

THE FEEDING HABITS OF TWO DEEP
SLOPE SNAPPERS, *PRISTIPOMOIDES ZONATUS*
AND *P. AURICILLA*, AT PATHFINDER REEF,
MARIANA ARCHIPELAGO

The lutjanid snappers belonging to the genus *Pristipomoides* are among the most prized and valuable commercial fish resources in tropical and subtropical regions of the Pacific Ocean (Polovina and Ralston 1987). These fishes normally inhabit escarpments with high vertical relief. During an intensive bottom fish survey conducted at Pathfinder Reef in the Mariana Archipelago, two species of snappers, *P. zonatus* and *P. auricilla*, comprised more than 68% of the total catch (Polovina 1985). Depth of capture data on these two species demonstrated overlap in their bathymetric distribution (Polovina et al. 1985; Ralston and Williams 1988).

Numerous feeding studies have been conducted on snappers that inhabit shallow (<100 m) water; however, published information on the diets of deep slope snapper species in the tropical Pacific is nearly nonexistent (see review by Parrish 1987). Kami (1973) noted prey items for four species of *Pristipomoides* in Guam with total sample sizes ranging from one to six individuals, and Kluegel (1921) presented information on the diet of *P. filamentosus* in Hawaii based upon four fish. The present paper examines how two coexisting species, *P. zonatus* and *P. auricilla*, partition food resources. With recent efforts to expand and develop commercial fisheries for tropical snappers as well as other deep dwelling bottom fishes, there is an increasing need to recognize the resources that support these fishes. The results presented here will therefore be useful for developing fishery management strategies and will lead to a better understanding of the ecology of tropical demersal communities.

Methods

Stomach and spew samples from 106 *P. zonatus* and 72 *P. auricilla* were collected at Pathfinder Reef during an intensive fishing experiment on 10–19 April and 5–7 May 1984. Located in the Mariana Archipelago at lat. 16°30'N, long. 143°05'E, Pathfinder Reef is a circular, volcanic pinnacle ris-

ing to about 16 m beneath the surface. The fishes, ranging from 30.2 to 44.4 cm fork length (\bar{x} = 38.4 cm, standard deviation = 2.81), were caught with hook and line on hydraulic-powered gurdies. The terminal rig and gurdy specifications are described in Uchida and Uchiyama (1986). While fishing, the vessel was usually allowed to drift over the banks and steep slopes, targeting species in the 150–275 m depth range. Our study species were captured mainly in depths between 180 and 220 m. Fishing was conducted around the entire perimeter of the bank during daylight hours (Polovina 1986).

Typical of feeding studies conducted on deepwater species with swimbladders, regurgitation of stomach contents posed serious problems (Bowman 1986). The rapid ascent to the surface forced most of the stomachs to evert and lose an unknown quantity of the contents. Many food items, however, were caught in the throat or gill rakers, picked out, and saved. These items, referred to as spews, and full stomachs were frozen and returned to the laboratory for analysis.

Laboratory procedures for examination of the samples were similar to those employed by Harrison et al. (1983). Briefly, food samples were sorted, counted, and identified to the lowest practical taxon. The volume of prey items was measured by water displacement. Fishes were predominantly identified by osteological and external anatomical characters and morphometrics. Invertebrates were identified by undigested hard parts and external morphological features including shells for gastropods and exoskeletons for crustaceans.

To analyze the data, we used percent frequency of occurrence to provide a qualitative picture of the food spectrum and percent volume of prey to describe relative biomass of prey items (Hyslop 1980). Because a high percentage of the diets was composed of urochordates, we did not employ any numerical analysis of the prey items. These pelagic, colonial tunicates (all *Pyrosoma* spp.) did not occur in discrete units and were thus difficult to count.

