

# DIETS OF FOURTEEN SPECIES OF VERTICALLY MIGRATING MESOPELAGIC FISHES IN HAWAIIAN WATERS

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## ABSTRACT

Fishes and zooplankton were sampled at four depths (70, 90, 110, 170 m) at night in the upper layers near Hawaii. Diets of the fishes were determined from stomach contents and preferences estimated by comparison with prey densities at the appropriate depth. Generally, the fishes fed on relatively large, pigmented or opaque crustaceans; other taxa and very small or translucent prey were rarely eaten. There were, however, differences in diet and preference between species; these were frequently correlated with morphological features, especially lens size and gill raker spacing. One group of four fishes which were very similar in both diet and morphology were separated by depth distribution and size. Comparison with other studies indicates that tropical species are perhaps more specialized and ecologically separated in diet than their counterparts in high latitudes.

Vertically migrating mesopelagic fishes are important components of oceanic ecosystems. In the tropical open ocean, abundance of larvae (Ahlstrom 1969) and estimates of biomass (Clarke 1973; Maynard et al. 1975) indicate that they are the dominant group of micronekton and greatly exceed the abundance of epipelagic forms. Standing crops are even higher in oceanic situations at higher latitudes (Frost and McCrone 1979) and coastal upwelling areas (Pearcy and Laurs 1966). Tropical oceanic faunas are much more diverse. At high latitudes and in quasi-neritic situations, one to three species typically make up the great majority of the standing crop (Pearcy and Laurs 1966; Zahuranec and Pugh 1971; Baird et al. 1975; Frost and McCrone 1979), while in the tropical open ocean the abundances of the dozens of cooccurring species are more evenly distributed (Clarke 1973, 1974).

The diets of these fishes are of interest both to assess their impact on lower trophic levels in oceanic ecosystems and to determine the degree to which cooccurring species are specialized with respect to their feeding habits; however, previous studies do not allow serious consideration of these aspects. Few have presented extensive data on more than one to three species. For the most part, prey have not been identified adequately enough to seriously discuss preference or dietary overlap, and there has been no consideration of bias due to

differing rates of digestibility and, therefore, ability to identify different prey types (Gannon 1976). Few studies have compared stomach contents of fishes with appropriate samples of the prey available; those that have done so have simply compared percentages of different prey types and have not considered biases or errors inherent in the samples taken for prey abundance.

This paper considers diets of 14 species of vertically migrating mesopelagic fishes based on data from collections taken near Hawaii in the central North Pacific Ocean. All species are primarily zooplanktivorous and are known (Clarke 1978) or suspected to feed principally in the upper 250 m at night. The diets of each species are compared with densities of zooplankton at each of the depths sampled. While problems in feeding studies mentioned above have by no means been completely eliminated, the methodology recognizes and at least qualitatively attempts to account for major sources of error. The results allow consideration of biases of the fishes as "samplers" of the potentially available prey and of dietary overlap between species or sizes cooccurring at the same depths in the water column.

## METHODS

### Field Collections

All specimens for this study were collected ca. 20 km off the coast of Oahu, Hawaii, (ca. lat. 21°10'-30' N, long. 158°10'-30' W) over bottom depths of 2,000-4,000 m. The depth ranges, vertical migra-

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tions, and other aspects of the ecology of the species considered have been reported for the same study area (Clarke 1973; Clarke and Wagner 1976) and other studies there summarized by Maynard et al. (1975).

Fishes were collected with a 3 m (10-ft) Isaacs-Kidd midwater trawl. To minimize the probability of fishes' feeding while in the net, the terminal section of the net was of ca. 3 mm knotless nylon mesh instead of the commonly used, finer plankton netting.

The trawl was launched and towed at ca. 2 m/s and the ship was slowed to ca. 1 m/s for retrieval. Total time for descent to and ascent from towing depth was 12-20 min. The trawl was towed at the desired depth for ca. 2 h. Zooplankton were sampled with 70 cm diameter, opening-closing bongo nets of 505  $\mu$ m mesh. Ship's speed of ca. 1 m/s was maintained for the entire tow; the nets were open at the desired depth for 30-33 min. Time-depth recorders attached to the nets indicated that the depths of the "horizontal" (2 h) portions of the trawl tows and the open part of the bongo net tows were within 5 m of each other and of the desired depth for each set of samples. All collections were preserved in ca. 5% formaldehyde in seawater solution immediately after the nets were on deck.

Four different depths (70, 90, 110, 170 m) were sampled (Table 1). In September 1973, two plankton tows followed by two trawl tows were made on

ambient light was essentially constant for all samples taken at a given depth, and there were probably no between-sample differences in vertical distribution of either the fishes or their prey at a given depth. Consequently, except for possible captures in transit to and from towing depth (see below), the fishes captured at a given depth were assumed to have been feeding on the same prey population sampled by the appropriate plankton tows.

