FEEDING HABITS OF STOMIATOID FISHES FROM HAWAIIAN WATERS

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ABSTRACT

Stomachs were examined from over 2,800 specimens of stomiatoids collected near Hawaii. Small *Vinciguerria nimbaria* ate mostly small copepods and ostracods, while large fish appeared to switch to large amphipods and small euphausiids. The remaining planktivorous species, sternoptychids and small gonostomatids, fed primarily on large calanoid copepods and small euphausiids. All of these appeared to feed by active, visual searching, and preferred prey were probably more visible than other zooplankton in appropriate size ranges. Diets and preferences of the planktivorous stomiatoids were similar to or identical with those of one or more species of myctophids which share the same habitat. The large gonostomatids ate micronekton but appeared to feed in the same manner as the small individuals and species.

The species from six other families, which appear to be morphologically adapted to ingest relatively large prey, did in fact feed mostly on prey 20% of their body length or longer. Only two species ate zooplankton as well. Most species with chin barbels were nearly or exclusively piscivorous, and those without barbels ate few or no fish. The barbel and analogous structures appear to be used primarily to attract and aid in the capture of relatively large fish. Apparent preferences for certain types of prey by the piscivorous species indicate that interspecific differences in barbel features are related to dietary specialization. Based on feeding incidence and estimates of stomach evacuation time, the piscivorous stomiatoids appear to consume a large fraction of the standing crop of planktivorous fishes each year.

Stomiatoid fishes are important components of the micronekton in most tropical and temperate oceanic areas (e.g., Maynard et al. 1975). Most species occur in the upper 1,000 m and undertake diel vertical migrations (Clarke 1974 and others cited therein). They include both small, planktivorous species and generally larger forms with certain morphological features apparently related to capture of relatively large prey.

Little is known of the feeding habits of these fishes and, consequently, of their role and importance in the pelagic food web. Diets of a few planktivorous species have been reported, but usually from few specimens and without identification of prey beyond major taxa. Clarke (1978) showed that some planktivores feed while at depth during the day. Knowledge of the prey of nekton-eating species has consisted mainly of incidental reports scattered throughout the literature rather than systematic investigations of large numbers of specimens.

This paper presents results of examination of stomach contents of over 70 species of stomiatoids from an extensive series of collections near Hawaii in the north central Pacific Ocean. Almost all the species are vertical migrators; the abundant, nonmigrating species of *Cyclothone*, *Sternoptyx*, and *Argyropelecus* (which are the subjects of separate studies by other investigators) are not included. Diets of the planktivorous species are compared with estimates of prey abundance in appropriate depth ranges in order to determine whether composition and apparent preference are similar to those of cooccurring, nonstomiatoid planktivores which feed in the upper layers at night (Clarke 1980). Data from the nekton-eating stomiatoids allows consideration of preference, feeding methods, and the impact of these predators on the planktivorous micronekton in the community.

METHODS

Specimens for this study were collected ca. 20 km west of the island of Oahu, Hawaii (ca. lat. 21°20-30′N, long. 158°20-30′W) in waters 2,000-4,000 m deep. Previous studies in this area have considered the vertical distribution and certain other aspects of the ecology of stomiatoids (Clarke 1974) and the feeding chronology of five species (Clarke 1978). Other investigations in the

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area have been summarized by Maynard et al. (1975).

Over 2,800 specimens of nine families were examined. Based upon preliminary results, morphology, and the literature, the species were separated into two groups, each of which was treated differently. Members of the Photichthyidae, Sternoptychidae, and Gonostomatidae were considered planktivores; and those of the Astronesthidae, Chauliodontidae, Idiacanthidae, Melanostomiatidae, Stomiatidae, and Malacosteidae as nekton-eating species.

All specimens of planktivorous species were taken with a 3 m Isaacs-Kidd midwater trawl which terminated in a 1 m diameter cone of ca. 3 mm mesh netting with a ca. 2 l nonfiltering cod end bucket. Towing procedures were the same as described in Clarke (1980). The trawl was lowered to a given depth as rapidly as possible, towed for 2-3 h at ca. 2 m/s, and retrieved as rapidly as possible. A time-depth recorder of the appropriate range was attached to the trawls; depth records were accurate to 2-4% of the depth fished. In addition to night tows at 70-170 m described in Clarke (1980), specimens were also taken from day tows at 400-800 m and night tows at 225-250 m made in September 1973 and November 1974 (Table 1). During some of the deeper tows, the trawl changed depth by as much as 50-100 m during the "horizontal" portion of the tow.

Since the most abundant planktivores were known to feed during the day (Clarke 1978), zooplankton were sampled at 400-500 m during the day (Table 1) with opening-closing 70 cm diameter bongo nets (505 μm mesh). The nets were lowered closed, opened for 0.5-1 h at ca. 1 m/s ship's speed, then closed, and retrieved. Time-depth recorders attached to the nets indicated vertical movement of up to 100 m during the open portions of the tows. Volume sampled by each net was estimated from the mouth area, duration of the open portion of the tow, and an estimated speed of 1 m/s.

All material was preserved immediately after capture and held in ca. 4% formaldehyde/seawater. Except for certain trawl samples where large numbers of *Vinciguerria nimbaria* were caught and only individuals with obviously full stomachs were selected, all specimens of each species considered were measured (standard length, SL, to the nearest millimeter) and stomachs examined. Intact prey items were identified, counted, and measured to the nearest 0.1 mm (prosome length for copepods, total length without telson for malacostracans, and total length or maximum dimension for other prey). Identifiable remains among partially digested material were recorded. Any remains of chaetognaths (the only gelatinous prey found) were counted as intact since they are probably degraded much more rapidly than other prey types.

Items in the mouth or esophagus were not counted; their limbs and bodies were not compressed, indicating that they had been taken after capture. Otherwise, there was no evidence of postcapture ingestion by the fishes. Most prey types found intact in the stomach were also recorded as digested remains that had almost certainly been eaten well before capture, and, conversely, several types of abundant zooplankton were rarely or never found in the stomachs, as would be expected if the fish were feeding indiscriminately in the net. There was no evidence that food was regurgitated during or after capture; I found no everted stomachs and no digested remains in the esophagus.

Zooplankton from the bongo net samples were counted from either the entire sample (euphausiids and other relatively large types) or 1/16-1/32 aliquots taken with a Folsom plankton splitter. For both plankton and intact prey items, euphausiids and most copepods (with the exception of unidentifiable copepodites, which were fairly common in all the plankton samples) were identified to species. Ostracods (mostly *Conchoecia*

TABLE 1.—Dates, local (Hawaiian Standard) times, and depths of tows with 3 m Isaacs-Kidd midwater trawl and 70 cm bongo plankton nets off Oahu, Hawaii. Times for trawls are for the period at depth; total times including descent and ascent are in parentheses. Times for bongos are for the open period only. Depth figures are the ranges during "horizontal" portions of tow or modal depth if the range was <20 m.

Date	Time	Depth (m)
Trawls:		
25 Sept. 1973	1523-1723 (1500-1750)	400
9 Nov. 1974	1540-1740 (1535-1802)	400-450
25 Sept. 1973	0748-0954 (0721-1028)	450-500
25 Sept. 1973	1148-1348 (1115-1435)	525
11 Nov. 1974	0818-1118 (0736-1154)	550-600
9 Nov. 1974	0808-1108 (0730-1132)	550-650
26 Sept. 1973	0820-1020 (0742-1120)	600
9 Nov. 1974	1230-1430 (1155-1500)	600-650
12 Nov. 1974	0756-1000 (0722-1100)	650 (briefly to 800)
26 Sept. 1973	1227-1427 (1142-1550)	700-800
10-11 Nov. 1974	2303-0100 (2250-0115)	250
11 Nov. 1974	0155-0505 (0145-0515)	225
Bongos:		
14 Sept. 1973	0930-1033	400-425
14 Nov. 1974	0808-0908	400-425
14 Sept. 1973	1103-1135	425-525
14 Sept. 1973	1241-1311	550

spp.) and amphipods were not further identified, and other prey types were identified only to major taxa. Prey types of the same genus or of similar size, pigmentation, etc. were often lumped for convenience of presentation of results. Densities of zooplankton (Table 2) were calculated from the counts (corrected for any subsampling) and estimated volumes filtered; however, since these are based on so few samples, they can be considered as only rough estimates of prey abundance at the depths where the fishes were caught. Furthermore, the densities of types under 1.0 mm long are underestimated due to mesh escapement; for most of these, densities are probably about 4-5 times higher than estimated from the samples (Clarke 1980).

The nekton-eating species were much less abundant than the planktivores, and their feeding incidence and number of prey per fish were lower; consequently, in order to gather as much data as possible I examined specimens from a wide variety of trawl samples taken between 1969 and 1978. These included both horizontal and oblique samples in the upper 1,200 m—mostly either above 350 m at night or deeper during the day. Almost all were taken with a 3 m Isaacs-Kidd trawl towed at ca. 2 m/s. The terminal section was of fine (333 μm) plankton mesh for about two-thirds of the samples. For a few rare species I also took material from collections with a 5 m Isaacs-Kidd, a 3 m Tucker, or a 2/3 Cobb pelagic trawl. Data from the more abundant fishes were grouped by arbitrary size classes or by time of capture. For the latter, "day" included all tows started and completed between sunrise and sunset plus a few dusk tows which were completed after sunset but fished at or near the day depths of the fishes. Similarly, "night" included tows taken wholly between sunset and sunrise plus a few dawn tows that fished at or near night depths of the fishes.

