

Abstract.—The feeding habits of the vermilion snapper, *Rhomboplites aurorubens*, were investigated to determine the role of this ecologically dominant and economically valuable species in the trophic ecology of southeastern U.S. reef habitats. Trophic ecology was studied by examining stomach contents and by comparing them to samples of benthic invertebrates and near-bottom plankton. Vermilion snapper fed on a variety of infaunal, epifaunal, and pelagic invertebrates, as well as on demersal and pelagic fishes and cephalopods. The diet was diverse but was dominated numerically by planktonic species. The benthic prey eaten were species associated with hard-bottom reef structure or were infaunal species from sand bottom areas adjacent to the reef. Many species were members of the hyperbenthos or demersal zooplankton and were apparently consumed in the water column during their nocturnal emergence from the sand or reef. Small crustaceans, especially copepods, sergestid decapods, and larvae of barnacles, stomatopods and decapods, dominated the diet of small (<50 mm SL) vermilion snapper. Larger decapods, fishes, and cephalopods were more important in the diet of larger vermilion snapper. Vermilion snapper, although reef associated, does not feed heavily on reef species, and may be important in transferring energy from the water column and adjacent sandy areas to the reef.

Planktonic and benthic feeding by the reef-associated vermilion snapper, *Rhomboplites aurorubens* (Teleostei, Lutjanidae)*

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The vermilion snapper, *Rhomboplites aurorubens*, is the most abundant lutjanid in the recreational and commercial fisheries of the southeastern U.S. (Grimes et al., 1982), and is a dominant component of the reef-associated ichthyofauna off the Carolinas and Georgia (Sedberry and Van Dolah, 1984). Because of its abundance and habit of foraging on small pelagic crustaceans (Grimes, 1979), vermilion snapper may be an important trophic link between the water column and those reef habitats where it schools during resting periods. If vermilion snapper also forages on infaunal benthos in adjacent sandy areas, it may be very important in the trophic coupling between the reef and surrounding expansive sandy areas. Vermilion snapper is also fed on by other predatory fishes (Sedberry, 1988) and thus may provide trophic links among top-level carnivores and the infauna, holozooplankton, demersal zooplankton (*sensu* Alldredge and King, 1977), and reef benthos.

Predation by fishes has been shown to be important in transferring energy from the water column or adjacent sand bottom areas to reef habitats (Bray et al., 1981; Meyer and Schultz, 1985; Rothans and Miller,

1991). Although information on feeding is available for some species of reef-associated fishes off the southeastern United States (Manooch, 1977; Grimes, 1979; Sedberry, 1985, 1987, 1988), the importance of reef bottom versus adjacent water column and sand bottom habitats as feeding grounds is poorly understood. These reefs support not only a variety of large sessile invertebrates (e.g., sponges, corals, tunicates) and associated motile organisms (Struhsaker, 1969; Wenner et al., 1983) but also a greater faunal abundance, diversity, and biomass than adjacent sand bottom areas of the open shelf (Struhsaker, 1969; Wenner, 1983; Wenner et al., 1983). Because of the rocky outcrops and the warming influence of the Florida Current, these reefs support tropical and subtropical families of fishes, and many economically valuable serranids, haemulids, sparids, and lutjanids, including vermilion snapper (Miller and Richards, 1980; Chester et al., 1984). The greater biomass and diversity of rocky reef habitats, compared with

sandy areas, may be the result of trophic links through reef-associated fishes, such as vermilion snapper, with other ecotopes on the shelf.

While an important component of regional reef ecosystems and fisheries, vermilion snapper and demersal-feeding fishes, such as red porgy (*Pagrus pagrus*) are being overfished (Low et al., 1985; Collins and Sedberry, 1991). As a result of this increased fishing pressure, vermilion snapper has increased in abundance relative to *P. pagrus* and other overexploited reef fishes off the southeastern United States, and the importance of its functional role in reef ecosystems may have changed. Increased fishing pressure since the late 1970's has also apparently caused a concomitant decrease in mean length and a decrease in size at maturity of vermilion snapper (Collins and Pinckney, 1988; Collins and Sedberry, 1991). If small vermilion snapper consume different prey than do large vermilion snapper and if average fish size is decreasing in the region, the trophic structure of reefs may be affected.

The objectives of this study were to describe the feeding habits of vermilion snapper and to evaluate its relative dependence on hard-bottom benthos, sand-bottom infauna, demersal zooplankton (Alldredge and King, 1977, 1985; Porter and Porter, 1977), holozooplankton (Cahoon and Tronzo, 1992) and nekton as food. An additional purpose was to describe differences in feeding habits with size.

Methods

Stomachs from vermilion snapper were collected during six cruises in 1980 and 1981 from 11 reef stations off South Carolina and Georgia. Stations were located in each of three depth zones representing the inner shelf (16–22 m depth, three stations), middle shelf (23–37 m depth, four stations) and outer shelf (46–69 m depth, four stations). Delineation of depth zones was based on distribution of fish assemblages as noted in previous studies and on community analysis of catches in the present study (Struhsaker, 1969; Miller and Richards, 1980; Sedberry and Van Dolah, 1984). Fishes were collected primarily with a roller-rigged 40/54 high rise trawl (Hillier, 1974); a few were captured with traps or hook-and-line. Sampling was conducted during the day and at night on hard-bottom reef habitat that was mapped for each station by means of underwater television. Detailed descriptions of station locations and fish sampling techniques have been described elsewhere (Sedberry and Van Dolah, 1984; Wenner et al., 1984).