### Laboratory Procedures

All nonlarval fishes from the trawls were identified and standard length (SL) measured to the nearest millimeter. The fishes from each depth were grouped by species and arbitrary size classes: 16-25 mm, 26-35 mm, 36-45 mm, 45-60 mm, and >61 mm. Certain species or size classes from each depth were eliminated from consideration because, based on previous evidence of depth-size distributions (Clarke 1973; Clarke and Wagner 1976), they were almost certainly taken in transit to and from towing depth. Among the size classes that were considered, a few possibly included specimens that were captured above towing depth and thus were not exposed to the same array of prey as sampled by the plankton nets; these groups are noted specifically in subsequent sections.

For each specimen examined, standard length was recorded and the stomach (anterior end of the esophagus to the pyloric constriction) removed. Prey items with bodies intact were noted separately and measured to the nearest 0.1 mm with an ocular micrometer. For the commonly occurring crustacean prey, the following measurements were used: copepods—prosoma length, ostracods—maximum carapace length, malacostracans—the distance from the anteriormost point exclusive of the antennae to the base of the telson. (The telson of malacostracans was too frequently separated to routinely include it in the length.) The dimensions measured for other intact prey were standard length for fishes, maximum diameter for nearly spherical items such as gastropod veligers, and total length for all others. Most intact copepods and euphausiids could be identified to genus and most copepodite VI stages of the former and juveniles and adults of the latter to species. Ostracods were almost all *Conchoecia* spp., but were not identified further. Other prey types were identified only to major taxa. Identifiable frag-

TABLE 1.—Sampling information for trawl and plankton collections at four different depths off Oahu, Hawaii. D + R = total time for descent and retrieval of trawl.

Depth (m)	Trawl				Plankton net	
	Date	Time at depth <sup>1</sup>	D + R (min)	Date	Time open at depth <sup>1</sup>	
70	24-25 Sept. 1973	2158-2400	13	24 Sept. 1973	2010-2040	
	25 Sept. 1973	0045-0245	12	24 Sept. 1973	2101-2131	
90	11-12 Nov. 1974	2300-0100	18	14 Nov. 1974	2353-0023	
110	26 Sept. 1973	0007-0207	13	25 Sept. 1973	2202-2235	
	26 Sept. 1973	0237-0437	15	25 Sept. 1973	2256-2328	
170	26-27 Sept. 1973	2318-0118	15	26 Sept. 1973	1953-2030	
	27 Sept. 1973	0150-0350	20			

<sup>1</sup>Hawaii standard time.

the same night at each of three depths (70, 110, and 170 m). For the 170 m collections the bongo nets failed to open and close properly on one of the tows. A single trawl sample from 90 m was taken in November 1974, and a single plankton sample taken at the same depth two nights later. All tows were taken between last light at dusk and first light at dawn and within 2 d of new moon. Thus

ments of digested prey among the remainder of the stomach contents were also recorded.

Prey items in the mouth were discarded, but items in the esophagus were included with the stomach contents. The bodies of items in the esophagus were compressed and the appendages were flattened against the body. Such items could conceivably have been eaten in the trawl, but several lines of evidence indicate that this is an unimportant source of error. Hopkins and Baird (1975) reported no evidence of net feeding even when a fine mesh cod end (which would presumably accumulate more zooplankton and restrict water flow) was used. Only a few of the species considered here had items in the esophagus at all frequently, and in all cases such items were the same or very similar to items frequently found among digested or partially digested matter in the stomach. Thus if there was significant net feeding, only some species did so and apparently selected prey from that in the cod end similar to their normal habits.

The species-size groups for which data are presented here are those from which a reasonable number of intact prey were recorded. If sufficient numbers of specimens were available, I examined specimens until about 100 intact items were recorded. For other groups, I examined all the fish collected, but eliminated from consideration those for which too few prey items were recorded either because of low numbers of specimens or low incidence of prey in the stomach.

Zooplankton from the bongo net samples were identified and counted from aliquots taken with a plankton splitter. Euphausiids and most adult copepods were identified to species—the former from between all and one-eighth of the sample and the latter from one-sixteenth to one-thirtysecond. Most immature copepods were identified to genus. Ostracods and amphipods from one-sixteenth to one-thirtysecond of the sample were counted and measured to the nearest 0.1 mm. Other taxa were counted from all to one-eighth of the sample. Flowmeters on the plankton nets gave suspect readings; consequently, volumes sampled by each tow were calculated from the duration of the open part of the tow and estimated speed (1 m/s). The densities (per cubic meter) of the different prey types were calculated from the volumes and adjusted counts.