Specimens were identified, measured, and classified into one of four categories: Damaged—the stomach ruptured or lost during capture, Empty—stomach completely empty or with only a trace of unidentifiable remains, Remains—prey completely disintegrated but identifiable to major taxon, Intact—prey in one piece or a few large pieces. Sizes (standard length of fishes, length without telson of crustaceans, and mantle length of squids) of all intact prey items were recorded. Depending upon size of the item and degree of digestion, the accuracy of these measurements was an estimated ±1-5 mm. Relative length of the prey items, as percentage of standard length of the predators, was used for presentation. Intact crustaceans and many of their remains could be identified to genus or species, but only a fraction of the intact fishes could be unquestionably identified. Where a fish prey could not be identified positively, a probable identification could be often given based on a process of elimination. Because of their photophores, myctophids and some stomiatoids could be identified as such at more advanced stages of digestion than other fishes; in most cases where an item was clearly not a myctophid, it was in good enough condition to be more precisely identified.

There was little evidence of postcapture ingestion of large items. A few very fresh items, i.e., those without a coating of stomach mucus or with the limbs not flattened against the body, were not counted. Most of these items were still partly in the esophagus and were usually types not found as digested remains in the same predator species, e.g., a euphausiid in an otherwise piscivorous species. As with the planktivores, there was no evidence of postcapture regurgitation of prey by nekton-eating species.

Most of the nekton-eating species proved to eat only small nekton (prey ≥10 mm long). Zooplankton (usually copepods) were very rarely found in their stomachs—always in near-perfect condition and never as digested remains. Certain species of these fishes, however, appeared to eat both small and large prey, and zooplankton were routinely found in their stomachs. In spite of the fact that many specimens of these species were taken by trawls with a fine mesh terminal section, there was little evidence that the data were biased by postcapture ingestion. As with the strictly planktivorous species, the types of prey found intact included only a narrow range of the types collected in the cod end of the trawl rather than a mixture as would be expected from indiscriminate ingestion in the net, and digested remains of the same types of prey were also recorded for these species. Finally, as will be shown below, the incidence of small items in the stomachs decreased with size of the fish; this would not be expected if these species were for some reason prone to ingestion after capture.

(At towing speeds of less than ca. 1.5 m/s, postcapture ingestion of both large and small items appears to be a serious problem. During the course of this study, I examined specimens from several tows taken at 1.0-1.5 m/s. Zooplankton—

TABLE 2.—Estimated densities of prey types from four plankton tows taken at 400-550 m during the day off Oahu, Hawaii. Data in the third column is from a tow taken in November 1974, the others from September 1973 (see Table 1). A "+" indicates present, but density <0.005/m^3. Except for the *Pleuromamma* spp., identifiable copepodites—usually stage V's—are included with adults.

Prey type		Density (No./m^3)			
	Depth of tow (m)	400-425	400-425	425-525	550
Copepods:					
Neocalanus spp.		0.05	0.02	0.12	0.07
Nannocalanus minor		0.01	—	—	0.07
Rhincalanus spp.		0.01	—	0.01	—
Eucalanus spp.		0.73	0.60	—	—
Clausocalanus spp.[1]		0.13	0.09	0.05	0.02
Pseudocalanidae[1]		0.57	0.69	0.17	—
Gaetanus/*Chiridius* spp.		1.18	0.60	0.14	0.07
Aetideidae <2.0 mm		0.60	0.55	1.49	0.14
2.0-2.9 mm		—	0.16	0.13	0.23
≥3.0 mm		—	—	0.03	0.39
Euchaeta media		0.15	0.53	0.40	—
Euchaeta spp.		0.02	0.05	—	0.02
Scottocalanus spp.		—	—	0.11	0.21
Lophothrix spp.		0.01	—	0.02	0.05
Scolecithricidae <1.0 mm[1]		0.44	0.35	0.19	0.12
1.0-1.5 mm		0.61	1.96	2.32	1.52
>1.5 mm		—	—	0.10	0.49
Metridia spp. ≤1.3 mm		0.33	0.05	0.23	0.39
>1.3 mm		—	—	—	0.02
Pleuromamma xiphias		—	—	0.51	2.08
Pleuromamma xiphias CV		0.47	1.09	0.17	0.16
Pleuromamma abdominalis		0.60	1.99	0.21	0.16
Pleuromamma abdominalis CIV, V		1.84	1.06	0.51	—
Pleuromamma gracilis		2.18	2.01	0.66	0.02
Pleuromamma gracilis CV		0.13	0.05	0.02	0.05
Lucicutia spp. ≤1.3 mm		0.13	0.02	0.05	0.23
>1.3 mm		—	—	0.04	0.12
Heterorhabdus papilliger		0.27	0.23	0.11	—
Heterorhabdus spp.		0.12	0.14	0.06	0.07
Heterostylites sp.		—	—	0.02	—
Haloptylus sp.		0.02	—	—	—
Augaptilidae		0.10	0.51	0.38	0.14
Arietellus sp.		—	—	0.01	—

Prey type		Density (No./m^3)			
	Depth of tow (m)	400-425	400-425	425-525	550
Candacia spp. ≤1.5 mm		0.03	0.07	0.01	—
>1.5 mm		—	—	0.03	0.14
Acartia spp.[1]		—	—	0.01	0.07
Unident. calanoid		0.72	2.08	0.55	1.04
Oithona spp.[1]		0.15	0.14	0.04	0.02
Oncaea mediterranea[1]		0.06	0.10	0.02	0.02
Oncaea conifera[1]		0.06	0.05	0.09	0.05
Oncaea spp. ≤0.6 mm[1]		0.21	—	0.27	—
Corycaeus spp.		0.01	—	0.04	—
Aegisthes spp.		0.16	0.02	0.13	0.09
Copilia spp.		0.07	—	—	—
Monstrilla sp.		0.01	—	—	—
Mormonilla sp.		—	—	0.04	0.07
Amphipod <2.0 mm		+	+	+	—
2.0-2.9 mm		+	+	+	+
≥3.0 mm		0.01	0.01	0.04	0.01
Ostracod ≤1.0 mm[1]		0.16	0.16	0.11	0.05
1.1-1.9 mm		0.30	0.12	0.26	0.11
≥2.0 mm		0.01	—	0.04	0.02
Euphausiids:					
Euphausia spp.		2.30	0.04	0.40	0.02
Stylocheiron spp.		0.02	0.01	+	—
Nematoscelis spp.		0.03	0.01	0.12	0.02
Thysanopoda aequalis		0.01	0.01	0.02	+
Thysanopoda spp.		0.01	+	0.01	0.01
Nematobrachion spp.		+	+	+	—
Euphausiid larva		0.01	0.03	—	+
Isopod		+	—	+	—
Megalops		—	—	+	—
Cyprus		0.16	0.06	0.03	+
Polychaete		0.01	0.01	+	—
Chaetognath		0.76	0.36	0.23	0.06
Pteropod		+	0.01	+	—
Fish larva		—	—	+	0.01

[1]Densities seriously underestimated due to mesh escapement.

up to 10-12 assorted copepods and ostracods, all apparently recently ingested—were found in several stomachs of fishes that otherwise had eaten only relatively large items. I also found several apparently freshly ingested euphausiids and sergestid shrimps in stomachs of fishes that otherwise appeared to be strictly piscivorous. Specimens from these slow tows were not included in the data presented here.)

Estimates of biomass and relative abundance of vertically migrating fishes in the study area and of feeding incidence of the nekton-eating stomiatoids were made from catches of a series of oblique 3 m Isaacs-Kidd trawl tows taken at approximately monthly intervals between August 1977 and November 1978. A time-depth recorder and a flowmeter were mounted on the trawl for all tows. All fishes were identified, species were grouped by taxa and known or probable feeding habits, and wet weights of each group determined for each sample. All nekton-eating stomiatoids from the series were examined and are included in the results below.

The 58 night tows in this series fished between the surface and ca. 350 m and covered the nighttime depth range of all vertically migrating species. The relative abundances of the different taxonomic and trophic groups were calculated based upon total numbers from all the night tows. Biomass (wet weight) per unit area of each group was calculated as in Maynard et al. (1975) for each sample. The overall mean of all samples and all seasons was used as the estimated average biomass. The 28 day tows covered the day depth ranges of the vertically migrating species (ca. 350-1,000 m), but for various reasons it was not possible to reliably estimate volume filtered (and therefore biomass per unit area) from these tows. The numbers of nekton-eating stomiatoids and of prey species in the catch and the numbers of prey found in the stomachs of the stomiatoids from both day and night tows were used to estimate feeding incidence relative to the numerical standing crop of prey species.

RESULTS

Photichthyidae

Vinciguerria nimbaria (Table 3) from three samples within its day depth range were divided into two size groups (16-25 mm and over 25 mm SL). Catches of three of the six size-depth groups were high, and only fish with visually apparent full stomachs were selected for examination (Table 3, columns 3, 5, 6). All fish of the other groups were examined, but total numbers of intact prey were still quite low for these.

Overall the most frequent items in the stomachs were small copepods and ostracods. *Oncaea* spp. were the dominant prey in most size-depth groups, and in all samples *Oncaea*—especially the small forms—were more frequent in the diets of the smaller fish than in those of the large. Beyond this, however, the diet composition varied between groups without much apparent relation to size or depth, e.g., *Clausocalanus* spp. and *Pleuromamma gracilis* were important fractions of the prey of the small fish from 400 m and both size groups from 450 to 500 m; candaciids and *Scolecithrix danae* were taken by most groups, but decidedly more frequently (as percentage of prey items) by the large fish from 400 m; the frequency of ostracods varied among the groups from 3% to 42% of the total items.

