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Feeding Ecology of Deepwater Lutjanid Snappers at Penguin Bank, Hawaii

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Abstract.—Deepwater snappers are a valuable component of fisheries on slopes and banks in Hawaii and in much of the world's tropics. Their ecology and trophic relationships in these deepwater habitats are poorly known. Line fishing in this study simultaneously collected six of the seven lutjanid species that commonly occur in the major deepwater snapper fishery at Penguin Bank, Hawaii. The catch rate of each species showed diel variability; the patterns of some species were distinctly different. The depth distribution of feeding, as indicated by depth of capture, differed considerably among species; all species were taken within several meters of the bottom. Size (fork length) of the predator species did not appear to be stratified by time of capture (daylight versus darkness) or median capture depth. Regurgitation of gut contents seemed to be reduced when fish were retrieved at a rate that was slower than used in commercial practice but rapid enough to prevent death or morbidity while hooked. The food remaining in line-caught specimens appeared to be representative of what was originally eaten. The six snapper species ate considerable amounts of a wide range of pelagic animals and demersal fishes and much smaller quantities of a few invertebrate benthic groups. *Etelis coruscans, Etelis carbunculus,* and *Aprion virescens* formed a distinct, primarily piscivorous feeding guild. *Pristipomoides filamentosus* and *Pristipomoides sieboldii* formed a distinct guild dominated by zooplankton feeding. The few specimens of *Pristipomoides zonatus* appeared somewhat intermediate in diet. Important planktonic prey groups included crustaceans, pteropods, and large, pelagic, colonial urochordates (e.g., salps). Urochordates made a significant contribution to the diet even for some of the primarily piscivorous species. Major diel and seasonal shifts in diet were found only in *P. filamentosus*; they involved the relative proportions of fish, and especially of the major planktonic groups. Our information on diet composition and depth and time of feeding (catch) suggests that considerable resource partitioning occurs among these deepwater snappers.

Deepwater lutjanid snappers represent an important resource throughout the tropical and subtropical oceans of the world. Many species of Lutjanidae are highly prized as food fish and typically have a high market value wherever they are found (Polovina and Ralston 1987). In the tropical Pacific, several genera of these fishes inhabit the slopes of land masses and banks at depths of 100–400 m. Understanding the trophic support for these fishes in this environment can provide important insight for management of their fisheries. Published studies of the diets of deepwater snappers are scarce, however, because these fisheries occur in isolated locations, and collecting gut contents from such deepwater fishes is difficult (Parrish 1987).

In Hawaii, deepwater lutjanid snappers are the mainstay of the commercial and recreational bottom fish fishery, contributing over 88% by weight and 93% by value of the total commercial deepwater bottom fish landings in 1990 (HDAR 1991). Bottom fishing is mainly concentrated on the steep slopes of deepwater banks. These banks and the deep slopes of island coasts have an aggregate area over six times that of shallow-water reefs in the state (Agegian et al. 1988). Similar grounds support existing or potential snapper fisheries in much of the Pacific and other tropical waters (Polovina and Shomura 1990). Our limited understanding of the ecology and production of deepwater banks suggests that these important habitats probably function very differently from shallow-water coral reef ecosystems. The interaction between currents, the daily tidal regime, and the physical structure

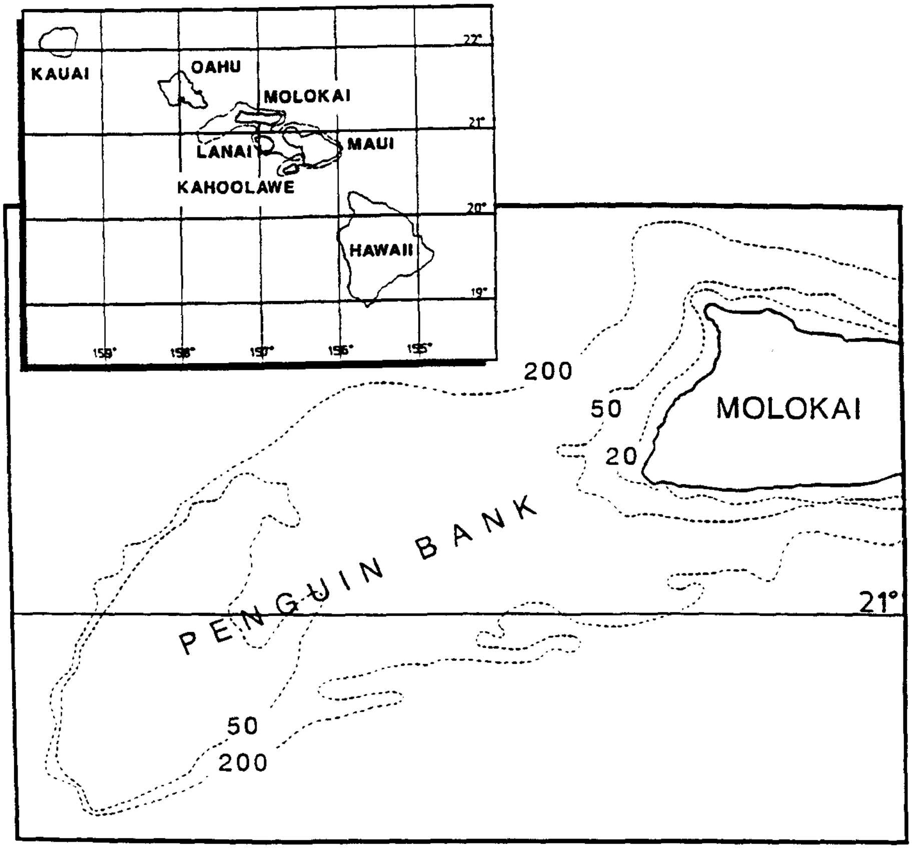

FIGURE 1.—Penguin Bank and immediate surroundings in the Hawaiian Archipelago. Bathymetric contours are in meters. The Molokai–Lanai–Kahoolawe–Maui bank complex is indicated generally by the bathymetric contour (200 m) in the inset.

of the banks may produce hydrographic features that are distinctive and have different effects on system productivity (Agegian et al. 1988).

The Molokai–Lanai–Kahoolawe–Maui bank complex (Figure 1), of which Penguin Bank is a large part, produces about 41% of the commercial bottom fish catch of the main Hawaiian Islands (based on 1990 landings statistics from the Hawaii Division of Aquatic Resources). In addition, there is a large but unrecorded recreational catch (Ralston and Polovina 1982; WPRFMC 1986). After recent heavy fishing pressure, there are indications that some stocks on these banks have been overfished and are declining (Ralston and Polovina 1982; Ralston 1984; Ralston and Kawamoto 1985, 1988; HDLNR 1986; WPRFMC 1986, 1988). Knowledge of these stocks is based almost entirely on data from landings by the commercial handline fishery. Some information is available on basic life history characteristics (e.g., growth parameters, reproductive data, size data, and mortality rates) of some major species in the fishery (Ralston 1981; Everson 1984; Kikkawa 1984; Kikkawa and Everson 1984; Uchiyama et al. 1984; Uchiyama and Tagami 1984; Sudekum et al. 1991). However, little is known about the habitat, food resources for bottom fish, or other characteristics of the environment that make it a productive fishing ground.

Except for some data on the diet of the greater amberjack *Seriola dumerili* (Humphreys and Kramer 1984), almost nothing is known about the feeding ecology of the commercial bottom fishes at Penguin Bank. Trophic information for these species from other localities also is sparse. One jack species (*Pseudocaranx dentex*) has been studied by Seki (1984a), two snapper species (*Pristipomoides auricilla* and *Pristipomoides zonatus*) by Seki and Callahan (1988), and two other jacks (giant trevally *Caranx ignobilis* and bluefin trevally *Caranx melampygus*) by Sudekum et al. (1991). All available diet information on deepwater groupers and snappers has been surveyed by Parrish (1987), including results from elsewhere in the Hawaiian Archipelago obtained by Kluegel (1921) and Seki (1984b) and previously unpublished results on diets of fishes from the Northwestern Hawaiian Islands (NWHI) and the Marianas.