The apparent search volume per fish (ASV) was used as an index of relative preference for the different prey types. For each type of prey noted

from the stomachs of each category of fish, the ratio of the total number of intact items to the density of that type was divided by the number of fish with intact items in the stomach. Fish examined but with no intact prey items in the stomach were eliminated because they provided no information on preference, they included fish that had not fed at all as well as those with variable amounts of digested material in the stomach, and finally their proportion of the total fish examined varied between categories. Thus the ASV's as calculated here apply to fish that had fed recently before capture and take no account of between-category differences in feeding success.

The ASV is the minimum volume the average fish of each category had to search to capture the observed number of a given prey type. The actual volume searched is larger to the extent that the fish are not 100% effective in detecting, capturing, and ingesting prey. If the fish were equally effective in detecting, capturing, and ingesting all types of prey, the ASV's would be equal. For a given category of fish, differences in ASV's between prey types indicate the degree to which the fish were "biased samplers" of the available prey and thus measure relative preference in the broadest sense, i.e., without specifying which aspects of predation were biased.

The ASV is similar to the index of preference recently derived by Chesson (1978); the relationship between the two indices is:

$$\alpha_i = \frac{V_i}{\sum_{k=1}^m V_k}$$

where for type  $i$  out of  $m$  prey types,  $V_i$  is the ASV and  $\alpha_i$  is Chesson's index. Unlike ASV,  $\alpha$  has no dimensions and is normalized. Assuming that predation does not substantially alter prey densities, i.e., that the number of prey eaten is low relative to the total available, both indices are equivalently related to the probability of a given type of prey being eaten:

$$P_i = \frac{V_i \rho_i}{\sum_{k=1}^m V_k \rho_k} = \frac{\alpha_i n_i}{\sum_{j=1}^m \alpha_j n_j}$$

where  $P_i$  is the probability of prey type  $i$  being eaten, and  $p_i$  and  $n_i$  are the density and number of

prey type  $i$  available. Like  $\alpha$ , the ASV is unaffected by negative or positive preference for other types of prey. As pointed out by Chesson (1978), most other indices of preference, including that of Ivlev (1961), are so affected and their biological meaning is not clear.

Preference could be affected by many characteristics of the prey, only one of which could be considered in this study. Other things being equal, large or more visible prey types could be detected at greater distances (Zaret and Kerfoot 1975; O'Brien et al. 1976) and thus have higher ASV's than small or translucent types. Consequently, in addition to measuring size of prey, I examined several samples of living zooplankton from the study area and noted, for as many prey types as possible, whether they were opaque or translucent in life and the presence of any pigment.

Ability to escape once detected and attacked would decrease ASV. Prey with bioluminescent organs could either be more readily detected than those without or conceivably use them to decrease probability of detection or capture. Aggregation or patchiness of prey could also affect ASV either way depending upon patch size, predator capacity, and the search behavior of the predator. Unfortunately, none of these behavioral aspects of predation could be investigated.

For each of the fish species considered here, I examined four morphological features which could affect preference. Relevant measurements were made to the nearest 0.1 mm with either an ocular micrometer or vernier calipers on at least five specimens spanning the size range of each species considered. The length of the premaxillary was taken as a measure of gape; the diameter of the lens, as a measure of visual ability; and the average space between gill rakers on the lower branch of the first arch, as a measure of minimum particle size that could be retained. These were expressed as linear functions of standard length determined by least squares regression. The filtering area of the gill rakers, which could not be directly calculated without knowledge of the angle at which the arch is held during feeding, was assumed proportional to the product of the length of the raker-bearing segments of the first arch and the length of the gill raker at the joint between the upper and lower branches. This product or "area" was expressed as a power function of standard length determined by linear squares regression on the logarithms.

Aside from being affected by characteristics of the fishes and their prey, ASV's could have been biased by problems in the methodology. Any feeding in the net (considered above) would tend to increase ASV for large prey retained there and also blur any differences in visibility or escape behavior. Differential rates of digestion and disintegration of prey would bias stomach content data toward more resistant and more easily recognizable prey (Gannon 1976). Counting only intact and measurable prey eliminated bias due to differential ease of identification. For example, if all identifiable parts had been counted, the data would have been heavily biased toward *Pleuromamma* spp. whose spots or "buttons" can be recognized even after the items have completely disintegrated and passed into the intestine, while certain other prey which cannot be identified positively if only one or two features are missing would have been underrepresented. Even among the crustaceans, the rate at which the prey disintegrates probably varies; Gorelova (1975) indicated that some small cyclopoid copepods remain intact even in the intestine of myctophids. Other types of prey are probably digested much faster than crustaceans. To at least qualitatively correct for the latter bias, I counted all recognizable remains of chaetognaths, heteropods, other gastropods, siphonophores, and tunicates as "intact" for calculation of ASV's.