Some of this variability was undoubtedly a consequence of small sample sizes from three groups, but part resulted from large numbers of certain prey types occurring in only one or a few of the fish from a given size-depth group. Examples include (see appropriate column of Table 3): All 7 *P. gracilis* from 1 of 6 fish with prey (column 1); all 5 amphipods from 1 of 3 fish (column 2); 4 of 5 *Undinula* spp. from 1, 4 of 5 *Sapphirina* spp. from another, and all 11 pelecypod larvae from another out of 18 fish (column 3); 13 of 41 *Clausocalanus* spp. in 1 and 34 of 73 *P. gracilis* in 3 others out of 20 fish (column 5); 14 of 15 *Scolecithrix danae* in 1 and 24 of 34 *P. gracilis* in 2 others out of 9 fish (column 6). The presence or absence of only one or two fish such as these had an important effect on percentages of certain items in the estimated diet of a size-depth group.

Vinciguerria nimbaria over 30 mm SL had eaten considerably larger items more frequently than smaller fish. The only large day-caught specimen (37 mm) contained remains of another fish, a 3.0 mm amphipod and two *Nematobrachion* spp., each ca. 15 mm long. Ten specimens over 30 mm were taken in a night tow at 70 m. Most items in the stomachs of these fish were on the borderline between "intact" and "remains" and difficult to count similarly to those from the day specimens, but it was clear that euphausiids—mostly *Stylocheiron* spp.—were the most frequent items and that small copepods were much less important than in the smaller fish. Remains of six to nine *Stylocheiron* each were found

TABLE 3.—Numbers of intact items of different prey types from stomachs of *Vinciguerria nimbaria* and *V. poweriae* from several depths and times. Remains of types not found intact are denoted by "r"; in column seven (*V. nimbaria*, Night, 70 m), numbers of nearly intact remains (see text) are given in parentheses.

	V. nimbaria							*V. poweriae*	
	Day						Night	Day	Night
Depth (m)	400		400-450		450-500		70	400-300	225-250
Size (SL, mm)	17-25	26-30	16-24	26-30	17-25	26-30	31-39	23-29	20-34
No. examined	14	8	18	13	20	9	10	11	16
No. w/intact prey	6	3	18	4	20	9	0	8	7
No. of intact prey	54	33	270	31	437	192	0	57	17
No. of prey type:									
Neocalanus spp.	—	—	—	—	1	1	r(4)	—	—
Nannocalanus minor	—	—	—	—	—	1	—	—	—
Undinula spp.	—	—	5	—	1	1	—	—	—
Clausocalanus spp.	3	—	1	—	41	13	—	—	—
Euchaeta spp.	—	1	—	—	—	4	r(2)	—	—
Aetideidae	—	—	—	—	—	2	r(1)	—	—
Scolecithrix danae	—	5	3	1	2	15	—	—	—
Scolecithricidae ≤1.0 mm	1	—	—	1	2	2	—	—	—
Scolecithricidae >1.0 mm	—	1	—	—	5	1	—	2	—
Pleuromamma abdominalis	—	—	—	r	3	1	—	1	—
Pleuromamma spp. CIV, CV	—	—	1	—	8	2	—	—	—
Pleuromamma gracilis	7	r	5	1	73	34	—	—	r
Lucicutia spp. ≤1.3 mm	3	r	3	—	20	9	—	—	1
Heterorhabdus spp.	—	—	1	—	2	1	—	—	—
Augaptilidae	—	—	—	—	—	1	—	—	—
Candacia spp.	1	1	2	—	4	6	r(1)	3	r
Paracandacia spp.	—	7	2	—	1	3	r(13)	1	2
Unident. calanoid	—	1	—	—	6	2	r(5)	—	—
Corycaeus spp.	—	1	10	—	11	1	r(1)	—	—
Oncaea mediterranea	9	2	66	6	82	13	r(2)	6	5
Oncaea conifera	10	2	43	4	55	17	—	7	—
Oncaea venusta	1	—	19	1	7	4	—	3	3
Oncaea spp. ≤0.6 mm	13	2	29	—	67	24	—	3	1
Sapphirina spp.	—	—	5	1	—	1	r(1)	—	—
Aegisthes spp.	—	—	—	—	—	1	—	—	—
Euphausia spp.	—	r	r	—	6	2	—	2	—
Stylocheiron spp.	—	—	—	—	—	r	r(28)	r	r
Nematobrachion spp.	—	—	—	—	—	—	—	1	r
Euphausiid larva	—	—	1	—	3	4	r(1)	—	—
Caridean larva	—	1	—	—	—	1	—	—	—
Amphipod <2.0 mm	—	1	4	—	2	—	—	1	—
≥2.0 mm	—	4	3	1	4	4	r(46)	—	—
Ostracod ≤1.0 mm	2	—	27	4	16	9	—	5	2
>1.0 mm	4	1	20	9	14	8	r(9)	16	3
Gastropod larva	—	—	8	—	1	1	—	6	—
Pelecypod larva	—	—	11	—	—	—	—	—	—
Heteropod (*Atlanta* spp.)	—	1	1	—	—	—	—	—	—
Chaetognath	—	1	—	—	—	1	r(1)	—	—
Fish larva	—	1	r	2	—	2	r(2)	r	r

in four of the large *V. nimbaria*. Amphipods were also apparently important items in the diet of these large fish, but similar to the above examples, about 38 of the approximately 46 amphipods recorded were eaten by only 2 of the 10 fish.

Vinciguerria poweriae was taken in small numbers in the same day tows as *V. nimbaria* and at night at 225-250 m (Table 3). Both the incidence of fish with intact prey and the number of prey per fish were lower at night, indicating that, like *V. nimbaria* (Clarke 1978), *V. poweriae* feeds during the day. The items and remains found in stomachs of both groups indicate that *V. poweriae's* diet is generally similar to that of *V. nimbaria* of the same sizes. The lower percentages of *Oncaea* spp., higher percentages of ostracods, and less diversity may have been an artifact of small sample size.

Sternoptychidae

Valenciennellus tripunctulatus and *Danaphos oculatus* (Table 4) were taken in day tows with and slightly deeper than the *Vinciguerria* spp. The small *Valenciennellus tripunctulatus*—mostly from the shallower tows—had eaten some *Oncaea* spp., ostracods, and small (1.0-1.5 mm) calanoids, but most of their prey and all of those of the larger fish were medium to large calanoids. Few prey were found in *D. oculatus*, but with the exception of a small scolecithricid and remains of an ostracod, all were large calanoids.

Gonostomatidae

The diet of *Gonostoma atlanticum* (Table 5) from day tows consisted of essentially the same

TABLE 4.—Numbers of intact prey from stomachs of *Valenciennellus tripunctulatus* from day samples at four different depths and of *Danaphos oculatus* combined from four different day samples. Remains of types not found intact are denoted by "r."

	Valenciennellus tripunctulatus				*Danaphos oculatus*
Depth (m)	400	400-450	450-500	525	400-600
Size (SL, mm)	22-30	23-29	28-31	29-34	28-40
No. examined	11	10	3	4	21
No. w/intact prey	11	10	3	4	10
No. of intact prey	84	44	7	34	21
No. of prey type:					
Neocalanus spp.	—	1	—	—	—
Eucalanus spp.	3	—	—	1	—
Clausocalanus spp.	4	1	—	1	—
Aetideidae <2.0 mm	4	—	—	2	3
>2.0 mm	10	3	1	—	8
Euchaeta media	12	4	2	6	5
Scolecithricidae <1.0 mm	4	2	—	—	1
≥1.0 mm	3	1	1	9	—
Pleuromamma xiphias	11	11	1	12	3
Pleuromamma xiphias CV	9	1	—	—	—
Pleuromamma abdominalis	3	2	2	1	—
Pleuromamma abdominalis CV	1	—	—	—	—
Pleuromamma gracilis	6	—	—	—	—
Heterorhabdus papilliger	4	1	—	—	—
Heterorhabdus spp.	2	—	—	—	—
Candacia longimana	—	—	—	1	1
Oncaea conifera	2	5	—	—	—
Oncaea spp. ≤0.6 mm	—	1	—	—	—
Corycaeus spp.	—	1	—	—	—
Ostracod ≤1.0 mm	—	2	—	—	—
1.1-1.9 mm	1	3	—	—	r
Unident. calanoid	5	4	—	1	—
Chaetognath	—	1	—	—	—

TABLE 5.—Numbers of intact prey from stomachs of four species of gonostomatid fishes taken day and night and combined from two or more samples within given depth ranges. In this table, a few stage V copepodites of *Pleuromamma xiphias* and *P. abdominalis* are included with adults. Prey types not found as intact items are denoted by "r." Additional remains from fish of column seven (225-250 m depth) included a penaeidean shrimp and a large *Metridia* sp. Data for *Gonostoma elongatum* and *G. ebelingi* over 120 mm SL are in Table 6.