Standard lengths (SL in mm) were measured at sea. Stomachs were removed, individually labeled, and fixed

in 10% seawater-formalin. Because of limited space and very large catches, only those stomachs that appeared to contain ingesta were preserved. No attempt was made in the field to determine the percentage of stomachs with food. Small (<50 mm SL) vermilion snapper were preserved whole and dissected in the laboratory. Fixed stomachs and small individuals were washed in tap water and transferred to 50% isopropyl alcohol.

Contents of individual stomachs were sorted by taxa and counted. Volume displacement of food items was measured in a graduated cylinder or estimated by using a 1×1 mm grid (Windell, 1971). The relative contribution of food items to the diet was determined by using three methods:

$$\text{percent frequency occurrence, } F = \frac{\text{number of stomachs with prey taxon}}{\text{number of stomachs with food}} \times 100$$

$$\text{percent numerical abundance, } N = \frac{\text{number of individuals of prey taxon}}{\text{total number of prey items}} \times 100$$

$$\text{percent volume displacement, } V = \frac{\text{volume displacement of prey taxon}}{\text{total volume of all prey items}} \times 100$$

These values are presented only for those prey species that occurred with a frequency of at least one percent or that made up at least one percent of the total number or volume of prey. Values of F , N , and V were also calculated for higher prey taxa, for stomachs pooled by 50-mm intervals of SL of vermilion snapper. The chi-square statistic (Tyler, 1979) was used to test for significance (0.05 level) of feeding heterogeneity between predator size classes.

To determine selection of prey type and predator feeding habitat, stomach samples were compared to samples from the potential prey environment by using Ivlev's index of electivity (Ivlev, 1961), calculated as

$$E = \frac{r_i - p_i}{r_i + p_i},$$

where: E = electivity for the i th potential prey species; r_i = percent by number of species i in the diet; and p_i = percent by number of species i in samples from the environment. Electivity values range from -1 to $+1$. Negative values imply that the species is avoided, not preferred, only incidentally ingested, or unavailable to the predator. Positive values imply that the predator prefers the prey species or that it is feeding on prey species that occur in a different habitat than that sampled by the prey sampler. A value near zero im-

plies no selectivity by the predator, that is to say the fish is feeding on the prey in proportion to the prey's relative abundance in samples taken in the habitat.

The electivity index was calculated for species that were numerically dominant in prey environment samples or in fish stomach samples. Dominant species included those that ranked among the five most abundant species within stomach or environmental samples pooled by depth zone. Prey samples and stomach collections were pooled by depth zone (inner, middle, and outer shelf) for comparison. Samples of benthic prey were obtained at the 11 reef sites during 1980 and 1981 with a diver-operated suction sampler (inner and middle shelf) or a grab sampler (outer shelf). Details of benthic sampling are provided elsewhere (Wenner et al., 1983; Wenner et al., 1984) and are only summarized here. Briefly, divers obtained five replicate suction samples during the day at each inner and middle shelf reef site by scraping the hard reef substrate enclosed by a 0.1-m² quadrat box while simultaneously sucking with an airlift device similar to that described by Chess (1979). Suction samples were collected in 1.0-mm mesh bags.

At the outer shelf stations, where water depth precluded the use of the suction device operated by divers, quantitative 0.1 m²-samples were collected in reef habitat with a modified Smith-McIntyre grab. After retrieval, each sample was sieved through a 1.0-mm sieve and retained organisms were identified and counted. Most (75.0%) grab samples were taken during the day.

Additional sampling was conducted to compare stomach contents with potential prey species occurring in the near-bottom water column above the reef. To determine extent of feeding on the near-bottom plankton, electivity values were calculated for samples obtained with an epibenthic plankton sled and compared with those from the suction and grab samples. The sled was similar to that described by Brattegard and Fosså (1991) but had a mouth opening of 0.5 m² and runners that permitted it to sample 0.5 m off the bottom. The sled also had a mouth-opening mechanism designed to fish only when it was in contact with the bottom. A 0.947-mm mesh net was attached to the sled and two ten-minute tows were made per station at night to minimize net avoidance. Sled collections for invertebrates were made only in 1981. These samples were analyzed for decapods, stomatopods, cumaceans, and mysids, and comparisons with fish stomachs were limited to these taxa. Underwater television and diver observations were used to direct invertebrate sampling to reef habitat. Further details of all fish and invertebrate sampling can be found in Sedberry and Van Dolah (1984) and Wenner et al. (1984).

Daytime submersible observations of vermilion snapper behavior were made during dives aimed at visually censusing (transects and point counts) reef fishes of the outer shelf on 14–15 July 1985. The submersible used was the *Sea Link I*, which provided a panoramic view (Askew, 1985) of shelf edge reefs and their fishes.

Results

Vermilion snapper was very abundant in trawl catches. Although it was relatively infrequent at inner shelf stations (mean catch per tow of 12.4), vermilion snapper was very abundant at middle (243.7 per tow) and outer shelf (140.1 per tow) stations.