The overall goal of our study was to identify and characterize key relationships between commercially important deepwater bottom fishes and their habitats and major food sources. Specific objectives were (1) to determine whether there is overlap among deepwater lutjanid snappers in their depth ranges or feeding periods, (2) to identify important prey groups in the diets of these species and estimate their relative importances, (3) to determine the extent of overlap in diet for these predators, and (4) to identify any diel or seasonal shifts in their diets.

Study Area

Penguin Bank is a large underwater feature immediately southwest of the island of Molokai, Hawaii (Figure 1). The top is relatively flat, with depths of 50–100 m; at the periphery, the bathymetry drops rapidly to over 500 m (Gregory and Kroenke 1982). Penguin Bank is similar in depth to the other banks in the Hawaiian Archipelago, and production dynamics on Penguin Bank are probably representative of many such banks in Hawaii and elsewhere in the tropics. Suitable habitat for bottom fish seems to be limited to a small and rather scattered fraction of the entire Penguin Bank area (C. R. Agegian, University of Hawaii, J. J. Polovina, Honolulu Laboratory, National Marine Fisheries Service, and S. Ralston, Tiburon Laboratory, National Marine Fisheries Service, personal communications).

Methods

Specimen collection.—Several areas of Penguin Bank known as commercially productive fishing grounds were chosen for specimen collection. These sites were surveyed hydroacoustically with a Raytheon model LSR-910M and a Simrad type EQ38-MK3 paper-recording fathometer, a RD Instruments series RDVM acoustic doppler current profiler, and a Furuno model CN106 color chromoscope.[1] Information was collected on bathymetry, substrate type, and fish aggregations. Some nearby areas on top of the bank also were fished to obtain adequate diet samples from the snapper *Aprion virescens*.

Specimens were collected between October 1987 and December 1989, primarily by conventional bottom handlines deployed from hydraulic fishing gurdies (Uchida and Uchiyama 1986:29). Five stations were fished with a Kali bottom longline developed at the National Marine Fisheries Service's Honolulu Laboratory (Shiota 1987). The use of rigid polyvinylchloride tubing in this gear in place of conventional gangions or dropper lines greatly reduced problems with fouling on the rough bottom. Stripped squid was used for bait for all handlining and longlining. All hooks were fished within a few meters of the bottom.

A handline fishing station consisted of a series of drifts made over a selected site after wind and current directions were determined. Drifts varied in response to local conditions and topography, but a typical station was occupied 1–3 h, during which time sampling occurred at depths ranging from about 100 to 250 m. An effort was made to sample the complete depth range fairly evenly throughout the diel cycle. Total fishing effort was 248 line-hours during daylight (0600–1830 hours) and 294 line-hours during darkness (1830–0600 hours). The shallow (0–150 m) and deep (150–300 m) depth ranges were each fished at least 90 line-hours during each period (daylight and darkness). In the standardized fishing, each 50-m depth interval from 50 to 300 m was handlined for a minimum of 25 line-hours. At least 20 line-hours of effort were exerted in each 2-h time interval throughout the diel cycle (Table 1). Effort was not equal for various times of day and depths, so most catch data were expressed as handline catch per unit effort (CPUE).

To determine if there were species-specific patterns of temporal and spatial distribution, the handline catch of each species, expressed as a fraction of the total handline catch of all species, was compared by chi square analysis (χ^2) to a uniform

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[1] Mention of products or names of manufacturers does not imply endorsement by the U.S. Government.

distribution of expected (equal) catch of all species. This procedure was used separately for each 2-h interval of the day and for each 50-m interval of depth fished.

Because regurgitation of gut contents is a problem when line-caught fish are brought to the surface rapidly by commercial fishing methods, various decompression schedules were tested. Lines were retrieved at different rates, and the general condition of each fish and the extent to which it had regurgitated were recorded. The most visible sign of barotrauma was the eversion of the stomach forward through the esophagus, caused by the expansion of gas in the swim bladder. To quantify the potential for loss of gut contents by regurgitation, each fish was assigned an integral value (ranging from 0 to 4) reflecting the degree of extrusion of the stomach into the mouth cavity. Time, depth, and location of capture, rate of ascent, and regurgitation state value were recorded for each specimen. The mouth and gills were examined for regurgitated material (which was included in diet analysis), and the specimen was weighed (to the nearest 0.01 kg), measured (standard length, fork length, and total length to the nearest 1 mm) and sexed (by macroscopic appearance of gonads after dissection). Fish were cooled quickly, and within 1 h after capture, the gastrointestinal tract was removed and frozen. Altogether, 589 fish were collected. All identifiable prey items from 219 of these predator specimens were used in trophic analysis.

Trophic analysis.—Diet composition was determined by examining the contents of the entire gastrointestinal tract of each specimen, following procedures similar to those described in Hyslop (1980), Harrison et al. (1983), and Parrish et al. (1985). All prey organisms were identified visually under magnification to the lowest feasible taxon. All prey individuals were counted, and the volume of individuals or groups of individuals was measured by liquid displacement. If a prey individual was in an advanced state of digestion, its volume was estimated by comparing it with intact individuals of similar size and known volume. Parts of partially digested prey were measured (e.g., with an ocular micrometer) to permit estimates of the sizes of the intact individuals.

TABLE 1.—Distribution of total standardized handline fishing effort applied simultaneously for six snapper species collected at Penguin Bank, Hawaii, in 1987–1989.

Effort distribution by time of day		Effort distribution by depth	
Time of day (hours)	Effort (line-hours)	Bottom depth (m)	Effort (line-hours)
0000–0200	27.8	50–100	25.4
0200–0400	20.2	100–150	188.8
0400–0600	29.1	150–200	188.9
0600–0800	41.9	200–250	110.1
0800–1000	37.8	>250	28.0
1000–1200	54.3		
1200–1400	37.4		
1400–1600	32.6		
1600–1800	43.0		
1800–2000	62.0		
2000–2200	128.8		
2200–2400	27.4		

Diet composition was expressed in terms of number and volume of prey items and frequency of occurrence of predator guts containing the prey. An index of relative importance (IRI) for each prey category in the diet was calculated with the method of Pinkas et al. (1971):

$$\mathrm{IRI} = F(N + V);$$

F = percentage of all predator individuals that contained that prey category,
N = percentage of total prey individuals that were of that category, and
V = percentage of total prey volume that was of that category.

To compare diets, the IRI of a particular prey category was expressed as a fraction of the sum of IRI values for all categories at comparable levels of systematic or ecological organization.

Diet overlap between predator groups was calculated by the Morisita–Horn C_λ formula (Horn 1966):

$$C_\lambda = \frac{2\sum_{i=1}^{s}(x_i y_i)}{\sum_{i=1}^{s} x_i^2 + \sum_{i=1}^{s} y_i^2};$$

s is the total number of prey categories, and x_i and y_i are the proportions of the total diet index of predator group x and y that are taken from prey category i. Values of C_λ can vary from 0 when diets of two groups are completely distinct to 1 when the diets are identical. Diet overlaps were classified with Langton's (1982) scale: low overlap, 0–0.29; medium overlap, 0.30–0.59; and high overlap, ≥0.60. Groups compared for diet overlap included different predator species, predators collected in different seasons and at different times of day, and different portions of the alimentary tract (i.e., stomach, mouth and hindgut).

TABLE 2.—Six deepwater snapper species collected in this study, by number and size caught, time of day, and depth of capture, at Penguin Bank, Hawaii, in 1987–1989.