	Gonostoma atlanticum				*Gonostoma elongatum*			*Gonostoma ebelingi*		*Diplophos taenia*	
	Day		Night		Day	Night		Day		Day + night	
Depth (m)	400-525		170-250		400-800	110-170	225-250	400-500	525-650	400-650 + 90	
Size (SL, mm)	22-45	46-65	25-44	46-54	34-78	29-88	93-120	34-77	94-117	53-93	103-171
No. examined	34	29	26	9	24	15	17	9	21	9	14
No. w/intact prey	25	21	7	4	6	9	2	7	4	8	9
No. of intact prey	74	46	10	5	22	18	3	20	9	13	19
No. of prey type:											
Neocalanus spp.	—	—	—	—	1	—	—	—	—	1	—
Undinula sp.	—	—	—	—	—	—	—	—	—	1	—
Eucalanus spp.	1	—	—	—	—	—	—	—	—	—	—
Aetideidae	2	2	—	1	4	—	—	2	3	—	—
Euchaeta media	r	1	—	1	—	—	—	1	—	—	—
Scottocalanus spp.	r	2	1	2	r	—	—	—	4	—	—
Amallothrix spp.	2	1	—	—	—	—	—	—	—	—	—
Pleuromamma xiphias	33	10	1	—	11	15	2	5	r	2	2
Pleuromamma abdominalis	8	3	2	—	—	1	—	—	—	4	—
Pleuromamma gracilis	—	1	—	—	—	—	—	—	—	—	—
Lucicutia spp.	1	—	1	—	—	—	—	—	—	—	—
Candacia longimana	6	3	1	r	2	—	r	r	—	—	—
Unident. calanoid	1	—	2	1	—	—	—	—	—	—	—
Oncaea spp.	3	—	—	—	1	—	—	6	—	—	—
Euphausia spp.	13	14	2	—	—	1	r	1	—	5	4
Stylocheiron spp.	2	—	—	r	r	r	r	r	—	—	—
Nematoscelis spp.	—	6	—	—	—	—	—	—	1	—	—
Nematobrachion sp.	—	—	—	—	—	—	1	—	—	—	—
Thysanopoda aequalis	—	3	—	r	1	—	—	1	—	—	2
Thysanopoda spp.	—	—	—	—	—	—	r	—	—	r	1
Euphausiid larva	—	—	—	—	—	—	—	—	—	—	1
Ostracod	1	—	—	—	—	1	—	4	1	r	—
Amphipod	—	—	—	—	2	—	r	—	—	—	7
Fish	1	—	—	—	r	—	r	r	—	—	2

types of copepods eaten by the sternoptychids plus small (8-12 mm) species of euphausiids. The euphausiids were over twice as frequent and, among the copepods, *P. xiphias* and *P. abdominalis* much less important in the diet of the larger of the two size groups of fish. *Gonostoma atlanticum* appears to feed by day (Clarke 1978); as expected, the remains and few intact prey items found in night-caught specimens were similar to those from day-caught fish.

Gonostoma elongatum were divided into three size groups. Specimens <90 mm SL from both day and night tows (Table 5) contained mostly large copepods, the majority of which were *P. xiphias*. Euphausiids or their remains were found in several specimens; only one, a *Thysanopoda aequalis*, was over 10% of the fish's length. Intermediate-sized *G. elongatum* (93-120 mm SL) were taken only at night, and most stomachs contained only digested remains. The frequency of euphausiids in the diet appeared higher than in the small fish, and one plus the remains of two others were over 10% of the fish's length. *Gonostoma elongatum* over 120 mm (Table 6) had eaten large prey in all but two cases. Relative sizes of most measurable items were about 10%, but values ranged from 3.8% to 27% (excluding two copepods and a somewhat suspicious pyrosome). Penaeidean shrimps and euphausiids were the most frequent items and remains, but fish were taken by several and squid by two of the large specimens.

Limited data for *G. ebelingi* and *Diplophos taenia* indicated that both diet and differences between size groups were similar to those of *G. elongatum*, but there were some differences in important prey types. Data for *G. ebelingi* came exclusively from day tows. Small fish (Table 5) had eaten small zooplankton—*Oncaea* spp. and ostracods—as well as the larger *P. xiphias* and euphausiids; the intermediate-sized individuals had eaten only large zooplankton. The largest fish (Table 6) had eaten only fish and crustaceans over 10 mm long; the relative sizes of intact items were 11-24%. *Diplophos taenia* (Table 5) were mostly from day tows. Small fish had eaten medium to large copepods and *Euphausia* spp. The large fish contained few copepods or their remains; most prey were small euphausiids or the large (5-6 mm) amphipod *Vibilia* spp. The two largest fish examined had eaten myctophids. One of the myctophids (*Lampanyctus* sp.) and a *T. tricuspidata* were relatively large (29 and 22%, respectively), but all other items were <10%.

Astronesthidae

Astronesthes indicus under 60 mm SL fed mostly on copepods and ostracods (Table 7). Small prey types, especially *Oncaea* spp., were more frequent in diets of fish under 30 mm SL. Of the two species of scolecithricid copepods eaten, the smaller *Scolecithrix danae* (ca. 1.5 mm prosome length) was more frequent in the diet of the fish under 30 mm than in the 31-60 mm fish, but the larger *Scottocalanus* spp. (over 3 mm PL) were more frequent in the larger fish. Euphausiids were only slightly more frequent in the diet of the 31-60 mm fish than in that of the smaller ones; remains of euphausiids, including five in one fish, were found only in the 31-60 mm group. The few individuals over 60 mm SL (Table 6) were mostly empty; only a myctophid and fish remains were found.

The smallest individual of *A. "cyaneus"* (15 mm SL) had eaten small zooplankton, but those 20-47 mm SL (Table 6) had eaten only *Euphausia* spp.—some up to almost one-half their own length. Fish remains were found in two of the three larger fish examined. The small and intermediate-sized *A. splendidus* had eaten a few copepods and a small euphausiid, but all other prey of all sizes were relatively large—an average of 41% of SL—and all but two were fish (Table 6). Small *A. "similis"* (Table 6) contained only fish remains; the large individuals contained fish and a single euphausiid whose relative length was considerably less than those of the fishes eaten. (See Clarke 1974, regarding differences between the two provisionally identified species and *A. cyaneus* and *A. similis*.)

The items found in *Heterophotus ophistoma* (Table 6) were unique in several respects, but the significance of these cannot be assessed from the insufficient data here. One of the small specimens contained squid remains—otherwise found in only two specimens of *G. elongatum*. The four large specimens contained two sergestids, a *Sternoptyx* sp.—the only nonmigrating fish found in any stomiatoid, and remains of a *Parapandalus* sp.—the only adult caridean shrimp found. All of these items were relatively smaller than prey of most other nekton-eating species.

Chauliodontidae

Chauliodus sloani (Table 6) had eaten mostly fish; only those <120 mm had taken crustaceans—mostly euphausiids—frequently. The

TABLE 6.—Summary of stomach analyses for nekton-eating stomiatoids. See text for definition of categories. Under "Time" (first column): D = day, N = night, B = both combined. Under "Remains recorded" (last column): e = euphausiid, s = sergestid, c = unidentifiable crustacean, m = myctophid, f = unidentifiable fish, sq = squid. See text for explanation of groups of unidentified *Eustomias* spp.

Family/species	Time	SL (mm)	No. specimens (damaged)	% of undamaged specimens			Relative lengths of prey in % of predator SL (No. of items)		Remains recorded
				Empty	Remains only	Intact items	Fish	Crustaceans	
Gonostomatidae:									
Gonostoma elongatum	D	138-207	11(0)	64	9	27	13-20(2)	10-13(3)	e,sq[1]
	N	126-210	10(0)	10	40	60	13-17(2)	6-27(6)	e,c,f,sq[2]
Gonostoma ebelingi	D	121-143	19(0)	58	32	11	—	11-24(3)	e,c,m,f
Astronesthidae:									
Astronesthes indicus	B	64-152	20(2)	83	11	6	29(1)	—	f
Astronesthes "cyaneus"	B	15-47	30(0)	60	23	17	—	24-48(6)	e,c[3]
	B	114-164	3(0)	33	67	0	—	—	m,f
Astronesthes splendidus	B	22-39	31(1)	53	23	23	32-63(5)	31-41(2)	e,m,f[4]
	B	41-58	17(0)	76	6	18	41-44(2)	—	c,m,f[5]
	B	66-95	14(0)	57	7	36	21-64(5)	—	m
Astronesthes "similis"	B	23-68	27(1)	73	27	—	—	—	m,f
	B	98-122	5(0)	40	20	40	25-41(2)	8(1)	f
Heterophotus ophistoma	B	35-70	8(1)	86	14	—	—	—	sq
	B	141-320	4(0)	25	25	50	7(1)	6-11(2)	c
Chauliodontidae:									
Chauliodus sloani	D	20-60	43(4)	62	18	20	33-45(7)	20(1)	e,m,f
	N	20-60	57(9)	58	23	19	31-63(6)	10-20(2)	e,m,f
	D	61-120	12(2)	50	20	30	21(1)	11-16(3)	e,f
	N	61-120	33(9)	54	25	21	22-42(6)	—	m,f
	D	121-255	24(6)	44	22	33	14-33(5)	13(1)	f
	N	121-232	23(11)	50	25	25	14-19(3)	—	c,f
Idiacanthidae:									
Idiacanthus fasciola	D	50-100	55(25)	90	10	—	—	—	m,f
	N	50-100	73(24)	88	4	8	16-22(4)	—	f
	D	101-200	38(6)	72	19	9	17-20(3)	—	m,f
	N	101-200	57(8)	78	14	8	9-20(4)	—	f
	D	201-375	37(1)	75	14	11	13-23(4)	—	f
	N	201-372	102(7)	84	6	9	10-23(8)	4-8(2)	f
Melanostomiatidae:									
Thysanactis dentex	D	121-167	29(0)	86	—	14	30-48(4)	—	—
	N	121-174	51(5)	67	13	20	21-42(5)	14-29(3)	f[6]
Eustomias bifilis	D	50-90	40(5)	91	—	9	19-20(3)	—	—
	N	50-90	95(2)	85	4	11	17-47(10)	—	m,f
	D	91-165	36(5)	74	13	13	8-21(4)	—	m,f
	N	91-170	60(2)	91	5	3	15-33(3)	—	f
Eustomias enbarbatus	B	56-219	26(3)	78	13	9	16-41(2)	—	f
Eustomias spp. (3,low)	B	50-160	46(4)	79	7	14	17-32(6)	—	f
Eustomias longibarba	B	66-152	50(3)	79	9	11	24-42(5)	25(1)	f
Eustomias gibbsi	B	61-141	35(3)	91	3	6	34-37(2)	—	f
Eustomias spp. (3,hi)	B	55-161	134(7)	83	9	8	17-34(10)	—	f
Eustomias "silvescens"	B	60-180	32(1)	68	6	26	23-48(8)	—	f
Eustomias spp. (2)	B	60-161	152(0)	80	8	12	17-76(18)	14(1)	f
Bathophilus kingi	B	24-140	3(2)	76	17	7	23-40(3)	—	f
Bathophilus spp.	B	26-90	27(3)	67	21	12	45-67(3)	—	f
Photonectes spp.	B	22-78	14(2)	42	25	33	34-72(4)	—	f
	B	132-240	10(0)	90	—	10	26(1)	16(1)	—
Leptostomias spp.	B	35-290	31(2)	83	7	10	13-29(3)	—	f
Melanostomias spp.	B	62-165	8(0)	75	12	12	33(1)	—	f
Stomiatidae:									
Stomias danae	B	42-183	12(0)	75	8	17	24-33(2)	—	f
Malacosteidae:									
Aristostomias spp.	B	33-140	25(8)	71	24	6	35(1)	—	m,f
Photostomias spp.	B	29-51	37(6)	68	13	19	—	9-30(4)	s,c
Photostomias sp. 1	B	52-102	73(4)	74	16	10	—	15-28(8)	s,c
Photostomias sp. 2	B	51-90	54(2)	67	21	12	—	29-42(6)	s,c
Photostomias sp. 2	B	91-140	38(1)	89	8	3	—	30(1)	s,c