Approximately 115 species of prey were identified in 255 stomachs that contained food. Fish with stomachs containing food were found at all times of the day; 22% of stomachs with food were collected between 0001 and 0600 hours local time; 17%, between 0601 and 1200 hours; 18%, between 1201 and 1800 hours; and 43%, between 1801 and 2400 hours. Although no attempt was made in the field to quantify proportions of stomachs with food, there were more stomachs with obvious contents at night (1801–0600 hr).

Most prey items found in vermilion snapper stomachs were planktonic or nektonic organisms (Table 1). Amphipods, mainly planktonic hyperiids and caprellids (e.g., *Lestrignonus bengalensis*, *Phtisica marina*), copepods, and decapods (e.g., larval forms, *Lucifer faxoni*) were the most frequently consumed taxa. These small crustaceans were eaten in large numbers by smaller vermilion snapper, but, with the exception of decapods, contributed little to prey volume (Table 2). Mysids, cumaceans, and doliolids were also frequently consumed. The overall diet was dominated volumetrically by squids and fishes.

Significant feeding differences between size classes were detected by the Tyler chi-square feeding heterogeneity index (Table 2). Several groups of crustaceans and fishes demonstrated significant differences in frequency between size classes of vermilion snapper. Decapods were important prey for larger fish but dominated the diet of fish between 50 and 100 mm SL. Small crustaceans, such as copepods, stomatopods and amphipods decreased in relative number and volume in the diet with increasing size of predator, although amphipods remained a frequent food item in all size classes examined. Barnacles and cumaceans varied in relative volume of prey for different size classes, but cumaceans increased in frequency in larger fish. Although squids and fishes were eaten by most size classes, they were volumetrically most important in

Table 1

Food items that occurred with a frequency (*F*) of at least one percent of stomachs with food, or that made up at least one percent of the total number (*N*) or volume (*V*) of food in vermilion snapper (*Rhomboplites aurorubens*) stomachs (*n*=255). All higher taxonomic groupings of prey are listed, regardless of their frequency, number, or volume. P=planktonic, H=holoplanktonic, D=demersal zooplankton; B=benthic, E=epifaunal, I=infaunal; N=nektonic.