Species	Number collected	Fork length (mm)		Time of day caught (hours)	Depth of capture (m)	
		Range	Median		Range	Median
Pristipomoides sieboldii	147	237–435	363	0036–2242	104–265	168
Pristipomoides filamentosus	232	267–654	388	0010–2348	49–256	107
Pristipomoides zonatus	7	322–410	387	0915–1806	150–190	164
Etelis coruscans	40	265–836	404	0540–1905	163–331	192
Etelis carbunculus	92	232–576	346	0150–2258	73–280	175
Aprion virescens	71	443–890	633	0615–1850	46–134	51
Total	589					

Statistical analyses were done on a microcomputer with the software package SAS PC Release 6.03 (SAS Institute 1985, 1988).

Results

Catch Composition

Six of the eight native lutjanid snapper species known from Penguin Bank were captured in this study (Table 2). The only common, native, deepwater lutjanid of this habitat not present in the catch was *Aphareus rutilans*.

Pristipomoides sieboldii and *Pristipomoides filamentosus* made up 64% of the catch; *P. zonatus* was caught only incidentally (1%). *Etelis coruscans* and *Etelis carbunculus* made up 23% of the catch. *Aprion virescens*, an important commercial species in summer, accounted for 12% of the total.

Spatial and Temporal Distribution of the Catch

The distribution of depths and times of catch of most of the six snapper species overlapped somewhat, but some distinct species differences were discernible. *Pristipomoides filamentosus* seemed to take bait most readily during the morning (0400–0800 hours) and evening (1600–2200 hours) (Figure 2A). *Pristipomoides sieboldii* seemed to feed in a less regular temporal pattern with several peaks during the day and night. The highest catch rates of the *Etelis* species were widely separated in time; *E. coruscans* took bait most readily during 0600–0800 hours and *E. carbunculus* during 1800–2000 hours (Figure 2B). *Aprion virescens* was caught throughout the daylight hours, and seemingly was inactive during most of the night. The pooled CPUE for all snappers (which are targeted as a group in the snapper fishery) fluctuated over a diel cycle, with peaks during 0400–0800 hours and 1800–2200 hours. The pooled catch rate declined from 2200–0400 hours.

Distributions of CPUE at discrete depth intervals indicated that *A. virescens* took bait most readily in the shallowest zone occupied by these species (Figure 3B). Its distribution overlapped with that of *P. filamentosus*; however, the CPUE of the latter was highest in a deeper zone (100–150 m) (Figure 3A). The CPUE of *E. coruscans* was very low in all except our deepest (250–300 m) standardized fishing zone. The catch depth distributions of the two *Etelis* species overlapped, but the CPU for *E. carbunculus* was highest at 200–250 m depth and substantial at shallower depths. The catch depth distributions of the *Pristipomoides* species overlapped with that of *E. carbunculus*, but the peak CPUE of each species was in a different depth range. The peak CPUE for *P. sieboldii* was at 150–200 m. *Pristipomoides zonatus* was caught in the same depth range as *P. sieboldii*, but too few *P. zonatus* were caught to determine the depth where CPUE peaked. The depth range of some of these species may extend deeper than 300 m. However, local underwater observations (S. Ralston, personal communication) and research elsewhere in the tropical Pacific (Ralston and Williams 1988) suggest that none of the species has major peaks in abundance at depths exceeding 300 m.

Chi-square goodness-of-fit analysis indicated that within each depth and time interval sampled, catches (relative abundances) of these species varied significantly from an "expected" uniform distribution of equal catch of all species (χ^2 = 11.73–521.04, df = 5, P = 0.01–0.005). The nonuniform

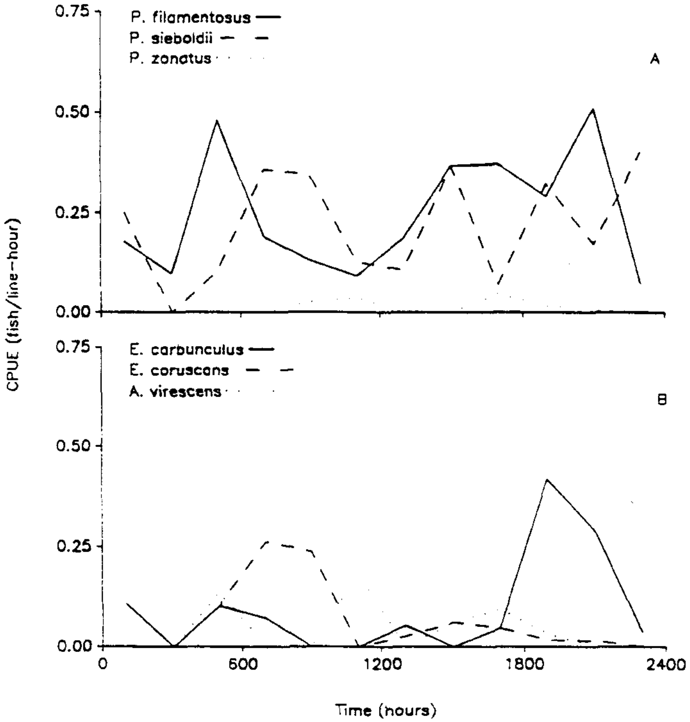

FIGURE 2.—Diel pattern of catch per unit effort (CPUE) of (A) three *Pristipomoides* species, and (B) two *Etelis* species and *Aprion virescens*, at Penguin Bank, Hawaii, 1987–1989.

dispersion of catches suggests that the differences in observed interspecific temporal and depth patterns of catch are related to real interspecific differences in patterns of predator occurrence and feeding.

To determine whether fish size was related to depth or time of capture, the catch data were tested by both median comparison tests and nonparametric correlation analysis. No significant correlation was found between fork length and capture depth for any of these species (Spearman's rank correlation analysis: $r_S = -0.13$–0.29, $P = 0.17$–0.92). For each of the species, median fork lengths of fish caught during daylight (0600–1830 hours) and darkness (1830–0600 hours) were not significantly different (Wilcoxon's signed-rank test: $Z = 0.98$–1.61, $P = 0.10$–0.32).

Fish Retrieval Rate and Regurgitation

The effect of fish retrieval rate on regurgitation was tested for all species by Spearman's rank correlation analysis. No clearly significant correlation was found between rate of ascent and regurgitation index ($r_S = -0.23$–0.01, $P = 0.06$–0.93). However, qualitative observations indicated that a retrieval rate of about 0.5 m/s was optimal in terms of fish condition and fishing success. Fish retrieved rapidly (≥ 2 m/s) or very slowly (≤ 0.1 m/s) exhibited signs of traumatic decompression, including extreme eversion of the stomach through the esophagus, and bulging eyes. However, fish retrieved at intermediate rates of ascent (about 0.3–0.6 m/s) usually showed less traumatic signs of decompression and were often lively at the surface. Size of fish did not seem to affect the extent of regurgitation: the Spearman coefficients comparing fork length with regurgitation index were nonsignificant for all species ($r_S = 0.01$–0.14, $P = 0.72$–0.94). No significant correlation could be found between regurgitation index and the depth at which a fish was hooked (depth range, 49–280 m: $r_S = -0.007$–0.27, $P = 0.22$–0.45).