The densities of small zooplankton were underestimated due to escapement through the 505  $\mu\text{m}$  mesh of the plankton nets used. Counts of ostracods and certain copepods from an available plankton tow from the study area with 333  $\mu\text{m}$  mesh on one frame and 505  $\mu\text{m}$  on the other indicated that—assuming that the 333  $\mu\text{m}$  sampled the small prey accurately—prey >1 mm long were adequately retained by the 505  $\mu\text{m}$  net. These included most of the prey eaten by the fishes. Two types of frequently eaten prey, large (0.6-0.8 mm) *Oncaea* spp. and ostracods <1.0 mm were underestimated by factors of roughly 4 and 5, respectively, in the 505  $\mu\text{m}$  sample, and their ASV's are overestimated by the same factors. There were insufficient numbers of other small prey types in the 333/505 sample to provide even roughly reliable estimates of error.

Any avoidance of the bongo nets by prey would result in erroneously high estimates of ASV. No studies have documented the extent of error due to avoidance by different prey types, but it can probably be assumed to be negligible for the great

majority of prey types eaten by the fishes considered here. Certain types, e.g., large (>10 mm) euphausiids, shrimps, or fish larvae, must certainly be able to avoid the bongo nets; consequently, high ASV's associated with such types must be considered as doubtful.

Uncertainty associated with the estimated densities from the plankton tows probably limits interpretation more than any other factor. Since only one or two pairs of zooplankton samples were available from each depth, the sampling error associated with estimated densities cannot be specified. Overall, the between tow, between net, and between aliquot differences in counts of abundant types indicated that the densities and therefore the ASV's are probably accurate to within a factor of 0.5-2× of the values given. Thus small differences in ASV's cannot be considered real. Absurdly high values of ASV frequently resulted for prey types that were very rare or absent in the plankton samples. Such types were frequently large forms that may have been "rare" because of net avoidance, and even for those that were truly rare, the potential sampling error was probably large due to insufficient volumes sampled. Consequently, after inspection of the data, all values >1.0 m<sup>3</sup> were lumped together.

## RESULTS

A total of 14 species of fishes comprising 51 size-depth-species categories (Table 2) yielded sufficient data to merit presentation and discussion. Although most prey items were identified to genus or species and all were measured to the nearest 0.1 mm, certain prey were grouped by higher taxa or size ranges for presentation of prey densities (Table 3) and to avoid dealing with low numbers in calculations of ASV's.

In the individual species accounts below, an attempt is made to summarize the major points in the tabulated data. For these purposes and subsequently throughout the paper, "microzooplankton" are operationally defined as those prey types too small (<1.0 mm) to have been accurately sampled by the plankton tows and thus those whose ASV's are overestimated. The remaining prey types or "macrozooplankton" are considered by species or as small (1.0-1.5 mm), medium (1.5-3.0 mm), or large (≥3.0 mm). For each category of fishes considered, the number of macrozooplankton prey types and their frequencies in the diet are

grouped by ASV values in 0.1 m<sup>3</sup> increments between 0 and 1.0 m<sup>3</sup> (Table 2).

### *Lampanyctus steinbecki* (Table 4)

The data for *L. steinbecki* are the most extensive of all species considered. Large numbers of at least two size classes were taken at each of the four depths sampled, and, in spite of the rather low numbers of prey per fish, the numbers identified for most categories were relatively high. The 18-25 mm fish from 90 and 110 m and 36-45 mm fish from 170 m may have included some individuals caught in transit above the towing depth.

Microplankton were of minor importance in the diets of all but the smallest size groups considered. Small macrozooplankton were eaten infrequently and had low ASV's for all sizes of fish. The most frequently taken prey were euphausiids and medium to large copepods. The ASV's for these and other large prey were usually relatively high. *Candacia longimana* was most consistent in this respect. The ASV's for *Pleuromamma xiphioides* at 90 m were markedly lower than at the other depths as were those for *Euphausia* spp. at 70 m. Neither of these exceptions appeared to result from differences in importance in the diet. *Pleuromamma xiphioides* was extremely abundant at 90 m (Table 3), and this, combined with the lower numbers of prey per fish at this depth, caused most of the reduction in ASV. *Euphausia* spp. were extremely abundant at 70 m (Table 3); most were *E. tenera*, a species eaten infrequently. As a consequence of these and similar differences between depths, there was no clear trend or consistency to the distribution of ASV's of the different prey types. Most types and most items had low ASV's at 90 m, ASV's were more nearly evenly distributed at 70 and 110 m, and the majority of prey had high ASV's at 170 m (Table 2).