Small intact items also recorded: [1]*Euchirella* sp.
[2]*Pleuromamma xiphias*, caridean larva, pyrosome.
[3]*Oncaea* spp., ostracod.
[4]*P. xiphias*, *P. abdominalis*, euphausiid larva.
[5]*P. xiphias*, *Euchirella* sp.
[6]Isopod.

fishes eaten by the smallest size group were relatively larger (30-63%) than the fishes from the larger *C. sloani* (14-29% with one exception) or any of the crustaceans (10-20%). Of the 28 fish eaten, 18 were myctophids of at least 5 different genera (*Ceratoscopelus*, *Hygophum*, *Notolychnus*, *Lampanyctus*, and *Triphoturus*); five others were definitely not myctophids and included one and probably a second *Vinciguerria nimbaria* and what was most likely a *Bregmaceros* sp.

TABLE 7.—Summary of stomach analyses of planktivorous sizes of *Astronesthes indicus* and *Thysanactis dentex*. For large prey types, the range of relative lengths in percentage of predator length is given in parentheses after the count. Data for larger fishes of both species are in Table 6.

	Astronesthes indicus				*Thysanactis dentex*			
Size (SL, mm)	15-30		31-60		43-90		91-120	
Time	Day	Night	Day	Night	Day	Night	Day	Night
No. examined (No. damaged)	23(0)	37(1)	43(1)	55(2)	78(1)	104(3)	37(0)	79(5)
Percent undamaged:								
Empty	70	67	86	77	57	44	73	68
Remains only	—	3	2	4	10	19	8	8
Intact items	30	31	12	19	32	38	19	24
Intact large items	4	8	2	9	16	21	16	22
No. of prey type:								
Eucalanus sp.	—	1	—	—	—	—	—	—
Aetideidae	3	—	—	—	8	8	—	2
Scolecithrix danae	3	6	1	2	—	—	—	—
Scottocalanus spp.	—	1	1	4	1	—	—	—
Pleuromamma xiphias	1	—	—	—	24	21	2	13
Pleuromamma abdominalis	—	—	—	—	5	3	—	3
Other calanoid	6	3	—	5	5	3	—	—
Oncaea spp.	16	9	1	4	—	—	—	—
Aegisthes sp.	—	1	—	—	—	—	—	—
Euphausia spp.	1(21)	2(19-35)	1(14)	4(12-30)	2(7-13)	3(10-13)	1(10)	3(10-11)
Nematoscelis sp.	—	—	—	—	—	1(11)	—	—
Thysanopoda aequalis	—	1(21)	—	—	8(12-19)	18(11-19)	1(10)	4(10-13)
Thysanopoda spp.	—	—	—	1(30)	1(24)	3(23)	1(22)	3(21-28)
Euphausiid larva	3	6	1	1	2	1	—	—
Decapod larva	—	1	—	—	—	1	—	—
Sergestes spp.	—	—	—	—	—	2(18-20)	—	1(11)
Ostracod	21	15	14	8	—	1	—	—
Fish	—	—	—	—	2(23-24)	3(15-36)	3(16-43)	7(18-53)

Idiacanthidae

All sizes of *Idiacanthus fasciola* had eaten fish nearly exclusively (Table 6). Of the 23 fish, 15 were myctophids of at least 5 genera (*Bolinichthys*, *Ceratoscopelus*, *Diaphus*, *Lampanyctus*, and *Triphoturus*). Only one of the others, possibly a stomiatoid, was definitely not a myctophid. The largest prey of all sizes of *I. fasciola* were about 20% of the predator's length, but the minimum and average relative size of prey were somewhat higher in the small *I. fasciola*. The only two crustaceans found were intact, but neither appeared to have been very recently ingested. No crustacean remains were found, and the two intact crustaceans were smaller than all (substantially smaller than most) of the fishes eaten. Two other, smaller items—a pyroosome and a copepod—found in *I. fasciola* were not counted because they showed no sign of digestion or compression. Thus *I. fasciola* must have occasionally fed in the net and may have ingested the crustaceans there. Whatever the case, crustaceans are certainly a very minor part of the diet.

Melanostomiatidae

Thysanactis dentex under 120 mm SL had eaten zooplankton as well as large prey (Table 7). The 43-90 mm size group had eaten small euphausiids—mostly *Thysanopoda aequalis* 11-19% of their length—and large, pigmented copepods—mostly *Pleuromamma xiphias*; however, several relatively larger (15-36% of SL) fishes, *Thysanopoda* spp., and sergestids were also found. Fish 91-120 mm had eaten copepods and small euphausiids much less frequently; the bulk of the diet was relatively large fish and crustaceans. With the exception of a single isopod, the items and remains from fish >120 mm (Table 6) included only relatively large prey: other fishes, a large *Thysanopoda* spp., and two sergestids. Of the 24 intact fishes from all sizes of *Thysanactis dentex*, 9 were definitely myctophids of at least 5 different genera (*Bolinichthys*, *Diaphus*, *Diogenichthys*, *Lampadena*, and *Triphoturus*), and 11 were definitely of other families, including 6 *Bregmaceros* spp. and 2 *Melamphaes* spp. Most of the high values of relative size were for the slender *Bregmaceros* spp. The three *B. japonicus* from the 91-120 mm SL *Thysanactis dentex* were 45-53% compared with 11-28% for the remaining fishes and large crustaceans. Among the prey from *T. dentex*, over 120 mm SL, the three *Bregmaceros* sp. (c.f. *B. macclellandi*) ranged from 39 to 42%, while with the exception of an unidentified fish at 48%, the remaining fish prey were 14-32%.

There were approximately 30 species of *Eustomias* in the collections, many of them either undescribed or of uncertain status. *Eustomias bifilis* was the only one for which large numbers were available, and only 4 others were represented by more than 25 specimens (Table 6). The remaining identifiable species were pooled according to pectoral ray and photophore counts along with specimens whose barbels had been damaged and could not be identified to species. Those designated "3, low" were all damaged specimens with 3 pectoral rays and 15 or fewer VAL and VAV photophores. *Eustomias bifilis* and *E. enbarbatus* were the only other species from the area with the same counts. Those designated "3, hi" included 69 specimens of at least 6 undescribed species and 65 damaged specimens, all with 3 pectoral rays and over 15 VAL and VAV photophores—the same counts as for *E. longibarba* and *E. gibbsi.* Those designated "2" included 6 damaged specimens and 146 others of about 20 species, which, like *E. "silvescens,"* had only two pectoral rays. The 2-rayed species have shorter and generally more ornate barbels than any of the 3-rayed species (cf. illustrations in Morrow and Gibbs 1964).

All prey items and remains from the 3-rayed species with low counts were fish. Of 20 intact items from *E. bifilis,* 11 were the myctophid *Bolinichthys longipes* and 6 were myctophids of at least 3 other genera (*Benthosema, Diogenichthys,* and *Hygophum*). One of the three unidentified items was definitely not a myctophid and was probably a *Howella* sp. The range of relative size of prey (15-34% of SL) was large, but there was no trend with the size of the predator. One and probably both of the intact fish found in *E. enbarbatus* were *Howella* sp. The six intact items from the damaged specimens (most of which were probably the abundant *E. bifilis*) included three *Bolinichthys longipes,* a *Benthosema,* an unidentified myctophid, and an unidentified fish.