Taxon and prey item	<i>F</i>	<i>N</i>	<i>V</i>	Taxon and prey item	<i>F</i>	<i>N</i>	<i>V</i>
Cnidaria				Hyperiidea			
nematocysts	1.2	0.1	0.1	<i>Euprone</i> sp. (H)	1.2	0.1	<0.1
Annelida				Hyperiidae undet. (H)	5.1	0.5	0.1
Total Polychaeta	11.9	1.8	2.5	Hyperiidea undet. (H)	5.9	0.7	<0.1
<i>Phyllodoce longipes</i> (I)	3.2	0.4	0.3	<i>Lestrigonus bengalensis</i> (H)	17.8	4.1	0.2
Mollusca				<i>Lycaea</i> sp. (H)	1.2	0.1	<0.1
Total Gastropoda	5.1	0.9	0.3	<i>Phronima</i> sp. (H)	2.0	0.7	0.3
<i>Natica pusilla</i> (B)	1.6	0.4	0.1	<i>Phronima sedentaria</i> (H)	1.6	0.3	<0.1
Total Pelecypoda	1.2	0.3	<0.1	<i>Phronimella elongata</i> (H)	2.0	0.8	<0.1
<i>Ervilia concentrica</i> (I)	1.2	0.3	<0.1	<i>Simorhynchotus</i> sp. (H)	1.6	0.2	<0.1
Total Cephalopoda	5.9	0.4	43.8	Total Decapoda	56.5	20.8	11.7
Loliginidae undet.	4.4	0.3	22.4	Decapoda undet. zoea (P)	3.2	0.2	<0.1
<i>Loligo plei</i> (N)	0.8	<0.1	21.1	Decapoda undet. larvae	2.0	0.2	<0.1
Crustacea				Natantia undet. zoea (P)	2.4	0.3	<0.1
Total Ostracoda	12.6	11.1	0.2	Natantia undet. shrimp	12.2	1.3	1.4
Ostracoda A (H)	11.1	11.0	0.2	Penaeidea			
Total Copepoda	43.5	13.4	0.5	<i>Lucifer faxoni</i> (H)	14.2	8.5	0.8
<i>Calanopia americana</i> (D)	2.8	0.5	<0.1	Penaeidae zoea (P)	1.2	0.1	<0.1
<i>Candacia curta</i> (P)	2.8	0.4	<0.1	<i>Sicyonia typica</i>	1.2	0.1	2.0
<i>Centropages furcatus</i> (H)	4.0	0.3	<0.1	<i>Solenocera atlantidis</i>	1.2	0.1	0.2
<i>Labidocera aestiva</i> (P,B)	6.3	0.7	0.1	Caridea			
<i>Labidocera</i> sp. (H)	1.6	0.2	<0.1	Caridea undet. shrimp	1.2	0.1	<0.1
<i>Oncaea</i> sp. (H)	1.6	0.3	<0.1	<i>Leptocheila</i> sp.	3.2	0.3	0.2
<i>Sapphirina</i> sp. (H)	1.2	0.1	<0.1	<i>Leptocheila papulata</i>	16.6	2.2	3.0
<i>Temora stylifera</i> (H)	9.5	1.6	<0.1	<i>Ogyrides</i> sp.	2.0	0.2	0.2
<i>Temora turbinata</i> (H)	21.7	5.3	0.2	<i>Processa</i> sp.	1.2	0.1	0.1
<i>Undinula vulgaris</i> (H)	3.2	0.6	<0.1	Anomura			
Total Cirripedia	16.2	3.1	2.5	<i>Albunea paretii</i>	4.7	1.4	0.2
Barnacle larvae (D)	15.4	3.0	2.5	<i>Ranilia muricata</i> zoea (P)	2.0	0.2	<0.1
Total Stomatopoda	9.9	2.2	1.0	Brachyura			
Stomatopod larvae (P)	8.3	2.0	0.8	Brachyura undet. zoea (P)	4.0	0.4	<0.1
Stomatopoda adults (D)	1.2	0.1	0.2	Brachyura undet.			
Total Mysidacea	16.6	5.2	0.8	megalopae (P,B)	7.9	1.1	0.2
<i>Anchialina typica</i> (D)	1.2	0.1	<0.1	Brachyura undet. crab	5.5	0.4	0.4
<i>Bowmaniella portoricensis</i>	9.9	1.0	0.3	Calappidae zoea (P)	2.0	0.2	0.1
<i>Bowmaniella</i> sp.	1.2	0.1	<0.1	<i>Ovalipes</i> sp. (P,B)	1.2	0.1	0.4
<i>Mysidopsis bigelowi</i> (B)	1.2	0.1	<0.1	Pinnotheridae zoea (P)	2.4	0.3	<0.1
<i>Promysis atlantica</i> (P)	2.0	3.6	0.4	Portunidae megalopae (P,B)	4.4	0.6	0.1
Total Cumacea	14.6	7.4	1.1	Portunidae crab (P,B)	2.8	0.2	0.2
<i>Cyclaspis varians</i> (D)	5.5	0.7	0.1	<i>Portunus</i> sp. (P,B)	2.0	0.2	0.2
<i>Oxyurostylis smithi</i> (D)	11.1	5.9	0.8	Xanthidae crab (B)	1.6	0.1	0.3
Total Isopoda	2.0	0.2	<0.1	Sipunculida (B)	1.2	0.1	<0.1
Total Amphipoda	47.4	13.7	1.8	Chaetognatha (P)	13.8	1.9	0.3
Gammaridea				Chordata			
<i>Ampelisca abdita</i> (D)	1.2	0.1	<0.1	Thaliacea			
<i>Ampelisca vadorum</i> (D)	2.0	0.1	0.1	Doliolida undet. (H)	8.3	7.4	1.2
Corophiidae undet.	1.6	0.3	<0.1	Larvacea	0.8	<0.1	<0.1
<i>Gammaropsis</i> sp.	2.0	0.2	<0.1	Cephalochordata			
<i>Lysianopsis alba</i>	1.6	0.1	<0.1	<i>Branchiostoma caribbaeum</i> (D)	3.2	0.4	0.1
<i>Photis</i> sp.	1.2	0.1	<0.1	Total Teleostei	27.7	6.9	32.2
<i>Rudilemboides naglei</i>	2.0	0.3	<0.1	Anguilliformes	0.4	<0.1	1.3
<i>Synchelidium americanum</i>	1.6	0.1	<0.1	<i>Prionotus</i> sp. larvae (P)	1.2	4.2	2.6
<i>Tiron tropakis</i> (I)	2.0	0.1	<0.1	<i>Sardinella aurita</i> (N)	1.6	0.2	12.4
Caprellidea				Teleostei undet. eggs (P)	2.0	3.0	<0.1
Caprellidae undet.	1.6	0.1	<0.1	Teleostei undet. larvae (P)	3.2	0.4	0.6
<i>Phtisica marina</i> (P,B)	14.6	2.4	0.3	Teleostei undet.	14.2	1.3	14.7

Table 2

Percent frequency occurrence (F), percent number (N), and percent volume (V) of higher taxonomic groups of food in the diet of vermilion snapper (*Rhomboplites aurorubens*), by length interval. An asterisk (*) indicates significant differences in prey frequency between one length interval and the adjacent larger interval, based on Tyler's (1979) test.