### *Lampanyctus nobilis* (Table 5)

*Lampanyctus nobilis* was taken from three depths; with the possible exception of the smallest size group from 110 m, the data were unlikely to have been seriously affected by catches in transit to and from towing depth.

The diet of *L. nobilis* was generally similar to that of *L. steinbecki* but with a greater frequency of large prey. Microzooplankton were hardly eaten (Table 2), and ASV's for the few types of small macrozooplankton were very low. The most fre-

TABLE 2.—Number of identified prey items, percentage of prey items <1.0 mm long, and distribution of types and percentages of prey items as a function of apparent search volume (see text) for each species, depth, and size category of fish examined. Given under each interval of apparent search volume are the number of types of macrozooplankton prey and, in parentheses, the percentage of total prey items whose apparent search volumes were in that interval.

Species, depth, standard length	No. prey items (% <1.0 mm)	Apparent search volume (m <sup>3</sup> )										
		0-0.10	0.11-0.20	0.21-0.30	0.31-0.40	0.41-0.50	0.51-0.60	0.61-0.70	0.71-0.80	0.81-0.90	0.91-1.0	>1.0
<i>Lampanyctus steinbecki</i> :												
70 m: 26-35 mm	44(14)	3(20)	3(14)	1(5)	1(2)	1(23)	—	2(9)	—	—	1(9)	2(5)
36-45 mm	33	3(24)	1(3)	3(9)	1(3)	—	2(30)	—	—	—	1(9)	3(21)
46-52 mm	16	—	1(37)	—	1(6)	—	—	1(6)	1(37)	—	1(13)	—
90 m: 18-25 mm	17(35)	3(24)	2(18)	—	2(18)	—	—	1(6)	—	—	—	—
26-35 mm	37(14)	9(35)	3(19)	1(11)	2(14)	1(8)	—	—	—	—	—	—
36-45 mm	99 (6)	15(48)	3(14)	—	1(12)	1(6)	—	—	—	—	1(13)	—
46-51 mm	11 (9)	1(9)	2(27)	2(18)	—	—	1(9)	—	1(9)	—	—	1(18)
110 m: 19-25 mm	17	1(12)	3(24)	—	3(35)	1(6)	1(24)	—	—	—	—	—
26-35 mm	47(21)	6(17)	—	2(11)	1(21)	—	1(11)	1(11)	—	—	1(6)	1(2)
36-45 mm	133 (4)	4(5)	4(8)	1(4)	1(4)	1(7)	—	1(2)	1(34)	2(26)	—	2(7)
46-50 mm	69 (3)	6(12)	2(9)	2(3)	3(16)	2(51)	—	—	—	—	—	3(7)
170 m: 36-45 mm	40 (7)	2(5)	—	—	—	—	—	—	—	1(7)	—	8(80)
46-54 mm	89 (1)	5(8)	3(10)	—	—	1(3)	—	—	—	—	—	10(77)
<i>L. nobilis</i> :												
70 m: 36-45 mm	56 (4)	5(32)	6(18)	1(2)	—	1(4)	1(23)	1(2)	—	—	—	4(16)
47-57 mm	18	2(33)	2(11)	1(17)	—	—	—	—	—	1(6)	—	2(33)
64-78 mm	9	—	1(56)	1(11)	—	—	—	—	—	—	—	3(33)
90 m: 36-45 mm	45 (9)	4(22)	4(18)	2(7)	2(9)	1(13)	—	—	—	—	—	3(22)
46-60 mm	33	9(39)	1(6)	2(12)	—	1(6)	—	2(21)	—	—	—	4(15)
110 m: 37-45 mm	32	1(6)	3(9)	1(6)	2(25)	—	—	1(9)	1(16)	—	—	4(28)
47-60 mm	28	1(4)	3(1)	—	—	—	—	1(11)	1(36)	—	—	3(39)
62-75 mm	61	2(3)	2(5)	1(3)	—	1(7)	—	—	1(30)	—	1(2)	7(51)
78-86 mm	25	—	—	2(28)	—	—	2(20)	—	—	—	—	6(52)