Trophic Analysis

Analysis with diet overlap indices based on percent IRI indicated that for each species, the com-

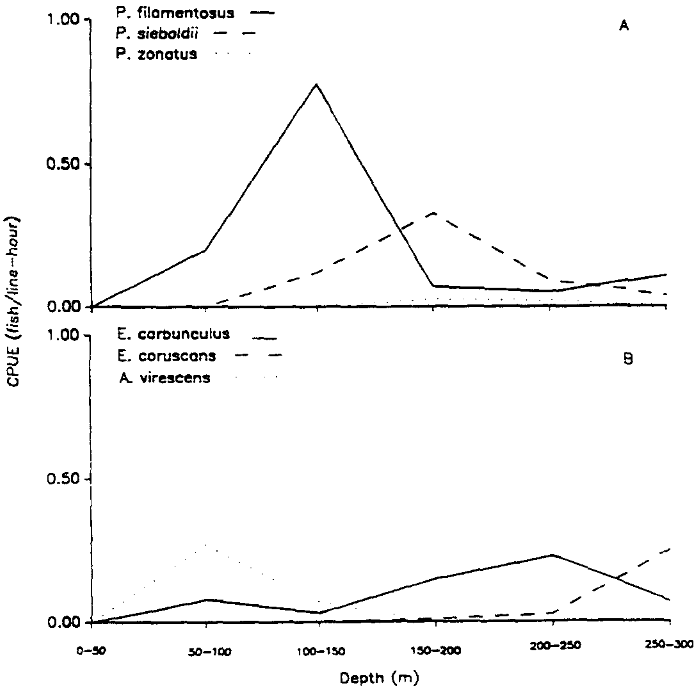

FIGURE 3.—Depth distributions of catch per unit effort (CPUE) of (A) three *Pristipomoides* species, and (B) two *Etelis* species and *Aprion virescens*, at Penguin Bank, Hawaii, 1987–1989.

position of prey items found in the hindgut, stomach, and mouth was similar ($C_\lambda > 0.5$ for diet overlap between gut locations for each snapper species). Therefore, all prey items from the entire alimentary tract of an individual were pooled for diet calculations.

As a group, the snappers ate large amounts of a wide range of pelagic animals and much smaller quantities of a few benthic groups (Table 3; Appendix Table A.1). Five of the snapper species were separable by diet into two general feeding guilds: (1) zooplanktivores that fed primarily on pelagic urochordates, planktonic crustaceans, and pteropods, and (2) species that were primarily piscivorous (Table 3). Zooplankton composed 92% and 97% of the total IRI in the diets of *P. filamentosus* and *P. sieboldii*, respectively. *Etelis coruscans*, *E. carbunculus*, and *A. virescens* were primarily piscivorous; fish accounted for 81–98% of the total IRI.

Pristipomoides species fed on pelagic urochordates (mainly thaliaceans); these prey were most prevalent in the diet of *P. filamentosus* (47% of total IRI). *Pristipomoides sieboldii* also fed on thaliaceans (16% of total IRI), but pelagic crustaceans (47%) and pteropods (29%) were more important prey items. Pelagic crustaceans and pteropods were also important in the diet of *P. filamentosus*. *Pristipomoides zonatus* fed on thaliaceans (38% of total IRI), but also preyed on fish (55%) and benthic crustaceans (6%). In the piscivorous guild, pelagic urochordates, cephalopods, and benthic crustaceans also were notable prey items.

The two feeding guilds were clearly distinguished by their C_λ values. Exclusive of *P. zonatus*, C_λ values ranged from 0.78 to 1.00 within guilds (Table 4), and little dietary overlap occurred between guilds (C_λ = 0.03–0.23). *Pristipomoides zonatus* (only six specimens) fell somewhat between guilds: it showed high overlap with the piscivorous guild (C_λ = 0.76–0.87) and medium–low overlap with the zooplanktivorous guild (C_λ = 0.18–0.55).

Major diel and seasonal diet changes were found only for *P. filamentosus*. Its C_λ value (based on

TABLE 3.—Diets of six deepwater snapper species collected at Penguin Bank, Hawaii, in 1987–1989. Gut contents of 219 fish were divided into 12 major systematic or ecological groups. Relative abundance of prey is expressed as percentage of total index of relative importance (IRI). Numbers in parentheses indicate the number of guts with any identifiable contents.

	Percent IRI in gut contents of					
Prey group	*Pristipomoides sieboldii* (60)	*Pristipomoides filamentosus* (54)	*Pristipomoides zonatus* (6)	*Etelis coruscans* (24)	*Etelis carbunculus* (33)	*Aprion virescens* (42)
Fish (juvenile and adult)	1.8	7.2	55.2	80.6	98.4	95.8
Fish larvae	0.3	0.04	0.0	0.0	0.0	0.2
Pelagic small crustaceans	47.2	31.1	0.0	1.0	1.0	0.4
Shrimp (adult)[a]	1.2	0.1	0.7	4.4	0.2	0.1
Crabs (adult)[a]	0.07	0.0	5.8	0.06	0.03	0.02
Polychaete worms	0.1	0.0	0.0	0.0	0.0	0.0
Cephalopods	1.5	0.5	0.0	2.9	0.3	0.7
Pteropod molluscs	28.9	13.0	0.0	0.0	0.0	0.01
Other small molluscs	0.4	0.2	0.0	0.0	0.02	0.0
Chaetognaths	0.1	0.0	0.0	0.0	0.0	0.0
Pelagic urochordates	16.4	47.3	38.4	11.1	0.02	2.7
Siphonophores	1.8	0.6	0.0	0.0	0.0	0.0

[a] Larvae are included in "Pelagic small crustaceans."

IRI) for day versus night samples was 0.50. Pelagic urochordates composed a much greater part of the total IRI of individuals caught at night (Table 5). Other major components of the diet (e.g., fish, pelagic crustaceans) were more prevalent in specimens caught during the day. Seasonally, pelagic urochordates were low in the summer IRI of *P. filamentosus*, increased in winter, and became strongly dominant in spring (Table 5). As urochordates increased, groups such as pelagic crustaceans, pteropods and fish, which had composed sizable percentages of the IRI in summer or winter, decreased to low spring levels. Seasonal C_λ values for *P. filamentosus* reflected the fluctuating importance of pelagic urochordates in the diet. Values of C_λ for summer versus winter (0.78) and spring versus winter (0.71) were similar. However, the shift of the major diet component from pelagic crustaceans in summer to pelagic urochordates in spring resulted in a C_λ value of 0.34 in the summer versus spring diet comparison. The diet of each piscivorous species was highly similar throughout the diel and seasonal cycles; the range of C_λ values was 0.62–0.99.

Discussion

Fish Retrieval Rate and Regurgitation

Regurgitation of gut contents due to rapid decompression remains a problem for trophic studies of deepwater physoclistous fishes. We found that retrieval at a very slow rate to allow resorp-

TABLE 4.—Values of the index of diet overlap (C_λ) between each pairwise combination of six deepwater snapper species collected at Penguin Bank, Hawaii, in 1987–1989. Values of C_λ are calculated based on percentage of index of relative importance (IRI).

Species	*P. filamentosus*	*P. zonatus*	*E. coruscans*	*E. carbunculus*	*Aprion virescens*
Pristipomoides sieboldii	0.78	0.18	0.08	0.03	0.04
Pristipomoides filamentosus		0.55	0.23	0.11	0.13
Pristipomoides zonatus			0.87	0.76	0.78
Etelis coruscans				0.97	0.98
Etelis carbunculus					1.00

TABLE 5.—Temporal trends in diet composition of *Pristipomoides filamentosus* at Penguin Bank, Hawaii, in 1987–1989. Gut contents were divided into eight major systematic or ecological groups. Relative abundance of prey is expressed as percentage of total index of relative importance (IRI). Numbers in parentheses indicate the number of guts in each period that contained any identifiable prey.