An interspecific comparison of the two snapper species requires some measure of diet overlap and niche breadth. Diet overlap (C_i) was computed by using the formula developed by Morisita (1959) and

modified by Horn (1966). C_1 is formulated as

$$C_1 = \frac{2 \sum_{h=1}^s p_{ih} \cdot p_{jh}}{\sum_{h=1}^s p_{ih}^2 + \sum_{h=1}^s p_{jh}^2};$$

where p_{ih} and p_{jh} are the biomass proportions of a prey item h in the diets of species i and j , respectively, and s is the total number of major prey taxa in the food spectrum. C_1 varies from zero, when there is no overlap between the diets of species i and j , to one, when all prey items are in equal proportions. Niche breadth (B) for each species was computed by using the formula developed by Levins (1968):

$$B_i = \frac{1}{\sum_{h=1}^s p_{ih}^2};$$

where again, p_{ih} is the biomass proportion of a prey item h in the diet of species i and s is the total number of major prey taxa. The breadth values range from one, when prey items consist only of one category, to s , when all food items are in equal proportion in the same diet. These breadth values were then normalized as $B_n = B/s$, which ranges from a value of zero, representing the most uneven distribution of prey composition in the diet, to one, representing a totally even distribution. For the calculation of both breadth and overlap indexes, only prey items identified at least to the family level were used.

Results

The diets of *P. zonatus* and *P. auricilla* differed considerably from each other (Table 1). By volume, the 106 food samples from *P. zonatus* collected for this study were composed of 59.0% invertebrates and 41.0% fishes. The dominant invertebrate prey included the pelagic tunicate *Pyrosoma* spp. and galatheid crabs, nearly all *Munida japonica*. The most frequently occurring fishes in the diet were the ophichthid eel, *Shultzidia johnstonensis*, and the symphysanodontids *Symphysanodon maunaloae* and *S. typus*. In general, *P. zonatus* preyed heavily upon benthic organisms. Many of the prey items, such as echinoderms, octopods, and the various benthic

crustaceans, must have been captured at the substratum. Conversely, the 72 food samples from *P. auricilla* were composed of 88.2% invertebrates and 11.8% fishes by volume; all were predominantly pelagic forms. Major invertebrate prey included the pelagic heteropod *Atlanta* spp., the pelagic tunicate *Pyrosoma* spp., and numerous species of cavolinid pteropods. Few fishes, most of them small and unidentifiable, were eaten by this snapper species.

The dietary overlap value (C_1) was calculated to be 0.04. Based on the Langton (1982) convention of 0.00–0.29 as the low overlap, 0.30–0.60 as the medium overlap, and >0.60 as the high overlap, very little overlap occurred between the diets of the two snappers at Pathfinder Reef.

The niche breadth values (B) calculated for the two species indicated *P. zonatus* had a higher food breadth (3.82, $s = 10$) than *P. auricilla* (2.05, $s = 6$), suggesting more food specialization among the latter. Evenness in the proportion of the diet attributed to each prey type, however, was similar for the two species ($B_n = 0.38$ in *P. zonatus*; $B_n = 0.34$ in *P. auricilla*).

Discussion

As previously mentioned, a few fragmentary reports (cf. Parrish 1987) from various localities have addressed the trophic relationships of any tropical snapper inhabiting waters deeper than 100 m. He further attributes this lack of information to the normally remote fishing localities and, most of all, to the loss of stomach contents through regurgitation during capture.

The problem of regurgitation has plagued trophic studies of demersal fishes, regardless of whether fishing involved trawls (Mauchline and Gordon 1984; Clark 1985; Bowman 1986) or hook and line (Kluegel 1921; Forster et al. 1970; Seki 1984). Likewise, most food samples for our study were salvaged, regurgitated spewings retained in the mouth, throat, or gill rakers of the fishes. It is possible that the material occurring as spews may consist predominantly of certain prey items more likely retained because of size or some morphological structure, thereby resulting in a biased interpretation of the diet. We nevertheless employ the assumption that what is recovered is representative of the diets at the time of capture.