<i>Triphoturus nigrescens</i> :												
70 m: 19-25 mm	108(44)	7(17)	1(2)	5(8)	1(13)	3(8)	—	1(3)	1(1)	1(2)	—	1(2)
26-37 mm	98(14)	12(31)	5(9)	3(4)	1(3)	4(6)	—	1(26)	1(5)	—	—	2(2)
<i>Notolynchus valdiviae</i> :												
90 m: 16-24 mm	51(51)	13(37)	1(2)	—	—	—	—	—	1(10)	—	—	—
110 m: 19-24 mm	136(57)	14(15)	3(15)	2(9)	1(1)	1(2)	—	—	—	—	—	—
170 m: 20-23 mm	89(25)	5(11)	2(2)	1(4)	3(8)	—	—	—	—	1(11)	—	5(38)
<i>Ceratoscopelus warmingi</i> :												
70 m: 46-69 mm	56(18)	6(21)	4(11)	2(4)	—	—	2(7)	1(2)	1(4)	—	—	7(34)
90 m: 38-45 mm	32(37)	4(22)	1(3)	3(16)	1(3)	—	—	1(6)	—	1(9)	—	1(3)
46-62 mm	153(20)	15(25)	5(18)	2(3)	2(4)	2(9)	2(3)	—	1(6)	—	1(5)	3(8)
110 m: 48-68 mm	53 (8)	1(4)	1(2)	3(9)	—	1(6)	—	—	—	—	1(13)	10(58)
<i>Bolinichthys longipes</i> :												
70 m: 17-26 mm	77(86)	3(4)	1(1)	—	3(6)	1(3)	—	—	—	—	—	—
90 m: 27-35 mm	125(86)	10(12)	2(2)	1(1)	—	—	—	—	—	—	—	—
36-47 mm	166(83)	12(10)	3(5)	1(1)	—	—	—	—	—	—	—	2(1)
110 m: 26-35 mm	236(88)	9(7)	2(2)	—	—	1(3)	—	—	—	—	—	—
36-49 mm	317(76)	8(3)	3(4)	1(1)	—	—	—	1(3)	—	—	1(5)	1(8)
<i>Diogenichthys atlanticus</i> :												
70 m: 17-21 mm	40(77)	4(10)	2(5)	—	1(3)	1(5)	—	—	—	—	—	—
<i>Benthoosema suborbitale</i> :												
70 m: 18-25 mm	28(54)	4(14)	1(4)	1(4)	2(7)	—	—	2(11)	1(4)	—	—	1(4)
26-30 mm	69(42)	9(19)	4(13)	1(16)	1(4)	—	1(3)	—	—	—	—	1(3)
110 m: 28-32 mm	47(45)	4(13)	3(15)	2(23)	—	1(2)	—	—	—	—	1(2)	—
<i>Diaphus schmidti</i> :												
70 m: 31-35 mm	154(30)	1(5)	7(8)	—	2(10)	2(4)	1(1)	1(1)	—	—	—	10(42)
36-40 mm	120(39)	4(7)	5(8)	6(7)	2(18)	1(4)	1(1)	—	2(2)	—	1(2)	5(11)
90 m: 27-35 mm	180(49)	9(11)	4(4)	3(6)	—	2(5)	—	3(14)	—	—	1(1)	5(9)
36-41 mm	78(46)	5(15)	6(9)	4(14)	1(8)	—	—	1(4)	1(1)	—	—	2(3)
<i>D. perspicillatus</i> :												
70 m: 46-56 mm	418(33)	4(2)	2(3)	2(2)	—	2(3)	—	2(8)	—	2(2)	1(5)	16(41)
<i>D. fragilis</i> :												
90 m: 34-44 mm	29(52)	2(7)	3(24)	2(7)	1(3)	—	—	—	—	1(3)	—	1(3)
<i>D. trachops</i> :												
170 m: 36-50 mm	29(10)	—	2(10)	—	2(10)	1(3)	—	—	—	—	1(3)	7(62)
<i>Melamphaes danae</i> :												
70 m: 17-22 mm	54(22)	4(15)	5(22)	—	—	1(2)	2(18)	—	—	—	—	4(22)
90 m: 19-22 mm	31(23)	1(3)	2(26)	1(16)	—	1(16)	—	—	—	—	—	2(16)
110 m: 19-22 mm	34 (9)	—	1(6)	3(12)	—	—	—	—	—	1(21)	1(3)	7(50)
<i>Bregmaceros japonicus</i> :												
70 m: 38-51 mm	41 (2)	5(24)	1(5)	—	—	2(15)	2(39)	—	—	1(12)	—	1(2)

quent prey were euphausiids and *P. xiphias*; except at 70 m and 90 m, respectively, ASV's for these forms were relatively high. Generally ASV's of other large prey were also high.