The prey of *E. longibarba, E. gibbsi,* and the other species with three pectoral rays and high photophore counts were, with one exception, fish. Of the 17 intact fish, 15 were myctophids including 7 and probably 8 *Bolinichthys longipes* and at least 2 other genera (*Benthosema* and *Ceratoscopelus*). The median relative size of fish prey for these *Eustomias* spp. (25%) was significantly higher ($P<0.05$, Mann-Whitney test, one-tailed probability) than that for the *Eustomias* spp. with three rays and low photophore counts (20.5%). One specimen of *E. longibarba* had eaten a large euphausiid, *Thysanopoda pectinata.*

One of the *Eustomias* spp. with two pectoral rays had eaten a sergestid shrimp, but all other prey of this group were fish. These *Eustomias* spp. appeared to eat fewer and different myctophids than did any of the 3-rayed species. *Eustomas "silvescens"* (cf. fig. 106A in Morrow and Gibbs 1964), the most commonly taken species of this group, had eaten three *Scopelosaurus* spp., three myctophids (two *Bolinichthys longipes* and a *Diaphus*), and two unidentified fish. Stomachs of the remaining species contained a total of 18 intact fish: 12 myctophids, 2 *Howella* sp., and 4 *Scopelosaurus* spp. (plus 2 more of the latter that were too digested to measure). Five and probably six of the myctophids were *Diaphus* spp., and only three and probably four were *B. longipes.* In the 3-rayed species of *Eustomias, Diaphus* was found only once, and *B. longipes* was the most common prey. Although data are too few to be certain, some of the 2-rayed species appeared to have diets that were restricted or included high proportions of relatively rare fishes. For one undescribed form, all four items were *Diaphus* spp.; for another, two out of four were *Howella* sp.; and for a third and fourth, two out of two items and two out of four remains, respectively, were *Scopelosaurus* spp. The median relative size of prey of the 2-rayed species (27%) was significantly ($P = 0.01$) higher than that for the 3-rayed species with low counts, but did not differ from that for the 3-rayed species with high counts.

The two crustaceans recorded from *Eustomias* spp. appear suspicious and indicative of postcapture ingestion, especially since no digested crustacean remains were found in any of the stomachs. The two items showed no obvious signs of having been eaten after capture, but neither were they much digested. The only indirect evidence that these were actual prey items and not eaten in the net is that I have found both crustaceans and their remains in the stomachs of several *E. bulbornatus,* a species which does not occur in the study area. Since at least one species of the genus appears to eat crustaceans, it is possible that others may do so occasionally.

Based upon a limited amount of data (Table 6), the remaining melanostomiatid genera, as well as *Stomias danae* (Stomiatidae) and the *Aristostomias* spp. (Malacosteidae), are piscivorous. All the identifiable fish eaten by these species were myctophids. All three items from *Leptostomias* spp. were *Notolychnus valdiviae.* The relative size of prey of the small *Photonectes* spp. and several of the *Bathophilus* spp. was high—

over 50% in several cases. The only crustacean found was a partially digested penaeidean shrimp, together with a myctophid, in a large *Photonectes* sp.

Malacosteidae

Only 24 items were found in the 100 *Malacosteus niger* examined (Table 8). The most frequent items were copepods; these included some small harpacticoids, but most were large aetideids or scolecithridids. Similar-sized *Pleuromamma xiphias* were conspicuously absent. Two fish (86 and 93 mm SL) had eaten somewhat larger prey, and remains of relatively large prey were found only in the three largest fish examined. The incidence of intact prey was much lower in the larger of the two size groups.

As indicated in Clarke (1974), two species of *Photostomias* occur near Hawaii; neither is identical with *P. guernei*, the only presently recognized species. The form designated species 1 here matures at about 60 mm SL and grows to ca. 100 mm SL, while species 2 matures at about 120 mm SL and grows to >150 mm SL. Individuals less than ca. 50 mm SL cannot be reliably separated. The data given in Table 6 are limited to specimens that were analyzed after I had learned to separate the species as well as possible; the text below, however, also includes prey identifications and relative sizes from 54 other specimens from earlier collections. These 54 specimens were no longer conveniently available to me after I had learned to separate the species, and could not be identified with certainty from notes taken at the time of examination.

Both species ate crustaceans exclusively, and with few exceptions the prey and identifiable remains were sergestid shrimps, mostly small *Sergestes* spp. Two large individuals of species 2 had eaten *Gennadas* spp., and an unidentified small specimen had eaten a *Nematobrachion*, the only euphausiid found. Aside from the *Gennadas* occurring only in species 2, there was no evidence of difference in diet between the two species. Except for a juvenile shrimp eaten by a small fish, relative length of prey was 15-42% of SL with a median of 28.5%.

TABLE 8.—Summary of stomach analyses of *Malacosteus niger* with list of all items and remains found.

Size (SL, mm)	No. examined (damaged)	% undamaged specimens: Empty	Remains only	Intact items
24-90	44(3)	71	2	27
91-188	56(0)	88	4	9

SL—items or remains:

SL	Items or remains
30	*Undeuchaeta plumosa*
37	*Candacia longimana, Chirundina streetsi*, aetideid CV, copepod remains
61	*Undeuchaeta major*
70	*Oncaea* sp.
70	remains of 3-4 copepods
71	2 *C. streetsi*, 2 *U. major, Euchirella curticauda*
80	2 *C. streetsi, U. plumosa, Lophothrix* sp.
81	aetideid CV
84	*Oncaea* sp.
85	*Oncaea* sp.
86	*Lophothrix* sp., *Euphausia hemigibba*, myctophid (10 mm SL)
87	*Sapphirina* sp.
93	*Nematoscelis tenella*
96	*Amallothrix* sp.
97	*Euchirella* sp., remains *Scaphocalanus* sp.
101	*Corycaeus* sp.
110	*Thysanopoda* sp. remains
111	*Gaetanus kruppi*, fish remains
188	fish remains

DISCUSSION

Vinciguerria nimbaria, V. poweriae, Valenciennellus tripunctulatus, Danaphos oculatus, and *Gonostoma atlanticum* and small *G. elongatum, G. ebelingi*, and *Diplophus taenia* were planktivorous, i.e., almost all prey were <5-10 mm long. Clarke (1978) showed that four of these species feed primarily by day, and the limited data here indicated that *Vinciguerria poweriae* does also.

The majority of the diets of *V. nimbaria* and *V. poweriae* <30 mm SL consisted of small copepods and ostracods. *Vinciguerria nimbaria* >30 mm SL appeared to feed mostly on substantially larger prey—amphipods and small euphausiids, but large calanoid copepods were not important at any size. In the western Pacific, *V. nimbaria*, apparently smaller than the smallest size group covered here, were also reported to feed mostly on small copepods and ostracods (Ozawa et al. 1977).

Certain prey types found in stomachs of *V. nimbaria*, e.g., *Scolecithrix danae, Paracandacia* spp., *Oncaea venusta, Stylocheiron* spp., were either absent or very rare in the daytime plankton samples, but most were present at moderately high densities within the nighttime depth range of *V. nimbaria* (Clarke 1980). Based on diel changes in state of digestion of prey, Ozawa et al. (1977) concluded that *V. nimbaria* fed at sunset and at sunrise; their evidence for feeding at sunrise is indirect and equivocal. Clarke's (1978) data do not preclude feeding during the upward migration at sunset, but give no indication of feeding at night or sunrise. Thus, while some of the prey types not present in the plankton by day may have been taken at sunset, it seems unlikely that any would remain intact until late afternoon (when two of the day trawls were made) the next day. *Vinciguerria nimbaria* could conceivably undertake short, irregular excursions to shallower water during the day, or alternatively, may have a strong preference for rare, but perhaps vulnerable "stragglers" from populations with shallower centers of abundance.

For several prey types, most of the items recorded were found together in one or a few of the fish examined. This indicates that *V. nimbaria* often feeds on patches or aggregations of certain prey types. My earlier observation (Clarke 1978) that *V. nimbaria* stomachs tend to be either quite full or nearly empty throughout the day is also indicative of encounters with patches of prey. Since patchiness would increase the variability of encounter rates by both individual fish and the plankton nets, this might explain why some prey types were poorly represented by the few plankton samples as well as the large apparent differences in diet between small samples of fish.

Wherever and however *V. nimbaria* feeds, it clearly showed preference for certain prey types. Some types which were abundant in the zooplankton samples, e.g., *Oncaea* spp., *Clausocalanus* spp., small ostracods, were eaten frequently by fish <30 mm SL; but many other types, e.g., *Eucalanus* spp., scolecithricids (except *Scolecithrix danae*), *Metridia* spp., large *Pleuromamma* spp., and chaetognaths, also abundant were either absent or poorly represented in the diet. The types poorly represented in the diet were mostly either larger, less pigmented, or more translucent than those frequently eaten, regardless of whether the latter were rare or abundant in the plankton. The diet and apparent preferences of small *V. nimbaria* are most similar to but not identical with myctophids such as *Benthosema suborbitale* and *Bolinichthys longipes* which feed on small zooplankton (Clarke 1980). *Vinciguerria nimbaria* >30 mm SL showed apparent preference for *Stylocheiron* spp. and amphipods, both of which were rather uncommon within the day depth range. In contrast to both the remaining planktivorous stomiatoids and several myctophids which also feed on large zooplankton (see below), *V. nimbaria* ignored the large calanoids which were fairly abundant at the deeper end of its depth range (Table 2).