Based upon depth of capture information, *P. zonatus* and *P. auricilla* occupy nearly the same habitat, and considerable spatial overlap occurs in their foraging zones (Polovina 1986; Ralston and

Williams 1988). During submersible dives at Johnston Atoll, Ralston et al. (1986) verified this cohabitation with visual observations of the two species. *Pristipomoides zonatus* were observed between 215 and 250 m (median, 230 m) and *P. auricilla* between 205 and 295 m (median, 240 m). Our dietary analysis suggests that these two demersal species partition food resources by selecting prey from different microhabitats. *Pristipomoides zonatus* is best described as a demersal carnivore, with its diet containing benthic and demersal invertebrates together with tunicates and small fishes. In contrast, *P. auricilla* feeds primarily on large pelagic plankton, as evidenced by the abundance of heteropods, pteropods, and tunicates among the prey items.

Kami (1973) also found tunicates (*Pyrosoma* spp.) in four of the five *P. auricilla* food samples in Guam. The differences in diet composition are consistent with the suggestion, based upon catch rates and the taking of a baited hook, that *P. zonatus* is the more aggressive predator of the two species (Polovina 1986).

Although our study revealed little overlap between the diets of *P. zonatus* and *P. auricilla*, the common occurrence of *Pyrosoma* spp. in the diets of both species seems significant. Similarly, these tunicates were also found among the stomach contents of three other congeneric species (Kami 1973; Parrish 1987). Kashkina (1987) reported intensive predation on pyrosomes, as well as salps, among

TABLE 1.—Diet composition of *Pristipomoides zonatus* and *P. auricilla* at Pathfinder Reef, Mariana Archipelago.

Species	<i>Pristipomoides zonatus</i> (N = 106)		<i>Pristipomoides auricilla</i> (N = 72)	
	% volume	% frequency	% volume	% frequency
Invertebrates				
Hydrozoa				
Siphonophora	—	—	3.2	20.8
Ctenophora	0.3	0.9	—	—
Polychaeta	0.3	0.9	5.4	15.3
Gastropoda	0.1	0.9	0.3	4.2
Atlantidae	—	—	0.9	12.5
Cavolinidae	0.2	4.7	38.1	72.2
Cephalopoda	0.3	0.9	7.4	2.8
Teuthoidea	—	—	0.2	1.4
Octopoda	0.1	0.9	—	—
Crustacea	2.6	10.4	5.5	44.4
Stomatopoda	0.3	0.9	0.3	1.4
Euphausiacea				
Euphausiidae	—	—	0.7	4.2
Decapoda				
Caridea	0.5	2.8	0.3	2.8
Pandalidae	1.2	2.8	—	—
Palinura	—	—	0.7	1.4
Anomura				
Galatheidae	19.6	28.3	—	—
Brachyura	17.1	13.2	0.2	1.4
Echinodermata				
Ophiuroidea	0.1	0.9	—	—
Tunicata				
Pyrosomatidae	16.3	34.9	25.0	37.5
Fishes				
Osteichthyes				
(Unid. fishes)	16.3	22.6	8.7	16.7
Anguilliformes	8.2	7.6	—	—
Ophichthidae	8.6	10.4	—	—
Myctophiformes	—	—	2.5	1.4
Ophidiiformes				
Ophidiidae	0.1	0.9	—	—
Perciformes				
Serranidae	4.0	1.9	—	—
Symphysanodontidae	3.1	5.7	—	—
Chaetodontidae	0.1	0.9	—	—
Gempylidae	—	—	0.6	2.8
Tetraodontiformes				
Balistidae	0.6	0.9	—	—

numerous pelagic and demersal fish species. Originally thought to be of little nutritional value, these tunicates have been found to contain filtered concentrations of phytoplankton and microzooplankton, thereby elevating the preys' food value. Regional and highly localized oceanographic processes will affect the distribution of such potential planktonic prey, and exploitation of these resources may influence the local distribution of predator species (Brock and Chamberlain 1968; Bray 1981). Deepwater snappers are most abundant on slopes of upcurrent exposure and near underwater headlands at Johnston Atoll (Ralston et al. 1986). These abundance patterns were attributed to planktonic concentrations created by mesoscale oceanographic processes as noted with other fishes on bank or slope habitats (Isaacs and Schwartzlose 1965; Pereyra et al. 1969).