Prey	Length intervals (mm SL)											
	1-50			51-100			101-150			>150		
	F	N	V	F	N	V	F	N	V	F	N	V
Cnidaria (nematocysts)	—	—	—	—	—	—	2.9	0.3	0.9	—	—	—
Annelida												
Polychaeta	7.1*	1.6	2.1	10.9	0.4	2.8	13.3	2.2	2.8	10.9	1.6	2.2
Mollusca												
Gastropoda	7.1	0.9	0.2	1.8	0.1	<0.1	5.7	1.6	1.0	6.0	1.4	0.1
Pelecypoda	—	—	—	—	—	—	2.9	1.2	0.2	—	—	—
Cephalopoda	—	—	—	1.8	0.1	1.0	4.8	0.6	24.2	13.4	1.0	51.4
Crustacea												
Ostracoda	28.6	3.7	1.5	24.4*	29.1	3.6	7.6	1.0	0.1	3.0	0.2	<0.1
Copepoda	82.1	33.9	12.0	60.0	15.3	4.0	41.0*	13.1	1.0	16.4	1.9	<0.1
Cirripedia	21.4	6.1	4.2	20.0	1.3	0.5	11.4	2.6	2.5	18.0	4.8	2.6
Stomatopoda	25.0	2.8	9.6	20.0*	4.6	8.4	3.8	0.4	1.5	4.5	0.3	0.3
Mysidacea	21.4	1.9	4.6	12.3	0.7	0.5	20.0	16.0	4.0	11.9	1.5	0.1
Cumacea	3.6	0.9	0.8	7.3*	0.4	0.4	21.0	21.7	5.0	14.9	4.3	0.3
Isopoda	3.6	0.2	0.2	—	—	—	—*	—	—	6.0	0.5	0.1
Amphipoda	35.7	20.3	12.7	49.1	12.9	6.2	49.5	14.2	4.0	46.3	11.5	0.9
Decapoda	35.7*	25.0	31.1	70.9*	29.4	42.0	52.4	14.1	19.0	58.2	14.3	7.9
Sipunculida	—	—	—	—	—	—	1.9	0.2	0.1	1.5	0.1	<0.1
Chaetognatha	21.4	1.6	3.4	10.9	1.3	0.9	11.4	2.3	0.8	16.4	2.3	0.1
Chordata												
Thaliacea	3.6	0.2	0.4	9.1	1.5	1.6	5.7	2.0	0.4	13.4	24.9	1.3
Larvacea	—	—	—	—	—	—	—	—	—	3.0	0.2	<0.1
Cephalochordata	—	—	—	1.8	0.1	0.2	2.9	1.0	0.2	6.0	0.4	0.1
Teleostei	7.1*	0.7	17.1	43.6*	2.9	27.8	21.9*	5.5	32.4	38.8	28.8	32.7
Examined stomachs												
with food:		28			55			105			67	
Mean SL (mm) of fish												
with food:		36.4			77.8			131.1			168.1	

the diet of larger vermilion snapper (Table 2). Squids and fishes were 76% of the prey volume for all vermilion snapper, but 84.1% of the prey volume (and only 29.8% by number) of fish greater than 150 mm SL.

Vermilion snapper fed sparingly on invertebrates closely associated with the reef habitat and collected in suction and grab samples during the day (Table 3). Electivity values were negative (usually -1.00) for all dominant species in benthic samples. Polychaete species that dominated those samples consisted mainly of tube-reef building species (*Filograna implexa*) and species associated with sponges and corals (*Exogone dispar* and *Syllis spongicola*) (Gardiner, 1975; Wendt et al., 1985); none of these were consumed by vermilion snapper. On the other hand, many species that dominated numerically in the diet (e.g., *Oxyurostylis smithi* and *Lucifer faxoni*) were collected in benthic samples but were not a major component of the daytime reef fauna.

Because abundance of these species in benthic samples was so low, electivity values were positive. Those species that were higher in relative abundance in stomachs than in benthic samples (e.g., *O. smithi*) may have been consumed in the water column during periodic emergence.

As in the case of benthic samples, most species of cumaceans, mysids, stomatopods, and decapods that dominated samples from the sled were not as relatively abundant in stomach samples (Table 4). Most electivity values were negative; however, fewer absences from stomach samples ($E=-1.00$) occurred with the dominant species from sled samples than with the benthic samples. The mysid *Promysis atlantica* at the inner shelf ($E=0.77$) and the decapod *Lucifer faxoni* at the middle shelf ($E=0.63$) were dominant species in sled samples that were positively elected as prey. *Lucifer faxoni* was by far the most abundant species in

Table 3

Relative abundance (percent of total number of individuals, N) and electivity values (E) for dominant benthic species in suction and grab samples and in vermilion snapper (*Rhomboplites aurorubens*) stomachs. Dominant species for each type of sample (benthic or stomach) include those that ranked in the five most abundant species in any depth zone for that type of sample.