The diets of the remaining planktivorous stomiatoids were nearly restricted to large calanoids and small euphausiids. The copepods eaten were fairly abundant within the day depth ranges of the fishes (Table 2), but were apparently preferred over similar-sized *Eucalanus* spp., augaptilids, and chaetognaths which were also fairly abundant. The latter types are very translucent compared with the types eaten and probably less detectable visually. The *Gonostoma* spp. and *D. taenia* have relatively smaller eyes than *V. nimbaria* (data given in Grey 1964). Thus, the apparent preferences of these gonostomatids may result from their being poorly equipped to detect small, translucent, or otherwise less visible prey. (The sternoptychid species both have relatively large eyes, but they are tubular and directed upward, and are difficult to compare with the others.)

The diets of the planktivorous stomiatoids except *Vinciguerria* spp. were not only similar to each other but to those of three common myctophids (*Lampanyctus nobilis, L. steinbecki,* and *Triphoturus nigrescens*), which also have relatively small eyes (Clarke 1980). Limited data on diet from Clarke (1978) indicates that the abundant myctophids of the *Lampanyctus niger* species group also feed similarly. Thus, although they feed at different depths and times, several coexisting species of fishes are utilizing the same resources and apparently feeding selectively for the same reasons; conversely, a relatively few species of large zooplankton—particularly *P. xiphias* and *Euphausia* spp.—are supporting a large fraction of the planktivorous fishes. Certain small zooplankton, e.g., *Oncaea* spp. and *P. gracilis*, also appear to be heavily grazed by *Vinciguerria* and several other fishes from the same area (Clarke 1980), but overall there is less interspecific overlap in diet and more evidence of different feeding mechanisms among species which eat small zooplankton.

Gonostoma elongatum, G. ebelingi, and *D. taenia* appear to be essentially planktivores that consume some large prey simply because they reach larger sizes than do the other planktivorous stomiatoids. All three have well-developed gill rakers, none have large fangs, and the cardiac portions of the stomach are not notably elongate. Similarly, to the small individuals, the large specimens usually contained several relatively small prey; relative size of most items was ca. 10% of SL with few over 20%. Most of the prey were crustaceans, euphausiids and sergistid shrimps, but some fish and squid were taken. The only evidence of selectivity was the repeated occurrence of the relatively uncommon amphipod, *Vibilia* spp., in *D. taenia.*

The remaining species—of six families—all appear basically adapted for capture and ingestion of relatively large prey. All have large fangs, none have well-developed gill rakers, and in most the cardiac portion of the stomach is elongate and, in some species, obviously capable of distension to accommodate prey over one-half the predator's body length. All these species except *Malacosteus danae* have eaten relatively large prey (usually at least 20% of SL) at all sizes and most of them exclusively such items. There was rarely more than one prey item in a stomach.

Juvenile *Thysanactis dentex* and *Astronesthes* spp.—especially *A. indicus*—were the only fishes of this group that routinely ate zooplankton. Those consumed by small *A. indicus* were ostracods and small copepods, generally similar to the diet of *Vinciguerria nimbaria*. The juvenile *T. dentex*, which were larger than the planktivorous stages of *A. indicus*, had eaten mostly large calanoids and small euphausiids, essentially the same eaten by similar-sized *Gonostoma* spp. In both species, however, the incidence of relatively large prey was as high in the small planktivorous stages as in the sizes which ate only large prey. Thus, rather than changing with growth from small to large prey (but of the same range of relative size), these species appear to prey on an increasingly narrower range of relative sizes of prey.

Most of the nekton-eating stomiatoids were principally or exclusively piscivorous. The *Photostomias* spp. were the only ones that never ate fish. The relatively large prey of juvenile *A. indicus* and *A. "cyaneus"* were euphausiids, but there was limited evidence that adults of both species are piscivorous. The smallest size group of *Chauliodus sloani* and all sizes of *T. dentex* had eaten some relatively large euphausiids or sergestids; usually these were relatively smaller than the fishes eaten. Otherwise, crustaceans were either a minor or suspect part of the diet.

The systematic examinations of fairly large numbers of specimens by Beebe and Crane (1939), Legand and Rivaton (1969), and Borodulina (1972), and many other isolated reports in the literature generally agree that species of the six families considered as nekton-eating here eat primarily or exclusively relatively large prey which are usually fish. The only well-documented exception is *Tactostoma macropus*, which appears to eat only euphausiids and sergestids (Borodulina 1972). Notes by Fitch and Lavenberg (1968) indicate that off California several congeners of piscivorous Hawaiian species routinely eat crustaceans and that one, *Bathophilus flemingi*, eats "small crustaceans almost exclusively." The discrepancies may be artifacts due to differences in towing speed (not given by Fitch and Lavenberg and most other studies). The same types of differences were observed between specimens from the same area collected at speeds of over or under ca. 1.5 m/s (see Methods).

There was evidence of selectivity by the predators among the potential prey fishes. All but one of the fishes identified from stomachs were vertically migrating species; in particular, the nonmigrating *Cyclothone* and *Sternoptyx*, which are abundant within the day depth ranges of the predators, were absent from the diets of all predators except *Heterophotus ophistoma*. Other stomiatoids, particularly the abundant *Vinciguerria* spp., were underrepresented, and the abundant myctophids of the *L. niger* complex were absent. Based on the relative abundances of different migrating fishes in the study area (Table 9), several species of predators took cer-

TABLE 9.—Relative abundance and estimated average biomass (wet weight) of vertically migrating fishes based on data from 58 oblique trawls taken at night near Oahu, Hawaii, in 1977-78. Total number of fishes caught was 14,084. Relative abundance is expressed as percent of total myctophids, the dominant group.

Species	Relative abundance as % of total myctophids		Average biomass ($gm/10^3/m^2$)
	Numbers	Biomass	
Stomiatoids:			
Small planktivores		1.2	5.4
Vinciguerria spp.	13.0		
Others	2.8		
Gonostoma spp., *Diplophus taenia*	7.6	18.1	80.8
Nekton-eating species		15.9	66.4
Astronesthes spp.	0.7		
Chauliodus sloani	0.4		
Idiacanthus fasciola ♀	1.2		
Thysanactis dentex	0.9		
Eustomias spp.	0.8		
Photostomias spp.	0.6		
Others	0.6		
Myctophids:		100	455.5
Lampanyctus "niger" complex	13.0		
Lampanyctus spp. (others)	25.6		
Ceratoscopelus warmingi	14.2		
Diaphus spp.	12.6		
Notolychnus valdiviae	12.0		
Triphoturus nigrescens	5.1		
Benthosema suborbitale	5.1		
Bolinichthys longipes	3.4		
Others	8.9		
Other planktivores:		6.2	27.6
Melamphaeidae	3.7		
Bregmaceros spp.	1.8		
Cheilodipteridae, Notosudidae, etc.	0.9		
Other nekton-eating species:		4.5	20.2
Eels	0.5		
Iniomi, Trichiuroids, Chiasmodontidae, etc.	1.3		

tain prey species much more frequently than would be predicted by random nonselective feeding. Examples include nonmyctophids, particularly *Bregmaceros* spp., in the diet of *Thysanactis dentex*; *Bolinichthys longipes* in *Eustomias bifilis*; *Howella* spp. in *E. enbarbatus*; *Diaphus* spp., *Howella* spp., and *Scopelosaurus* spp. in the *Eustomias* spp. with two pectoral rays; and *Notolychnus valdiviae* in *Leptostomias* spp. The probability of drawing at random, e.g., two *Howella* spp. or two *Scopelosaurus* spp. out of two fish from the fauna is very low.

The relative sizes of fish prey for most species of predators were 20-30% of SL. Many of the values over 30% were for relatively slender prey such as *Bregmaceros* or *Scopelosaurus.* Only the *Bathophilus* and *Photonectes* spp. and small *Chauliodus sloani* appeared to take prey >30% routinely. The values for *I. fasciola* were mostly <20%; this species is, however, so slender that the relative size in terms of head length or body weight would be more like those for the other species.

If the weights of predator and prey were both similarly related to the cube of the length, then 20-30% relative length gives a value of 0.8-2.7% of body weight per item. If anything, this is probably an underestimate of average prey size, since the predators are for the most part slenderer than their prey. Also the stomiatoids seem to be softer bodied than most of their prey and may have a higher water content (cf. Blaxter et al. 1971); this would mean that relative prey size in terms of dry weight is higher. Borodulina (1972) gives lengths (SL ?) and wet weights of 14 fish prey and stomiatoid predators. The relative lengths of prey were 12-52% and relative weights 0.1-2.8%. The latter are probably underestimates of relative weight since some losses of prey weight must have occurred even in specimens still intact enough to be measured.

With the exceptions of *A. indicus* and *T. dentex,* all species with chin barbels fed exclusively or nearly so on relatively large fish. The barbel is rudimentary in *C. sloani,* which was also piscivorous except at the smallest sizes, but *C. sloani* has an elongated first dorsal ray with a light organ on the tip. Of the other nekton-eating species without barbels, fish were absent from the diets of the *Photostomias* spp. and eaten only by the largest *M. niger* and *A. "cyaneus."* The large gonostomatids also lack a barbel. Fish were less frequent than large crustaceans in their diets and were relatively smaller than fishes eaten by the predators with barbels. *Tactostoma macropus,* the only melanostomiatid known to eat primarily crustaceans (Borodulina 1972), has the smallest and most rudimentary barbel in the family.