Polovina (1986) suggested that fishing may selectively deplete one species, such as *P. zonatus*, preferentially over another (*P. auricilla*) and thereby alter the species composition in a given locality. With the small degree of dietary overlap between the two species in this study, such selective removal of *P. zonatus* will decrease predation pressure on the demersal prey resources of this species and, as evidenced in Larson (1980), may ultimately allow greater niche breadth for coexisting predator species.

In conclusion, this study has provided qualitative insight into dietary habits of two sympatric, deepwater species and has permitted some inferences regarding their ecology. Much more study is needed to comprehend fully the role of these predators in the ecosystem. Logistical constraints, including the problem of regurgitation, will continue to make quantitative assessments of diet a difficult task until new capture methodologies are developed. However, the rewards in improved understanding of deepwater ecology and increased ability to manage these valuable stocks suggest that the efforts will be justified.

Acknowledgments

We thank G. W. Boehlert, R. E. Bowman, C. B. Grimes, J. D. Parrish, J. J. Polovina, S. Ralston, and the two anonymous reviewers for their helpful comments on various drafts of the manuscript. This paper is a result of the Resource Assessment Investigation of the Mariana Archipelago at the Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA.

Literature Cited

- BOWMAN, R. E.
1986. Effect of regurgitation on stomach content data of marine fishes. *Environ. Biol. Fishes* 16:171-181.
- BRAY, R. N.
1981. Influence of water currents and zooplankton densities on daily foraging movements of blacksmith, *Chromis punctipinnis*, a planktivorous reef fish. *Fish. Bull., U.S.* 78: 829-841.
- BROCK, V. E., AND T. C. CHAMBERLAIN.
1968. A geological and ecological reconnaissance off western Oahu, Hawaii, principally by means of the research submarine "Asherah." *Pac. Sci.* 22:373-394.
- CLARK, M. R.
1985. The food and feeding of seven fish species from the Campbell Plateau, New Zealand. *N.Z. J. Mar. Freshwater Res.* 19:339-363.
- FORSTER, G. R., J. R. BADCOCK, M. R. LONGBOTTOM, N. R. MERRETT, AND K. S. THOMSON.
1970. Results of the Royal Society Indian Ocean Deep Slope Fishing Expedition, 1969. *Proc. R. Soc. Lond., B Biol. Sci.* 175:367-404.
- HARRISON, C. S., T. S. HIDA, AND M. P. SEKI.
1983. Hawaiian seabird feeding ecology. *Wildl. Monogr.* 85, 71 p.
- HORN, H. S.
1966. Measurement of "overlap" in comparative ecological studies. *Am. Nat.* 100:419-424.
- HYSLOP, E. J.
1980. Stomach contents analysis—a review of methods and their application. *J. Fish Biol.* 17:411-429.
- ISAACS, J. D., AND R. A. SCHWARTZLOSE.
1965. Migrant sound scatterers: Interaction with the sea floor. *Science* 150:1810-1813.
- KAMI, H. T.
1973. The *Pristipomoides* (Pisces: Lutjanidae) of Guam with notes on their biology. *Micronesica* 9:97-117.
- KASHKINA, A. A.
1987. Feeding of fishes on salps (Tunicata, Thaliacea). *J. Ichthyol.* 26:57-64.
- KLUEGEL, E.
1921. The food of Hawaiian food fishes. M.S. Thesis, Univ. Hawaii, Honolulu, HI, 18 p.
- LANGTON, R. W.
1982. Diet overlap between Atlantic cod, *Gadus morhua*, silver hake, *Merluccius bilinearis*, and fifteen other northwest Atlantic finfish. *Fish. Bull., U.S.* 80:745-759.
- LARSON, R. J.
1980. Competition, habitat selection, and the bathymetric segregation of two rockfish (*Sebastes*) species. *Ecol. Monogr.* 50:221-239.
- LEVINS, R.
1968. Evolution in changing environments. Princeton Univ. Press, Princeton, 120 p.
- MAUCLINE, J., AND J. D. M. GORDON.
1984. Feeding and bathymetric distribution of the gadoid and morid fish of the Rockall Trough. *J. Mar. Biol. Assoc., U.K.* 64:657-665.
- MORISITA, M.
1959. Measuring of interspecific association and similarity between communities. *Mem. Fac. Sci., Kyushu Univ., Ser. E Biol.* 3:65-80.
- PARRISH, J. D.
1987. The trophic biology of snappers and groupers. *In* J. J.