	Inner shelf			Middle shelf			Outer shelf		
	Relative abundance			Relative abundance			Relative abundance		
	Fish stomachs	Benthic samples	E	Fish stomachs	Benthic samples	E	Fish stomachs	Benthic samples	E
Dominant species — benthic samples									
<i>Chone americana</i>	—	0.33	-1.00	—	0.81	-1.00	—	0.59	-1.00
<i>Erichthonius brasiliensis</i>	0.09	2.89	-0.94	—	0.30	-1.00	—	0.13	-1.00
<i>Erichthonius</i> sp. A	—	0.08	-1.00	—	—	—	—	3.75	-1.00
<i>Exogone dispar</i>	0.44	3.71	-0.79	—	0.47	-1.00	—	0.01	-1.00
<i>Filograna implexa</i>	—	20.42	-1.00	—	63.87	-1.00	—	21.90	-1.00
<i>Luconacia incerta</i>	—	3.27	-1.00	0.05	1.03	-0.90	—	0.18	-1.00
<i>Malacoceros glutaeus</i>	—	0.41	-1.00	—	0.81	-1.00	—	0.02	-1.00
<i>Phyllochaetopterus socialis</i>	—	0.21	-1.00	—	0.12	-1.00	—	12.40	-1.00
<i>Pista palmata</i>	—	0.09	-1.00	—	0.08	-1.00	—	8.60	-1.00
<i>Podocerus</i> sp. A	—	2.87	-1.00	—	0.27	-1.00	—	0.14	-1.00
<i>Spiophanes bombyx</i>	—	0.39	-1.00	—	0.46	-1.00	—	5.81	-1.00
<i>Syllis spongicola</i>	—	2.14	-1.00	—	1.90	-1.00	—	1.38	-1.00
Total	0.53	36.81		0.05	70.12		0.00	54.92	
Dominant species — stomachs									
<i>Bowmaniella portoricensis</i>	0.18	0.09	0.32	1.80	0.10	0.89	0.50	0.22	0.37
<i>Leptochela papulata</i>	0.35	0.04	0.81	3.45	0.09	0.95	1.86	0.12	0.88
<i>Lucifer faxoni</i>	12.05	0.18	0.97	9.79	0.01	0.99	0.62	0.04	0.87
<i>Oxyurostylis smithi</i>	15.74	0.67	0.92	2.46	0.14	0.89	—	—	—
<i>Phtisica marina</i>	0.09	0.01	0.75	1.80	0.03	0.97	7.20	0.40	0.90
<i>Phyllodoce longipes</i>	1.14	0.06	0.89	0.05	0.04	0.10	0.12	0.20	-0.22
<i>Promysis atlantica</i>	11.79	—	1.00	0.05	<0.01	0.88	—	—	—
<i>Rhudilemboides naglei</i>	1.06	0.05	0.91	—	<0.01	-1.00	—	0.04	-1.00
Total	42.40	1.10		19.40	0.42		10.30	1.02	
Number of stomachs with food:		49			138			68	

sled samples at the inner shelf and was also abundant in stomach samples but demonstrated negative electivity at the inner ($E=-0.53$) and outer ($E=-0.39$) shelf sites. At the middle shelf, *L. faxoni* was the most abundant species in the analyzed taxa in fish stomachs and ranked third in abundance in sled samples. Many of the species that were high in relative abundance in fish stomachs also occurred in sled samples; however, electivity values were not always positive. The relative abundance of cumaceans, mysids, stomatopods, and decapods in fish stomachs, compared with their abundance in sled samples, indicated that vermilion snapper often selected crustaceans in higher proportions than was their availability to the plankton sled at night (Table 4). Included were several orders of Crustacea, particularly the cumacean *Oxyurostylis smithi* and the mysid *Promysis atlantica* at inner shelf stations, the decapods *Lucifer faxoni* and *Leptochela papulata* at middle shelf stations, and the decapods

Leptochela papulata and *Solenocera atlantidis* at the outer shelf.

Comparing dominant species in the diet of vermilion snapper with their relative abundance in benthic (lower half of Table 3) and sled (lower half of Table 4) samples indicated high positive selectivity for most prey species from both environments sampled. For suction and grab samples, this was due to the extremely low abundance (<1%) of all the dominant prey in the benthos. For the sled samples, many dominant prey species were also dominant in the environment.

Discussion

The vermilion snapper is well adapted to foraging in the water column (Davis and Birdsong, 1973; Grimes, 1979). Grimes (1979) reported that the diet of vermilion snapper was dominated by planktonic organisms

Table 4

Relative abundance (percent of total number of individuals, N) and electivity values (E) for dominant species of decapods, cumaceans, mysids and stomatopods in sled samples and vermilion snapper (*Rhomboplites aurorubens*) stomachs. Dominant species for each type of sample (sled or stomach) include those that ranked in the five most abundant species of decapods, cumaceans, mysids and stomatopods in any depth zone for that type of sample.

	Inner shelf			Middle shelf			Outer shelf		
	Relative abundance			Relative abundance			Relative abundance		
	Fish stomachs	Sled samples	E	Fish stomachs	Sled samples	E	Fish stomachs	Sled samples	E
Dominant species — sled samples									
<i>Bowmaniella portoricensis</i>	0.30	5.56	-0.90	5.52	10.45	-0.31	4.30	5.45	-0.12
<i>Lucifer faxoni</i>	20.57	66.77	-0.53	29.93	6.79	0.63	5.38	12.29	-0.39
<i>Mysidopsis furca</i>	—	0.67	-1.00	0.17	4.49	-0.93	—	22.28	-1.00
<i>Neopontonides beaufortensis</i>	—	4.10	-1.00	—	3.35	-1.00	—	0.77	-1.00
<i>Periclimenes iridescens</i>	—	3.18	-1.00	—	3.75	-1.00	—	0.84	-1.00
<i>Pontophilus gorei</i>	—	—	—	—	0.03	-1.00	—	7.33	-1.00
<i>Promysis atlantica</i>	20.12	2.57	0.77	0.17	7.24	-0.95	—	0.63	-1.00
<i>Thor manningi</i>	—	0.05	-1.00	—	0.43	-1.00	—	2.44	-1.00
Total	40.99	82.90		35.15	36.63		9.68	52.03	
Dominant species — stomachs									
<i>Bowmaniella portoricensis</i>	0.30	5.56	-0.90	5.52	10.45	-0.31	4.30	5.45	-0.12
<i>Cyclops varians</i>	1.05	0.05	0.91	3.18	1.45	0.37	—	0.41	-1.00
<i>Lucifer faxoni</i>	20.57	66.77	-0.53	29.93	6.79	0.63	5.38	12.29	-0.39
<i>Leptochela papulata</i>	0.60	0.39	0.21	10.54	2.07	0.67	16.13	1.61	0.82
<i>Oxyrostylis smithi</i>	26.88	1.38	0.90	7.52	1.19	0.73	—	0.42	-1.00
<i>Promysis atlantica</i>	20.12	2.57	0.77	0.17	7.24	-0.95	—	0.63	-1.00
<i>Solenocera atlantidis</i>	—	—	—	—	0.03	-1.00	4.30	1.12	0.59
Total	69.52	80.82		56.86	32.56		30.11	22.70	
Number of stomachs with food:		49			138			68	

