat starting at about 70 mm SL (Fig. 3). No fish smaller than 70 mm were collected from the reefs, and smaller red snapper were rarely observed on these reefs from SCUBA visual surveys. No fish larger than 160 mm SL were caught from the open habitat but were present on the reefs. This finding suggested that red snapper had shifted to reef habitat by 160 mm SL but also may have avoided trawl gear as described earlier for age-0 red snapper (Bradley and Bryan, 1975) and age-0 summer flounder (*Paralichthys dentatus*) (Szedlmayer and Able, 1993). However, no large (150–300 mm) red

snapper were observed over open habitat by a SCUBA visual survey despite our observations that red snapper are attracted to SCUBA divers. Thus we suggest that a shift in habitat was more likely the cause of this absence than trawl avoidance.

The distinct diet shift as red snapper changed habitats was independent of increasing size and suggested that different benthic habitats play a critical role in the early life history of this species. This separation was completely independent of "a priori" knowledge of sample location and fish size. For example, the MDS analysis showed almost complete separation based on habitat rather than fish size (Fig. 5). These differences between open and reef habitat were readily apparent when prey taxa were separated into lower taxonomic categories. For example, fishes such as *Halichoeres* spp., *Serranus* spp., and *Centropristis* spp., were found only in the diets of reef-collected red snapper. These species are closely tied to reef structure (Nelson and Bortone, 1996). Prey shrimp also showed distinct differences in red snapper diets between habitats. Over open habitat, Mysidacea, Penaeidae, and Sergestidae were important components. After the shift to reef habitat, Mysidacea were absent and Penaeidae and Sergestidae were greatly reduced, and Sicyoninae, Hippolytidae, and Alpheidae became the dominant shrimp components. The latter are all families typically associated with reef habitats (Chance, 1970; Pequegnat and Heard, 1979). One exception was the increased feeding on Squillidae, an open habitat crustacean, at the largest size classes of this study (220–250 mm SL; Fig. 9). For crabs, the separation was not as clear, because of the dominance of Portunidae, which can be assigned to both open and reef habitats. However, increases in reef crabs were still apparent with habitat shift, i.e., Diogeninae, Porcellanidae, and Leucosidae can all be considered reef prey. Although Bradley and Bryan (1975) pooled "juvenile" red snapper over open and reef habitats, they did show a marked increase in fish prey above 175 mm FL. This increase was almost exclusively due to Batrachoididae or toadfishes, which are typically found in reef habitat. We did not observe any toadfish prey in our juvenile red snapper collections, but its presence in this earlier study is consistent with present findings showing a shift to feeding on reef-habitat prey.

Red snapper diet shifted to greater percentages of reef-prey with movement to reef habitat, but with this shift they also continued feeding on other prey. This flexibility in feeding habits allows red snapper to take advantage of prey from wide-ranging habitats. Similar diet shifts related to habitat shifts have been shown in schoolmaster snapper, (*L. apodus*) (Rooker, 1995). The schoolmaster snapper shifted from nearshore mangroves to coral reef habitats near 70 mm SL; diets of fish ≤ 70.0 mm SL were dominated by crustaceans, particularly amphipods and crabs. Fish >70.0 mm SL fed on fishes and to a lesser extent crabs, shrimps, and stomatopods. Similar diet shifts were also shown for several fish species of Puget Sound. For example in pile perch (*Rhacochilus vacca*), striped seaperch (*Embiotoca lateralis*), and quillback rockfish (*Sebastes maliger*), the smallest juveniles preyed on open-habitat plankton and benthic fauna, and medium-size

and larger fish (>121 mm) of all three species shifted their diets to include reef-associated prey (Hueckel and Stayton, 1982). However, at larger sizes these three species were not totally dependent on reef-associated prey.

We have examined red snapper diets based on specific volume of food. Although many other studies have used an index of relative importance (IRI; Pinkas et al., 1971; Cortes, 1997), we were specifically interested in the nutritional value of particular prey, and prey separation into open-habitat or reef-habitat. With IRIs these separations would be more difficult to define, e.g., pelagic prey with high numbers might be considered more important, but actually provide little nutritional value to red snapper diets (Macdonald and Green, 1983). Future studies on the effects of red snapper predation on prey distributions may be better suited for using IRIs.

In summary, red snapper diets from open habitat showed prey taxa associated with open sand-mud substrate and the planktonic environment. Open-habitat prey, such as chaetognaths, are known to be pelagic as well as benthic, as are sergestid shrimp, calanoid copepods, mysids, and stomatopods (Williams, 1968; Manning, 1969; Gosner, 1978; Stuck et al., 1979; Alldredge and King, 1985; Lindquist et al., 1994). Red snapper shifted diets to reef-associated prey with their habitat shift, and this diet shift was independent of fish size. These diet shifts were clearly apparent for both fish and shrimp prey but less so for crab prey. As shown with marine fish species from Puget sound, red snapper diets from reef habitat were not restricted to reef-associated prey. For example, squids were an important prey over both open and reef habitats in the present study and our findings agree with those of Bradley and Bryan (1975). The squids *Loligo* sp., and *Lolliguncula* sp. are both abundant in nearshore coastal waters and are not typically associated with reef structure (Gosner 1978; Laughlin and Livingston, 1982; Hopkins et al., 1987). Availability and ease in capture could be a key as to why squid are important for red snapper over size ranges of 40 to 240 mm SL. This flexibility in feeding habits allows red snapper to take advantage of prey from wide-ranging habitats, but clear shifts to additional reef prey supports the hypothesis that reef structure provides new prey resources.

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