- Polovina and S. Ralston (editors), Tropical snappers and groupers: Biology and fisheries management, p. 405-463. Westview Press, Boulder and Lond.
- PEREYRA, W. T., W. G. PEARCY, AND F. E. CARVEY, JR.
1969. *Sebastes flavidus*, a shelf rockfish feeding on mesopelagic fauna, with consideration of the ecological implications. J. Fish. Res. Board Can. 26:2211-2215.
- POLOVINA, J. J.
1985. Variation in catch rates and species composition in handline catches of deepwater snappers and groupers in the Mariana Archipelago. Proc. Fifth Int. Coral Reef Congr., Tahiti 5:515-520.
1986. A variable catchability version of the Leslie model with application to an intensive fishing experiment on a multi-species stock. Fish. Bull., U.S. 84:423-428.
- POLOVINA, J. J., R. B. MOFFITT, S. RALSTON, P. M. SHIOTA, AND H. A. WILLIAMS.
1985. Fisheries resource assessment of the Mariana Archipelago, 1982-85. Mar. Fish. Rev. 47(4):19-25.
- POLOVINA, J. J., AND S. RALSTON (editors).
1987. Tropical snappers and groupers: Biology and fisheries management. Westview Press, Boulder and Lond., 659 p.
- RALSTON, S., R. M. GOODING, AND G. M. LUDWIG.
1986. An ecological survey and comparison of bottom fish resource assessments (submersible versus handline fishing) at Johnston Atoll. Fish. Bull., U.S. 84:141-154.
- RALSTON, S., AND H. A. WILLIAMS.
1988. Depth distributions, growth, and mortality of deep slope fishes from the Mariana Archipelago. U.S. Dep. Commer., NOAA Tech. Memo. NMFS, NOAA-TM-NMFS-SWFC-113, 47 p.
- SEKI, M. P.
1984. The food and feeding habits of the grouper, *Epinephelus quernus* Seale 1901, in the Northwestern Hawaiian Islands. In R. W. Grigg and K. Y. Tanoue (editors), Proceedings of the Second Symposium on Resource Investigations in the Northwestern Hawaiian Islands, vol. 2, May 25-27, 1983, University of Hawaii, Honolulu, Hawaii, p. 179-191. UNIHI-SEAGRANT-MR-84-01.
- UCHIDA, R. N., AND J. H. UCHIYAMA (editors).
1986. Fishery atlas of the Northwestern Hawaiian Islands. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 38, 142 p.

MICHAEL P. SEKI

Southwest Fisheries Center Honolulu
Laboratory
National Marine Fisheries Service, NOAA
2570 Dole St.
Honolulu, HI 96822-2396

MICHAEL W. CALLAHAN

Hawaii Cooperative Fishery Research Unit
University of Hawaii
Honolulu, HI 96822