and he noted that the diet of juveniles (<100 mm TL) was dominated volumetrically by copepods. In the present study, decapods dominated the diet volume of fish less than 101 mm SL. The feeding habits of vermilion snapper changed considerably with size in the present study, although pelagic prey dominated in all size classes. As vermilion snapper grows, it switches from a diet of many small crustaceans, to a diet dominated by a few large cephalopods, fishes, or decapod crustaceans. The switch to different prey taxa and to fewer, larger prey individuals was similar to ontogenetic diet changes noted by Sedberry (1983) for several demersal fishes from the outer continental shelf. In contrast, Schmitt and Holbrook (1984) found that black surfperch (*Embiotoca jacksoni*) switched to larger prey, but that gross taxonomic composition of the diet did not change and that surfperch continued to feed on macrocrustaceans, in spite of growth and changes in body size and foraging behavior. Vermilion snapper, like many other fishes (Sedberry, 1983), apparently becomes capable of taking larger prey as it grows and switches from picking plankton to pursuing and cap-

turing active nektonic species, such as Spanish sardine (*Sardinella aurita*), and squids.

Grimes (1979) suggested that vermilion snapper is a nocturnal forager and that selective feeding by vermilion snapper on demersal zooplankton, such as cumaceans, indicates nocturnal foraging. These crustaceans are infaunal in the sand or epifaunal in reef crevices during the day but emerge at night (Anger and Valentin, 1976; Alldredge and King, 1985), becoming prey for vermilion snapper and other fishes that forage on near-bottom zooplankton at night. Demersal zooplankton demonstrating nocturnal emergence and found in the diet of vermilion snapper included syllid polychaetes, some calanoid copepods, cumaceans, amphipods, decapods, barnacle and stomatopod larvae, chaetognaths and cephalochordates (Williams and Bynum, 1972; Fincham, 1974; Anger and Valentin, 1976; Hobson and Chess, 1976; Alldredge and King, 1977; Hammer, 1981; Alldredge and King, 1985; Cahoon and Tronzo, 1988). These taxa are dominant members of the demersal zooplankton (Porter and Porter, 1977) and emerge from benthic habitats at night when they

feed, molt, reproduce or disperse (Aldredge and King, 1985). This behavior makes them subject to intense predation by vermilion snapper or other specialized nocturnal predators (Robertson and Howard, 1978).

Demersal zooplankton are approximately as abundant as holozooplankton on the continental shelf off North Carolina (Cahoon and Tronzo, 1992), and the nocturnal emergence of demersal zooplankton probably increases overall food availability at night, while allowing planktivorous fishes to feed under the cover of darkness. Small vermilion snapper are prey for diurnal lutjanids and crepuscular serranids (South Carolina Wildlife and Marine Resources Department¹; Parrish, 1987; Sedberry, 1988) and would be subject to predation during the day.

Vermilion snapper also consumes holoplanktonic species such as copepods, hyperiids, *Lucifer faxoni*, and doliolids, as well as nektonic squids and fishes. As noted by Grimes (1979), squids were especially important in the diet of large juveniles and adults. These larger size classes of vermilion snapper also fed more on fishes, which included schooling pelagic species such as Spanish sardine, *Sardinella aurita*. Spanish sardine makes up 9.4% of fishes caught in trawls on the southeastern continental shelf². Predation by vermilion snapper on nektonic foragers such as squids and Spanish sardine provides a trophic link between the pelagic nekton and the reef. In the role as an abundant consumer of nekton, holoplankton, and demersal zooplankton, vermilion snapper may be important in transferring energy from benthic sand habitats and the water column to the reef, in the form of feces. Feces that disintegrate just above the reef provide fine particles and nutrients for filter- and suspension-feeders, and fecal pellets that are less refractile can be used directly by small crustaceans and other organisms living in the reef (Rothans and Miller, 1991). Vermilion snapper appear to be relatively inactive during the day, hovering or moving slowly in large schools along the reefs within a meter of the bottom (pers. observ. by GRS from *Sea Link I*). By feeding in the water column at night and swimming just above the reef during the day, vermilion snapper enhances the transfer of this organic matter to the benthos. During these diurnal resting periods, vermilion snapper probably deposit feces, derived from water column noctur-

nal foraging, onto the reef. Bray et al. (1981) also found that a planktivorous reef fish functioned as a trophic link between the plankton and benthos by importing organic carbon to the reef in the form of feces. Meyer and Schultz (1985) found that grunts (*Haemulon* spp.) feeding on sand flats transferred significant amounts of nutrient and organic matter to reefs, thus enhancing coral growth.