Although there were no major between-depth differences in diet composition, ASV's were generally higher for fish from 110 m than for those from 70 and 90 m (Table 2). Among the fish from 110 m,

TABLE 3.—Density estimates of prey types at each of the four depths sampled. A "+" indicates presence, but with estimated density  $<0.005 \text{ m}^{-3}$ . Undetermined subadult copepodite stages of copepods are designated by "C" and specific stages by "C" plus the appropriate Roman numeral; otherwise, copepods are all adults (CVI). Prey types  $<1.0 \text{ mm}$  long, whose densities are probably underestimated due to mesh escapement, are starred.

Prey type	Density ( $\text{m}^{-3}$ )				Prey type	Density ( $\text{m}^{-3}$ )			
	70 m	90 m	110 m	170 m		70 m	90 m	110 m	170 m
<b>Copepods:</b>					<b>Euphausiids:</b>				
<i>Neocalanus</i> spp. CII, CIII	1.98	0.57	0.82	0.02	<i>Euphausia</i> spp.	6.40	0.30	0.52	0.01
<i>Neocalanus</i> spp. CIV, CV	0.62	0.42	0.23	0.05	<i>Stylocheiron</i> spp.	0.26	0.24	0.17	1.08
<i>Neocalanus</i> spp.	0.05	0.03	0.13	0.05	<i>Nematoscelis</i> spp.	0.02	0.01	0.07	1.17
<i>Calanus tenuicornis</i>	0.92	2.43	2.72	0.62	<i>Thysanopoda aequalis</i>	0.03	0.24	0.04	+
<i>Nannocalanus minor</i>	0.98	0.46	0.04	—	<i>Thysanopoda</i> spp.	0.01	—	0.02	+
<i>Undinula vulgaris</i>	0.08	0.02	—	—	<i>Nematobrachion sexspinosus</i>	—	+	+	+
<i>U. darwini</i>	0.12	0.36	0.01	—	Euphausiid larvae	0.44	0.24	0.11	0.07
<i>Eucalanus</i> spp.	0.06	0.02	0.02	0.01	<b>Ostracods:</b>				
* <i>Acrocalanus</i> spp.	0.09	—	0.04	0.01	* $< 1.0 \text{ mm}$	0.50	0.46	0.11	0.37
* <i>Clausocalanus</i> spp.	1.26	1.11	2.45	0.47	1.0-1.4 mm	1.40	1.67	0.60	1.18
*Pseudocalanidae	0.60	0.19	2.23	0.80	1.5-1.9 mm	0.89	1.04	0.36	0.97
<i>Euaetideus acutus</i>	0.45	0.38	1.00	0.01	2.0-2.9 mm	0.09	0.19	0.04	0.09
<i>Chiridius</i> + <i>Gaetanus</i> spp.	—	0.35	0.15	0.17	$\geq 3.0 \text{ mm}$	—	0.05	0.01	—
Aetideidae—C $<2.0 \text{ mm}$	0.35	0.96	0.58	0.25	<b>Amphipods:</b>				
Aetideidae—C 2.0-3.0 mm	0.28	0.96	1.02	0.22	1.0-1.9 mm	0.49	0.35	0.13	0.07
Aetideidae—CV, CVI $>3.0 \text{ mm}$	0.27	0.59	0.55	0.08	2.0-2.9 mm	0.15	0.09	0.09	0.17
<i>Euchaeta media</i>	0.16	0.19	0.58	0.01	$\geq 3.0 \text{ mm}$	0.03	0.03	0.07	0.12
<i>Euchaeta</i> spp.	0.09	0.16	0.04	—	<b>Carideans:</b>				
<i>Euchaeta</i> spp. C $\leq 2.0 \text{ mm}$	0.11	0.68	0.92	0.39	juveniles and adults	+	+	+	+
<i>Euchaeta</i> spp. C $>2.0 \text{ mm}$	0.17	1.37	0.30	0.28	larvae	0.50	0.07	0.08	0.07
<i>Scolecithrix danae</i>	0.08	0.03	+	—	<b>Penaeideans:</b>				
* <i>Scolecithrix bradyi</i>	0.74	0.38	0.81	0.06	juveniles and adults	0.02	0.03	0.02	0.01
* <i>Scolecithricella</i> spp. $<1.0$	0.45	0.32	0.23	0.35	larvae	0.03	0.05	0.01	—
<i>Scolecithricella</i> spp. $\geq 1.0$	1.68	3.49	5.97	1.17	<b>Mysids</b>				
<i>Lophothrix</i> spp. CV, CVI	0.49	0.41	0.03	—	Brachyuran zoëae	0.02	0.03	0.01	+
<i>Scottocalanus</i> spp. CV, CVI	0.21	0.15	0.22	0.04	Brachyuran megalopae	0.69	+	0.02	+
Unident. <i>Scolecithricidae</i> / <i>Phaennidae</i>	0.23	0.36	0.35	0.14	Anomuran larvae	0.03	0.05	0.01	0.07
<i>Pleuromamma xiphias</i>	1.29	5.01	1.42	0.43	Other crustacean larvae	0.02	—	0.01	0.03
<i>P. xiphias</i> CV	0.93	0.65	0.67	0.82	Chaetognaths	—	+	+	+
<i>P. abdominalis</i>	0.34	0.63	0.49	0.09	Larvaceans	2.97	3.32	1.08	0.15
<i>P. abdominalis</i> C	3.87	0.38	0.81	1.82	Other tunicates	0.14	0.76	0.17	—
<i>P. gracilis</i>	2.57	2.37	5.34	1.42	Siphonophores	0.29	1.37	0.16	+
<i>P. gracilis</i> CV	0.72	0.65	0.68	0.72	Polychaetes	0.71	1.26	0.12	0.01
<i>Centropages</i> spp.	0.09	0.02	—	—	Heteropods	0.07	0.20	0.04	0.03
<i>Lucicutia</i> sp..	0.74	0.35	0.31	0.99	*Gastropod larvae + pteropods $<1.0 \text{ mm}$	0.39	0.07	+	+
<i>Heterorhabdus papilliger</i>	0.84	0.61	0.79	0.17	*Pelecypod larvae	2.82	0.21	0.17	0.03
<i>Heterorhabdus</i> spp.	0.01	—	0.08	0.14	Other invertebrate larvae	0.12	0.02	0.01	—
Augaptilidae	0.16	0.24	0.29	3.38	Miscellaneous	0.11	—	0.27	—
<i>Candacia longimana</i>	0.24	0.24	0.44	0.05	Fish eggs	0.01	—	0.01	+
<i>Candacia</i> spp. CV, CVI	0.34	0.93	0.51	0.41	Fish larvae	0.04	0.09	0.06	0.01
<i>Paracandacia</i> spp. CV, CVI	1.23	1.84	0.44	—		0.21	0.14	0.08	0.04
Pontellidae	0.01	—	—	—					
* <i>Acartia</i> spp.	0.38	0.22	0.44	0.01					
Unident. calanoids	0.13	—	—	0.07					
* <i>Oithona</i> spp.	0.81	0.80	0.51	0.07					
* <i>Oncaea</i> spp. $>0.6 \text{ mm}$	0.54	0.53	0.60	1.00					
* <i>Oncaea</i> spp. $\leq 0.6 \text{ mm}$	0.04	—	0.01	0.22					
<i>Corycaeus</i> spp.	2.89	1.11	1.38	0.49					
Other cyclopoids	0.15	0.92	0.27	0.08					