Although there are no directly supportive data or citations, it is undoubtedly true that in the open ocean, crustaceans far outnumber fishes at lengths <15-20 mm; for lengths >25-35 mm the opposite is probably true. It is also probably true that a fully metamorphosed fish is a faster swimmer than a similar-sized crustacean and, other things being equal, more likely to evade capture when attacked by a predator. Thus a predator which preferred items 20-30% of its length and actively searched for prey would have a diet similar to those of *A. indicus* and *A. "cyaneus."* The small predators would encounter crustaceans much more frequently and probably capture those encountered more frequently than they would fish, while the large predators would almost be forced into piscivory due to the relative rarity of appropriate-sized crustaceans. If the predator preferred prey only 10% of its body length, the diet would resemble those of the large *Gonostoma* spp., where even the largest individuals (100-200 mm) would still encounter more crustaceans than fish in the appropriate size range.

Most of the fishes with barbels must either reject crustaceans encountered or feed other than by active search. A plausible and likely hypothesis (which has been suggested by others) is that they are "passive" and use the luminescent bodies in the barbel to attract prey. Bertelsen (1951) developed a similar hypothesis for the ceratioid angler fishes. Since several of the prey fishes are not known to be bioluminescent themselves, it is most probable that the barbel mimics food of the prey species—most of which appear to be primarily visual feeders (see above)—rather than a conspecific of the prey. The large crustaceans apparently are not similarly attracted; this is not surprising in view of their very different eyes and probably different diet and feeding behavior. Thus the barbel may be an adaptation for attracting and perhaps aiding in capture of relatively large fish. This mechanism could allow these stomiatoids to subsist on relatively large prey whose densities are quite low (on the order of $1/m^2$ of sea surface, see Maynard et al. 1975) with less energy expenditure than would be required for active search and capture. Furthermore, assuming the findings of Pandian (1967) are generally true, the fish, which appear to be preferentially attracted, would be more efficiently digested and converted than crustaceans.

Chin barbels (and the first dorsal ray of *Chauliodus*) are not fully developed until after metamorphosis; for most species covered here, the smallest specimens examined (Tables 6, 7) are roughly the size at which the barbel appears fully developed. The *Astronesthes* spp. are quite small at metamorphosis, and it is not surprising that they apparently eat some of the zooplankton encountered regardless of whether or not they possess a barbel. Likewise, newly metamorphosed *C. sloani* would be expected to encounter so many more appropriate-sized crustaceans than fish that it would include some of the former in its diet. Bertelsen (1951) has similarly suggested that juvenile ceratioids eat some items as a result of visual detection and capture rather than by use of their lures. (The *Bathophilus* and *Photonectes* spp. are almost as small at metamorphosis as *C. sloani*, but, perhaps because they can handle relatively larger prey, appear to feed in the passive mode immediately after acquiring a barbel.) *Astronesthes indicus*, however, continues to feed like the barbelless *A. "cyaneus,"* i.e., as would be predicted for an actively searching species, until at least up to ca. 60 mm. *Astronesthes indicus* is unique in that the barbel is not fully developed shortly after metamorphosis but changes considerably as the fish approaches adult size (Gibbs 1964); consequently, it may not begin to feed passively until later.

Thysanactis dentex has a well-developed barbel, metamorphoses at rather large size, and appears to capture fish as frequently as the other species with barbels; but it also feeds on zooplankton until it is fairly large and includes relatively large crustaceans in its diet at all sizes. It thus appears to feed as an actively searching visual predator as well as by using the barbel. In spite of the advantages suggested for passive feeding, *T. dentex* is obviously successful at combining both methods; except for *Idiacanthus fasciola*, it is by far the most common species of the barbelled stomiatoids in the study area (Table 9).

Assuming that the above hypotheses are valid, then evidence for selective feeding by some species indicates that interspecific differences in barbel morphology and, perhaps, methods of deployment have evolved to specialize in attraction of a restricted type of prey, i.e., some of the species may be analogous to devoted aficionados of fly fishing in *Homo sapiens*. Although even the "generalist" *T. dentex* showed some evidence of preference for certain fishes, most evidence of restricted diets was from *Eustomias*, which is the most speciose genus considered and also has the most varied and ornate barbels. If sufficient data become available, it would be pertinent to compare the degree of preference in *Eustomias* with, e.g., *Bathophilus* or *Aristostomias*, in which all the species have similar and rather plain barbels. Regardless of whether the barbel is used or not, the advantages of specialization in diet, such as increased efficiency of capture, must be great. The overall density of prey in the study area is low compared with other oceanic areas, and much current ecological theory (e.g., Schoener 1971; Werner and Hall 1974) would predict broad diets rather than restriction to a single prey type such as *Scopelosaurus* spp., whose density is <1% of the already low total fish density.

The *Photostomias* spp. have no obvious features that would predict a diet restricted almost totally to sergestids. Though they lack a barbel, this would not explain the total absence of fish from the diet. The absence of caridean shrimps from their diet, as well as from those of the other species, may be related to stouter exoskeleton and heavier spines in these shrimps than in sergestids, but there are no such features to suggest why the very abundant large euphausiids and penaeid shrimps are also nearly completely ignored. *Photostomias* must either be able to attack and detect only sergestids or have some method of luring only them into proximity.

Malacosteus niger is the only "nekton-eating" predator which does not vertically migrate (Clarke 1974). Zooplankton densities within most of its depth range are low both day and night, but by day it overlaps with several abundant vertically migrating fishes as well as sergestids (Walters 1977) and large euphausiids (Hu 1978). Since this species is apparently well adapted for ingestion of large prey, has one of the largest gapes of all stomiatoids (Morrow 1964), and is so poorly adapted for small prey—no gill rakers or floor to the mouth, it is all the more perplexing that it had eaten so few relatively large items. It appears to subsist on a rather odd assortment of copepods.

Among the nekton-eating species, there were few differences between day- and night-caught fish in the incidence of intact prey, and none of the differences were sufficiently large to allow any inference about feeding chronology. There is some indirect evidence for night feeding. Most of the predators are found with their prey both day and night; however, some prey, the *Bregmaceros* and *Melamphaes* spp., occur well below their predators during the day (Clarke and Wagner 1976) and could only have been eaten at night or during migration. The absence of nonmigrating species in the diets also indicates less or no feeding during the day. Finally, if the lures of these predators are used to attract fish which are themselves actively searching for prey, the high frequency of species which feed in the upper layers at night and the low frequency of day-feeding, but vertically migrating, stomiatoids also indicates night feeding by the predators.

The average biomass of the nekton-eating stomiatoids in the study area was a substantial fraction of that of their prey (Table 9) and indicates that they are probably an important source of mortality to the prey species. An estimate of the stomiatoids' impact on the prey populations can be made from the catch and stomach content data from the 1977-78 series of oblique trawl tows and estimates of stomach evacuation time. The entire series of tows caught 17,543 vertically migrating planktivorous fish of the types eaten by the stomiatoids: Myctophids, exclusive of the *Lampanyctus niger* complex, plus other nonstomiatoid planktivores. The same tows caught 822 nekton-eating stomiatoids, exclusive of *Photostomias* spp. A minimum of 111 fishes or fish remains were found in the stomachs of these predators. If the totals from this extensive series of samples are taken as representative of the average state in the study area, then on the average the nekton-eating stomiatoids consume 0.63% of the prey numbers over a period of time equal to that required to evacuate the stomach.

This estimate is likely to be low because both feeding incidence of the predators and their numbers relative to the prey are probably underestimated. There were 107 stomiatoids whose stomachs were ruptured, and any prey they might have contained are not included. In fact, it is possible that individuals with distended stomachs were more susceptible to damage during capture and consequently, that the incidence of prey in the damaged specimens might have been higher than in the undamaged ones. The numbers of both predators and prey caught by the trawls are both negatively biased due to avoidance of the net, but there is evidence that the larger stomiatoids, especially *Astronesthes* spp., are much better avoiders than the small planktivores (Clarke 1973, 1974). Unless there was a difference in bias between stomiatoids with full and empty stomachs, this would also result in an underestimate of the percent of the prey population consumed.

There are no available data to directly estimate the time required to evacuate the stomach for these fishes, but studies of other fishes fed comparable sized meals indicate that evacuation time is no longer than 4 d and probably less. Evacuation times determined at temperatures similar to those encountered by the stomiatoids at night (15°-25°C) are mostly less than a day (Pandian 1967; several studies summarized by Magnuson 1969); at temperatures similar to those of the day depths (4°-5°C) values are 2-4 d (Tyler 1970; Popova and Sytina 1977). If evacuation time were 4 d, the annual consumption by stomiatoids would be 57.5% of the average standing crop of prey (0.63% × 365/4); if the time were 1 d, consumption would be 2.3 times the standing crop.

Although annual production by vertically migrating planktivorous fishes probably exceeds the average standing crop (Clarke 1973), the estimated consumption by piscivorous stomiatoids indicates that the latter account for a large and possibly predominant share of the former's production. Though stomiatoids appear to be the most abundant piscivores, consumption of the migrators by other, similar-sized predators, e.g., scopelarchids, chiasmodontids, trichiuroids, eels, and squids, is also likely to be substantial. The migrating planktivorous fishes, in turn, appear to be the dominant group of plankton consumers in the tropical open ocean (Clarke 1973; Maynard et al. 1975). Together, these indicate that a large fraction of primary production is eventually channeled into small predators, smaller than the average planktivore in many other parts of the ocean, rather than into large, commercially harvestable species.

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