	Percent IRI in gut contents collected during				
Prey group	Day (35)	Night (19)	Summer (15)	Winter (25)	Spring (14)
Fish (juvenile and adult)	10.0	1.7	13.6	9.4	1.6
Fish larvae	0.1	<0.01	0.2	0.03	<0.01
Pelagic small crustaceans	42.6	6.6	57.2	29.9	9.3
Shrimp (adult)[a]	0.1	0.1	<0.01	0.02	0.7
Cephalopods	0.4	0.4	0.8	0.3	0.4
Pteropod molluscs	18.1	5.9	10.2	22.2	4.8
Pelagic urochordates	28.2	84.8	15.0	37.7	83.3
Siphonophores	0.5	0.7	2.9	0.4	0.03

[a] Larvae are included in "Pelagic small crustaceans."

tion of gases from the swim bladder is not a satisfactory solution. Fish retrieved at the slowest rates often showed the same signs of barotrauma as those retrieved rapidly. Their inactivity when landed and lack of the usual signs of life suggest that death or debilitation is common after a long period on the line. Such fish may have reduced physiological capability to resorb gas from the bladder (perhaps because of loss of nervous control of the oval; Harden Jones 1957). However, fish retrieved at an intermediate rate (about 0.5 m/s) appeared to be less severely affected and often contained intact stomachs or retained a substantial amount of prey in the mouth, gills, and gill rakers. Our results suggest that retrieving at moderate rates produces specimens usable for diet studies and is a practical procedure for a field sampling program.

Subsurface handling of individual fish by divers may be one way of reducing the problem of barotrauma in physoclistous fishes (Parrish and Moffitt 1993). However, this technique is not feasible with intensive fishing operations such as those used in the present study.

Our results suggest that the entire gastrointestinal tract should be examined to obtain the maximum diet information from a given sample. In this study, the diversity and composition of prey found in the intestines were sufficiently similar to those found in the stomach and mouth that prey from all parts of the alimentary tract could be pooled for dietary analysis. However, some of the soft-bodied prey (especially larval fishes) seemed to be underrepresented in the intestinal samples. Movement of food through the digestive tract of these fishes seems to be fairly rapid. "Palu" (a fish attractant composed of minced fish and oats) was found in the hindgut of three species (*A. virescens, P. filamentosus, E. coruscans*) caught 1–2.5 h after it was first released in the water.

Trophic Analysis

Our data indicate that a distinct feeding guild with a strongly zooplanktonic diet occurs among the lutjanid snappers at Penguin Bank. These results, together with the reports for deepwater snappers elsewhere in the tropical Pacific (Parrish 1987), suggest that zooplanktivory may be an important trophic mode among *Pristipomoides* species. Examination of our data from all Penguin Bank cruises showed that zooplankton dominated the diets of *P. filamentosus* and *P. sieboldii* throughout the year, and levels of piscivory remained low. The diet composition of species of the piscivorous guild (*A. virescens, E. coruscans,* and *E. carbunculus*) remained relatively constant throughout the day and seasons of the year. *Pristipomoides zonatus* may have a more generalized diet than species in the planktivorous or piscivorous guilds. Our six specimens of *P. zonatus* contained substantial amounts of both benthic–demersal and pelagic forms. This same trend was reported for a larger sample (N = 106) of this species occurring in the Marianas (Seki and Callahan 1988).

As is commonly the case with analysis of fish gut contents, most of the fish prey we found in these deepwater snappers were not identifiable even to major groups. The identifiable fish prey were diverse systematically and ecologically, and included relatively sedentary species, fishes with generally demersal habits at a variety of depths, fishes of the water column near bottom, and mesopelagic species (Appendix). There was rather good correspondence between what is known of the common depth ranges of the various prey fishes and the depths at which the particular snapper species that ate them were collected.

The deep-feeding *Etelis* species contained a deepwater demersal cardinalfish *Epigonus* sp. and three identifiable mesopelagic fishes: the bristlemouth *Argyripnus brocki* and the lanternfishes *Benthosema fibulatum* and *Diaphus* sp. All these mesopelagic species have been identified as components of the distinctive "mesopelagic-boundary community" of Hawaii, which inhabits coastal waters over bottom depths of perhaps 100–700 m in a band surrounding islands and banks (Reid et al. 1991; S. B. Reid, University of Hawaii, personal communication). Of these species, at least *Benthosema fibulatum* and some *Diaphus* species perform some diel vertical migration and could be eaten well above the bottom at some times of the day. A number of the other, primarily demersal, prey species in the snapper diets also range higher in the water column at times and may be subject to midwater predation, especially during their younger life stages. The deepwater snappers may eat such prey only at the bottom, but these prey could provide a short link with productivity originating higher in the water column.

Monacanthidae (many identifiable as *Pervagor* sp.) were the most nearly ubiquitous prey fish, occurring in all the snapper species except one and composing at least a few percent of the diet of some. Species of *Pervagor*, especially the fantail filefish *P. spilosoma*, occasionally become extremely numerous and widely consumed by piscivorous fishes in Hawaii, at least in shallow waters (Tinker 1978; Brock 1984, 1985; Sudekum et al. 1991). At such times, this species seems to modify its usual behavior and occupies much of the water column as well as its usual demersal habitat (T. A. Clarke and S. B. Reid, University of Hawaii, personal communication). The abundance of monacanthids was not monitored at the specific times and locations of our collections. However, visual censuses made from submersibles on the top and upper slopes of Penguin Bank at 61–117 m depth between October 1985 and February 1988 (overlapping our study) showed that *P. spilosoma* was among the few most abundant fish species present on artificial reefs (F. A. Parrish, Honolulu Laboratory, National Marine Fisheries service, personal communication). The abundance of monacanthids in snapper diets may indicate opportunistic feeding during sporadic abundance of a particular prey.

Fishes recognizable as larval stages occurred with fairly high frequency in the guts of *P. sieboldii*, *P. filamentosus*, and *A. virescens*, but numbers and volumes eaten and the corresponding IRI values were rather low (Appendix). It seems likely that many larval fishes were among the unidentified fish remains or other unrecognizable gut material. The identified larval fish material was concentrated in the zooplanktivorous guild, but some was consumed by the shallowest feeding piscivore. This suggests that the larval fishes occurred and were captured along with invertebrate plankton.

For most of these snapper species, diet data from other sources are based on 1–60 specimens, except for 209 specimens of *P. zonatus* (Parrish 1987). These uneven data suggest that fish prey vary from fairly important to strongly dominant in the diets of these species in other localities. Results for *P. filamentosus* from the NWHI (Parrish 1987) indicated somewhat greater piscivory than at Penguin Bank. *Aprion virescens* and *E. carbunculus* in the NWHI were strongly piscivorous (as at Penguin Bank), and *P. zonatus* appeared more intermediate between piscivory and planktivory (Parrish 1987).

The diets of Penguin Bank snappers contained no identified prey fish species in common with snappers in the other Pacific localities reported. (In all the studies, relatively few prey fishes were identified to species.) Prey families shared by deepwater snappers at Penguin Bank and at other Indo-Pacific localities included Congridae, Apogonidae, Myctophidae, Synodontidae, Balistidae, and Ostraciidae, as well as unidentified tetraodontiform fishes (Parrish 1987).

Cephalopods (including octopus and squid) at Penguin Bank were eaten by all but one snapper species studied there, sometimes providing several percent of the diet (Appendix). The two *Etelis* species, which occurred deepest of all the snappers, contained deepwater ommastrephid and chiroteuthid squid. An early juvenile onychoteuthid species with somewhat shallower distribution was eaten by the shallower-feeding *P. sieboldii*. Cephalopods (including Ommastrephidae) have been found in the diets of all except two deepwater snapper species reported from elsewhere in the Pacific (Parrish 1987). They were fairly important in the diet of *P. filamentosus* in the NWHI.