Benthic polychaetes ranking high in relative abundance in the suction and grab samples were not important in the diet of vermilion snapper, and electivity values for all dominant species in the benthic samples were negative. The dominant crustaceans in benthic samples were epibenthic species such as the corophoid amphipod, *Erichthonius brasiliensis*, and the caprellid amphipod *Luconacia incerta* which attach to sessile invertebrates and are usually closely associated with the reef substratum (McCain, 1968; Bousfield, 1973). Because *E. brasiliensis* and caprellid amphipods have also been found in nocturnal zooplankton samples (Williams and Bynum, 1972; Hobson and Chess, 1976), they may be consumed by predators at night in the water column. Some motile benthic crustaceans such as mysids, cumaceans, and decapods that were common in vermilion snapper stomachs were much higher in relative abundance in stomachs than in benthic samples. Vermilion snapper apparently prey on these benthic crustaceans during their periodic migrations into the water column. The polychaetes that dominated benthic samples apparently do not undertake such migrations.

Vermilion snapper feed on many of the same prey species as the benthic-feeding sparid *Stenotomus chrysops*, an abundant demersal fish of the continental shelf (Sedberry and Van Dolah, 1984; Sedberry, 1988; Sedberry et al.²). Submersible observations indicate that *S. chrysops* feeds during the day on the benthos, living in sand adjacent to reef habitat, whereas vermilion snapper were not observed to forage in this manner. Vermilion snapper apparently consumes sand-dwelling benthos at night, when they emerge from the bottom, while *S. chrysops* feeds on benthos during the day when demersal zooplankton has burrowed in the bottom. This provides a temporal partitioning of prey resources between these two dominant species of reef-associated fish.

For reef fishes of the southeastern shelf, there is large variation in the degree of dependence on hard substrate as a habitat for prey (Sedberry, 1985, 1987, 1988). Of the three most abundant species in our reef trawl catches (*S. chrysops*, *Haemulon aurolineatum*, and *R. aurorubens*), all occur over sand bottom, although they are much more abundant over reefs (Wenner, 1983; Sedberry and Van Dolah, 1984). The

¹South Carolina Wildlife and Marine Resources Department. 1984. Final Report. South Atlantic OCS area living marine resources study. Phase III. Volume 1. Prepared by Marine Resources Research Institute, SCWMRD, for Minerals Management Service, Washington, D.C., under contract No 14-12-0001-29185, 223 p.

²Sedberry, G. R., C. A. Barans, C. A. Wenner, and V. G. Burrell Jr. The ichthyofauna of sandy bottom habitat on the continental shelf off the southeastern U.S. Manuscr. in prep.

former two species feed primarily on sand bottom benthos (Sedberry, 1985, 1988). Although *H. aurolineatum* and *S. chrysops* feed heavily on sand infauna and are not completely dependent on reef habitat, vermilion snapper is more restricted to reef habitat and does not range far from a home reef (Fable, 1980). Wenner (1983) collected only 2 specimens in 11 trawling tows in sand bottom habitat on the southeastern continental shelf, whereas *S. chrysops* and *H. aurolineatum* are dominant species in sand habitats (Wenner, 1983; Sedberry²). Vermilion snapper did not, however, feed directly on reef fauna, and its attraction to reefs may be behavioral rather than trophic.

Although vermilion snapper feeds extensively on demersal zooplankton, many individuals also feed opportunistically on concentrations of holoplankton that occur on the southeastern shelf. Copepods, such as *Undinula vulgaris* and especially *Temora turbinata*, that were frequent food items for vermilion snapper are epipelagic oceanic species that are transported landward across the continental shelf (Hopkins et al., 1981). Off the southeastern United States, upwelling at the shelf edge and cross-shelf transport of deep, highly productive oceanic water provide mechanisms for shoreward movement of shelf-edge biota, including copepods (*U. vulgaris*, *T. turbinata*, *Oncaea* spp.), doliolids, sergestid decapods (e.g., *Lucifer faxoni*), and other abundant oceanic zooplankters (Yoder et al., 1983; Paffenhöfer et al., 1984). Vermilion snapper, one of the most abundant fishes at shelf edge depths (Sedberry and Van Dolah, 1984), apparently takes advantage of this abundant resource and performs the function of transferring some of this oceanic productivity to bottom habitats on the continental shelf.

In conclusion, vermilion snapper feeds on a variety of prey above the substrate, much of which is demersal zooplankton. Although it is unknown how much of the biomass of the daytime benthos is composed of nocturnally emerging demersal zooplankton, it is apparent that these organisms are an important food source for vermilion snapper and other reef fishes. Demersal zooplankton, such as mysids, cumaceans, ampeliscid amphipods, and certain decapods, composed at least eight percent of the total volume of food for vermilion snapper in the present study and are more important in the diet of smaller size classes. While a small contribution, these benthic species provide a feeding opportunity for vermilion snapper and may be more important in the diet during periods of low productivity of holoplankton. Nektonic fishes and cephalopods provide the greatest volume of food for larger vermilion snapper. Because it is prey for other reef predators, vermilion snapper is an important trophic link among several habitats on the southeastern continental shelf.

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