Several groups of small malacostracans and the larvae of a few groups of large ones made up the bulk of the pelagic crustacean prey category in our study (Appendix). For some small crustaceans (e.g., amphipods, ostracods, isopods), it is not clear whether the habitat was pelagic, benthic, or both. However, these groups commonly occurred in fish guts with other clearly pelagic groups. Larval, juvenile, and adult lobsters, shrimp, and especially crabs and stomatopods were found in the diets of the snappers. Among identified stomatopod prey, species of *Squilla* and *Lysiosquilla* are moderately common as adults in shallow waters of Hawaii and may occur deeper as well. Adults of *Odontodactylus* spp. are unknown from shallow waters in Hawaii, but they have been trawled occasionally from deeper, soft bottoms (well below 100 m). Most of the large crustaceans in the diet were clearly benthic inhabitants as adults (e.g., the deepwater galatheid crab *Munida* sp.). Diet studies of deepwater snappers from other localities (Parrish 1987; Seki and Callahan 1988) have revealed amphipods, euphausids, isopods, crab and stomatopod larvae, and adult benthic crabs (including *Munida* sp. and other galatheids), stomatopods, shrimp, and lobsters.

Pelagic pteropods, including a major component from the family Cavolinidae, were eaten by three snapper species at Penguin Bank and were important prey for two species (Table 3, Appendix). Pteropods of the family Cavolinidae were a minor component of the diet of *P. zonatus* in the Marianas, fairly common in *P. multidens* in Western Samoa, and very abundant in *P. auricilla* in the Marianas (Parrish 1987; Seki and Callahan 1988).

The abundant pelagic urochordates, which were found in all the snapper species at Penguin Bank, included Salpida (probably a dominant group, but difficult to identify as remains), Doliolida, and Pyrosomida (Appendix). Pelagic urochordates (dominantly *Pyrosoma* sp.) have been identified in the diets of all except two deepwater snappers studied elsewhere in the Pacific (Parrish 1987). Siphonophores (dominantly Calycophora), a minor prey item for two snapper species at Penguin Bank (Appendix), have also been found in the diet of *P. auricilla* in the Marianas (Parrish 1987).

Pelagic urochordates and siphonophores might seem at first to offer little nutrition and to be unlikely preferred prey. Both are gelatinous, and the filter-feeding urochordates contain an indigestible cellulose tunic. However, both groups can concentrate large amounts of captured plankton prey in their guts (up to 20% of the body weight in some urochordates; Kashkina 1986), thus increasing their overall value as food. Both groups are colonial and form large interconnected aggregations of many individuals. They may enable snappers to forage with high efficiency. The frequency and abundance with which these soft-bodied megaplankton, together with the ciliary-feeding pteropods, appear in diets of most deepwater snappers sampled in the Pacific (Parrish 1987) suggest that they make a substantial contribution to the nutrition of demersal deepwater fish populations.

It is widely believed that these snapper species are strongly demersal (*A. virescens* less so than the others). This belief is based on behavior of related species, interpretation of sonar chromoscope images, much experience of commercial and recreational fishers, results of considerable experimental fishing, and underwater observations (including our own at Penguin Bank). The many strikes at our hooks near the bottom (none during the short time of lowering and retrieving the line) indicate that species with the full range of diets were in an active feeding state at the bottom during much of the day and night.

Animals from all the major pelagic prey categories consumed (Table 3) have been reported at times in substantial quantities at depths where these snappers were collected. In many cases, these prey were reported to be near bottom (Struhsaker 1973; Wiebe et al. 1979; Kashkina 1986; Grassle and Morse-Porteous 1987; Bathmann 1988; Childress et al. 1989; Reid et al. 1991; L. P. Madin, Woods Hole Oceanographic Institution, personal communication). These reports (some from Hawaii) are consistent with a pattern of near-bottom feeding by snappers. However, all available evidence does not exclude the possibility that significant feeding occurs far above the bottom.

Regardless of the level in the water column where feeding occurs, it is clear that planktonic animals provide an important conduit for transferring production from lower trophic levels in the water column to some large snapper species. These snappers occupy a demersal habitat that does not seem to be highly productive. The planktonic subsidy from the water column, facilitated by vertical migration of the zooplankton, may be important in maintaining fishable stocks of these deepwater snappers.

Spatial and Temporal Distribution

A baited hook does not represent a natural prey item for these snappers, but for the purpose of this study, an increase in CPUE was assumed to represent an increase in feeding activity. Diel cycles in feeding activity appear to be common and somewhat species-specific among the lutjanid snappers on Penguin Bank. Peak feeding of all these snappers as a group occurred during the morning and evening.

Nakamura (1967) and Shomura and Nakamura (1969), sampling with nets at depths of 60–200 m around the Hawaiian island of Oahu, reported marked increases in the abundance of zooplankton during early morning and evening. They observed strong diel fluctuations in abundance of ostracods, euphausids, pteropods, and larval fish, all of which are prey species for the zooplanktivorous snappers. Many zooplanktonic species migrate to surface waters at night to feed and return to deeper water during the day (Levinton 1982). This vertical migration could increase the availability of these prey to deepwater snappers during dawn and dusk as the zooplankton migrate past snappers occupying steep slopes or sites of high bottom relief.

The apparent diel distribution of zooplankton in the water column and the increased feeding activity by *Pristipomoides* species during early morning and evening suggest that these snappers are opportunistic zooplanktivores. However, pelagic urochordates, which were important in the diets of these snappers in our study, were less abundant than some of the other vertically migrating zooplanktonic groups in the net collections of Nakamura (1967) and Shomura and Nakamura (1969).

In general, the diets of the planktivorous *Pristipomoides* species had a higher percentage of thaliaceans at night and more pelagic crustaceans and fish during the day. This trend may reflect the difference in visibility of these prey and the role of vision in their capture. Small crustaceans and fishes would be more visible during the day, while the nearly transparent thaliaceans would be hard to see. At night, the relatively low visual acuity of the fish eye would result in much reduced ability to resolve smaller prey targets (Hobson 1991; McFarland 1991). However, many thaliaceans are bioluminescent, which along with their colonial habit could make them much more visible than small crustaceans or fishes. Their slow locomotion and bulky colonial form may make them more vulnerable to capture by random encounter in the dark.

Shomura and Nakamura (1969) reported that abundance of thaliaceans in Hawaiian waters was relatively low in summer and fall, higher in winter, and highest in spring. We found a similar trend in the abundance of thaliaceans in the diet of *P. filamentosus* on Penguin Bank. Kashkina (1986) reviewed a number of studies that reported high abundance of thaliaceans in portions of the "Hawaiian range" and elsewhere where there was upward mixing of nutrient-rich waters in spring. He suggested that such conditions stimulated planktonic production and provided food for increased thaliacean populations.

Resource Partitioning

Some of the snapper species caught in our study exhibited considerable overlap in diel feeding schedules. However, niche overlap was probably minimized by partitioning of prey and peak feeding depth. Within the piscivorous guild, dietary overlap was high. However, these species seemed to be stratified by bottom depth of peak feeding activity (Figure 3B). Little niche dimension overlap was evident between *A. virescens* and the other members of the piscivorous guild (or other snappers), because *A. virescens* fed most actively during daylight and much higher in the water column than the other species. Potential overlap seems most likely between *E. carbunculus* and *P. zonatus*, as all three niche dimensions measured showed considerable overlap. However, we collected too few *P. zonatus* to permit estimating the degree of overlap with confidence. For the two strongly zooplanktivorous *Pristipomoides* species, both diets and diel feeding schedules overlapped considerably. However, peak feeding activity seemed to occur at a bottom depth about 50 m deeper for *P. sieboldii* than for *P. filamentosus*. Moderate overlap in all three measured niche dimensions seemed to occur between *P. filamentosus* and *P. zonatus*, but interpretation was difficult because of the small sample size of *P. zonatus*. Based on diet composition and depth and time of catch, strong niche overlap between the planktivorous and piscivorous guilds seems unlikely.

Fishery Implications

Recent studies indicate that *P. filamentosus*, *E. coruscans*, and *E. carbunculus* have suffered significant growth overfishing around the main (inhabited) Hawaiian Islands and that *A. virescens* may have suffered some such effects (Ralston and Kawamoto 1988; Somerton and Kobayashi 1990a). Major reductions in spawning stock biomass of the first two species are raising concern among fisheries managers that they also may be experiencing recruitment overfishing (WPRFMC 1991).

Imposing size limits for retention of snappers has been suggested as a way to reduce the mortality of immature fish, increase the yield per recruit, and protect against recruitment overfishing (Somerton and Kobayashi 1990b). However, capture and release seems to result in high mortality, and the full benefits of a minimum size limit would be realized only if catches of undersize fish were minimized. This would be possible if undersize fish were naturally segregated from the larger fish by capture depth or time. However, the results presented here do not indicate that such stratification occurs. A possible approach to size-selective line fishing may be a judicious choice of hook size (Ralston 1990).

It seems unlikely that any foreseeable developments in gear or techniques will permit the fishery to harvest these stocks with high selectivity by species. However, our results are consistent with the reports of fishers that considerable selectivity can be achieved by choice of depth fished.

Population parameters and the ecology of individual species are often poorly known in tropical multispecies fisheries. Thus, groups of species such as deepwater snappers are sometimes analyzed and managed as a unit by approaches such as the total-biomass Schaefer model (TBSM) (Ralston and Polovina 1982). However, a thorough understanding of trophic relationships among the species making up the fishery is important for management of any multispecies fishery, and application of the TBSM may be inappropriate if such relationships remain unknown (May et al. 1979; Pauly 1979). The large differences in trophic roles of some of the snapper species at Penguin Bank suggest caution in lumping these species together in a TBSM analysis.

This study has not fully revealed the sources or production processes supporting these snapper populations. It is plausible that the productivity of the bank as a whole is enhanced by its hydrography. However, much of the food of these snapper species comes from pelagic (planktonic or nektonic) animals. This suggests that the occurrence and abundance of snappers on these grounds is not the result of some concentrated benthic food resource that is highly specific to localized bottom features. Bank features may provide some other localized resource (e.g., vertical relief, protective cover) that is important to snappers.

The distribution of these snappers may be affected by the upward deflection of deeper currents where the currents encounter the higher relief of banks, resulting in a higher local abundance of plankton (e.g., Brock and Chamberlain 1968). In an ecological study of the bottom fish resources of Johnston Atoll, Ralston et al. (1986) found *P. filamentosus* in much higher densities on the upcurrent side of the atoll than on the downcurrent side. They postulated that this was related to increased availability of allochthonous planktonic prey in the neritic upcurrent areas due to oceanic currents deflected by the atoll.

Although deepwater banks in Hawaii and the Pacific support highly productive fishery resources, their ecology remains relatively obscure. The results presented here are based on our collections from the south-central portion of Penguin Bank. These results provide a substantial contribution to knowledge of the trophic ecology of lutjanid snappers that support important deepwater fisheries on the bank and elsewhere throughout the Hawaiian Archipelago and other tropical seas.

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Appendix follows

Appendix: Diets of Deepwater Snappers

TABLE A.1.—Diets of six deepwater snapper species collected at Penguin Bank, Hawaii, in 1987–1989. Shown are the percentages of predator individuals that consumed each prey (*F*), the percentages of all numbers (*N*) and volume (*V*) provided by each prey, and each prey's index of relative importance (IRI) in gut contents. The number of guts with any identifiable contents is indicated beside each snapper species in parentheses. Prey categories followed by an asterisk are also included in the larger ecological category "Pelagic small Crustacea." Values for the highest systematic levels are underlined. Values of IRI were calculated separately for each prey category (line entry); values may be compared across categories at comparable systematic levels.

Prey category	Percent frequency (*F*)	Percent number (*N*)	Percent volume (*V*)	IRI
	Pristipomoides sieboldii (60)			
Fish (all)[a]	21.7	1.4	22.8	527.4
Fish (juvenile and adult)	10.0	0.4	21.2	216.7
Congridae				
Tetraodontiformes (all)	1.7	0.1	3.0	5.2
Monacanthidae	1.7	0.1	3.0	5.2
Pervagor sp.				
Ostraciidae				
Fish unidentified	8.3	0.4	18.2	154.8
Fish larvae[a]	15.0	1.0	1.6	40.0
Pelagic small Crustacea[a]* (including shrimp and crab larvae)	91.7	44.7	18.2	5.758.8
Euphausiacea*	38.3	14.0	1.0	577.3
Copepoda*	26.7	10.2	0.8	292.6
Amphipoda*	43.3	4.5	0.3	211.0
Hyperiidea	3.3	0.1	0.01	0.4
Gammaroidea	5.0	0.2	0.01	1.0
Caprellidea	1.7	0.06	<0.01	0.1
Amphipoda unidentified	38.3	4.2	0.3	171.7
Isopoda*	18.3	1.8	0.1	34.5
Shrimp (all)	38.3	5.1	8.3	511.6
Shrimp (adult)[a]	35.0	4.0	0.3	150.0
Pandalidae				
Shrimp unidentified	35.0	4.0	0.3	150.0
Shrimp larvae*	1.7	0.1	0.01	0.2
Alpheidae larvae	1.7	0.06	<0.01	0.1
Zoea unidentified	10.0	1.0	8.0	89.3
Crabs (all)	30.0	1.9	1.6	106.7
Munida sp. (Galatheidae)				
Crabs (adult, unidentified)[a]	5.0	0.2	1.5	8.4
Crab larvae (megalopa)*	28.3	1.8	0.1	53.3
Lobster (Palinuridae) larvae*	1.7	0.06	<0.01	0.1
Stomatopoda larvae*	26.7	1.9	7.1	240.9
Squilla spp. larvae	11.7	0.6	1.0	18.3
Lysiosquilla spp. larvae	6.7	0.6	5.0	37.2
Odontodactylus spp. larvae				
Stomatopoda larvae unidentified	10.0	0.7	1.2	18.8
Mysidacea*	15.0	1.5	0.1	23.4
Ostracoda*	30.0	5.6	0.4	181.1
Crustacea unidentified*	30.0	2.3	0.2	74.0
Polychaeta[a]	13.3	1.2	0.1	17.3
Cephalopoda[a]	11.7	0.5	15.5	186.5
Squid (all)	3.3	0.1	0.3	1.5
Onychoteuthis sp.	1.7	0.06	0.3	0.6
Squid unidentified	1.7	0.06	<0.01	0.1
Octopoda unidentified	1.7	0.06	<0.01	0.1
Cephalopoda unidentified	6.7	0.3	15.2	103.2
Pteropoda (all)[a]	93.3	35.2	2.6	3,532.3
Cavolinia spp.	60.0	9.0	0.7	580.3
Clio spp.	46.7	7.6	0.6	381.7
Cuvierina spp.	58.3	8.1	0.6	507.4
Diacra spp.	46.7	5.5	0.4	275.7
Pteropoda unidentified	33.3	5.0	0.4	179.6
Other small molluscs[a]	26.7	1.8	0.1	51.9
Cymatium/Bursa	1.7	0.06	<0.01	0.1
Mollusca unidentified				
Micromolluscs unidentified	25.0	1.8	0.1	47.1

TABLE A.1.—Extended.

Percent frequency (*F*)	Percent number (*N*)	Percent volume (*V*)	IRI	Percent frequency (*F*)	Percent number (*N*)	Percent volume (*V*)	IRI
***Pristipomoides filamentosus* (54)**				***Pristipomoides zonatus* (6)**			
20.4	3.2	33.8	752.2	66.7	33.3	76.9	7,346.8
18.5	2.5	33.5	665.2	66.7	33.3	76.9	7,346.8
				16.7	5.6	12.8	306.1
3.7	0.4	4.8	19.0	16.7	5.6	12.8	306.1
1.9	0.2	2.4	4.8	16.7	5.6	12.8	306.1
				16.7	5.6	12.8	306.1
1.9	0.2	2.4	4.8				
16.7	2.1	28.8	515.0	50.0	22.2	51.2	3,673.4
3.7	0.7	0.3	3.7				
46.3	49.1	12.6	2,859.9				
7.4	2.1	0.04	15.9				
7.4	1.2	0.02	9.3				
1.9	0.2	<0.01	0.3				
1.9	0.2	<0.01	0.3				
9.3	1.2	0.02	11.6				
9.3	1.2	2.0	29.6	16.7	5.6	0.02	92.9
7.4	0.7	0.8	11.1				
1.9	0.2	0.4	1.0				
5.6	0.5	0.4	5.1				
3.7	0.5	1.2	6.3				
14.8	6.3	0.1	95.5	33.3	16.7	6.3	765.7
				16.7	5.6	2.1	127.6
				16.7	11.1	4.2	255.2
14.8	6.3	0.1	95.5				
9.3	21.6	10.9	301.0				
5.6	19.5	8.5	155.2				
5.6	0.7	1.6	12.6				
1.9	0.2	0.4	1.0				
5.6	1.2	0.5	9.8				
3.7	1.4	0.03	5.3				
11.1	11.1	0.2	125.3				
22.2	3.5	0.07	79.6				
5.6	0.5	7.2	42.9				
5.6	0.5	7.2	42.9				
55.6	21.1	0.4	1,193.2				
22.2	4.9	0.1	111.4				
22.2	6.3	0.1	143.2				
13.0	2.1	0.04	27.8				
25.9	6.5	0.1	171.7				
9.3	1.2	0.02	11.6				
9.3	2.1	0.04	19.9				
1.9	0.2	<0.01	0.3				
7.4	1.9	0.04	14.6				

TABLE A.1.—Continued.

Prey category	Percent frequency (*F*)	Percent number (*N*)	Percent volume (*V*)	IRI
		***Pristipomoides sieboldii* (60)**		
Chaetognatha[a]	13.3	1.1	0.09	16.4
Pelagic urochordates[a]	46.7	4.7	38.3	2,006.0
Thaliacea	38.3	4.2	34.3	1,476.6
Pyrosoma sp.	8.3	0.4	3.0	27.9
Doliolum sp.	1.7	0.1	1.0	1.9
Siphonophora[a]	40.0	5.2	0.4	223.3
Diphyidae	40.0	5.1	0.4	218.1
Abylidae (calycophoran)	1.7	0.1	0.01	0.2
Siphonophora unidentified				
		***Etelis coruscans* (24)**		
Fish (all)[a]	62.5	30.4	85.7	7,253.4
Fish (juvenile and adult)	62.5	30.4	85.7	7,253.4
Argyripnus brocki				
Benthosema fibulatum				
Diaphus sp. (*adenomus*?)	4.2	0.9	0.03	3.8
Epigonus sp.	4.2	0.9	0.1	4.2
Sphyraenidae				
Parupeneus sp. (Mullidae)				
Naso sp. (Acanthuridae)				
Naso hexacanthus				
Dactyloptena orientalis				
Pegasus papilio				
Tetraodontiformes (all)				
Balistidae				
Monacanthidae				
Pervagor sp.				
Monacanthidae unidentified				
Tetraodontiform unidentified				
Antennarius pictus				
Fish unidentified	54.2	28.6	71.3	5.411.3
Fish larvae[a]				
Synodontidae larvae				
Fish larvae unidentified				
Pelagic small Crustacea[a]*	16.7	5.4	0.02	89.7
Copepoda*				
Isopoda*				
Shrimp (all)[a]	29.2	13.4	0.06	392.4
Heterocarpus ensifer	4.2	2.7	0.01	11.2
Shrimp unidentified	25.0	10.7	0.04	268.8
Crabs (all)[a]	4.2	0.9	0.4	5.6
Hippoidea	4.2	0.9	0.4	5.2
Crabs (adult, unidentified)				
Crab larvae (megalopa)*				
Stomatopoda (adult)				
Odontodactylus hanseni				
Crustacea unidentified*	16.7	5.4	0.02	89.6
Cephalopoda[a]	16.7	4.5	11.3	263.3
Squid (all)	4.2	1.8	3.3	21.2
Chiroteuthis sp.				
Nototodarus hawaiiensis	4.2	1.8	2.8	19.0
Squid unidentified				
Octopoda unidentified				
Cephalopoda unidentified	12.5	2.7	6.7	117.1
Pteropoda[a]				
Diacra sp.				
Other small molluscs[a]				
Pelagic urochordates[a]	20.8	45.5	2.4	999.7
Thaliacea	20.8	45.5	2.4	999.7
Salpidae				
Pyrosoma sp.	20.8	45.5	2.4	999.7

[a] A major systematic or ecological group in Table 3.

TABLE A.1.—Extended. Continued.

Percent frequency (*F*)	Percent number (*N*)	Percent volume (*V*)	IRI	Percent frequency (*F*)	Percent number (*N*)	Percent volume (*V*)	IRI
***Pristipomoides filamentosus* (54)**				***Pristipomoides zonatus* (6)**			
66.7	20.2	45.1	4.350.7	83.3	44.4	16.8	5.104.4
50.0	16.3	36.6	2.645.9	83.3	44.4	16.8	5.104.4
22.2	3.9	8.7	278.2				
18.5	3.2	0.06	59.7				
14.8	2.1	0.04	31.8				
3.7	1.1	0.02	4.0				
***Etelis carbunculus* (33)**				***Aprion virescens* (42)**			
90.9	78.9	95.7	15.871.3	92.9	67.6	91.6	14.783.1
90.9	78.9	95.7	15.871.3	88.1	64.1	91.5	13.704.8
3.0	2.2	0.2	7.2				
3.0	2.2	0.02	6.8				
				2.4	0.7	0.03	1.8
				2.4	1.4	0.2	3.9
				11.9	4.9	0.3	61.7
				2.4	0.7	0.5	3.0
				2.4	0.7	0.03	1.8
				2.4	0.7	0.1	2.0
15.2	32.2	41.3	1.114.6	9.5	5.6	5.2	102.9
				2.4	0.7	0.1	1.8
15.2	32.2	41.3	1.114.6	4.8	2.8	4.8	36.6
12.1	22.2	28.5	615.0				
6.1	10.0	12.8	138.4				
				4.8	2.1	0.2	11.1
				2.4	0.7	1.0	4.0
81.8	42.2	54.2	7.886.7	78.6	48.6	84.1	10.426.4
				9.5	3.5	0.1	34.6
				4.8	2.1	0.04	10.2
				4.8	1.4	0.08	7.1
18.2	7.8	1.4	167.0	14.3	4.2	0.01	60.5
3.0	1.1	<0.01	3.4				
				2.4	0.7	<0.01	1.7
9.1	3.3	0.7	36.7	7.1	2.8	<0.01	20.2
9.1	3.3	0.7	36.7				
3.0	1.1	0.2	4.1	7.1	2.1	0.2	16.5
3.0	1.1	0.2	4.1	2.4	0.7	0.2	2.2
				4.8	1.4	<0.01	6.7
				2.4	0.7	0.08	1.9
				2.4	0.7	0.08	1.9
18.2	6.7	1.4	146.7	7.1	2.1	<0.01	15.1
6.1	6.7	1.7	50.9	11.9	3.5	4.9	100.0
6.1	6.7	1.7	50.9				
3.0	2.2	0.3	7.6				
3.0	1.1	1.4	7.7				
3.0	3.3	0.01	10.1				
				2.4	0.7	<0.01	1.7
				9.5	2.8	4.9	73.3
				2.4	0.7	<0.01	1.7
				2.4	0.7	<0.01	1.7
3.0	1.1	<0.01	3.4				
3.0	1.1	0.2	4.1	16.7	19.7	3.2	382.3
3.0	1.1	0.2	4.1	14.3	11.3	3.2	206.7
				2.4	8.5	0.02	20.2