there was a trend for higher ASV's in the larger fish; about half the prey taken by the two largest size groups had ASV's of  $1.0 \text{ m}^3$  or more.

### *Triphoturus nigrescens* (Table 6)

A large fraction of the diet of the smaller *T. nigrescens* were microzooplankton—mostly *Oncaea* spp. The most frequent prey among the macrozooplankton was *P. xiphias*; it and several other medium to large prey types had moderately high ASV's. Few prey had high ASV's and those with low ASV's included all sizes. If the ASV for *Oncaea* spp. is reduced by a factor of 4 to roughly correct

for undersampling, it is still equal to or greater than those for the medium to large macrozooplankton. This indicates that preference for *Oncaea* by small *T. nigrescens* is similar to that for several larger prey types.

The microzooplankton were a small fraction of the diet of the larger *T. nigrescens*, and the corrected ASV for *Oncaea* spp. is relatively low. *Pleuromamma xiphias* was the most frequent prey species and had one of the higher ASV's. Most of the other prey were medium to large types, and some of these had moderate to high ASV's. The largest fraction of both items and prey types, however, had low ASV's (Table 2). These included both

TABLE 4.—Stomach contents of *Lampanyctus steinbecki*: number of fish examined, number with intact prey, total number of prey, and number of each prey type for each depth and size category. The apparent search volume (see text) for each prey type is given in parentheses after the number eaten. Rarely eaten prey types ("Other prey") are given by depth and size categories below the main body of the table. Copepodite stages of copepods are designated as in Table 3.

Depth	70 m			90 m			110 m				170 m		
	26-35	36-45	46-52	18-25	26-35	36-45	46-51	19-25	26-35	36-45	46-50	36-45	46-54
Standard length, mm	23	14	7	18	38	103	12	15	22	50	45	20	53
No. examined	18	11	6	8	25	55	7	12	19	42	41	16	35
No. with intact prey	45	33	16	18	39	101	11	18	47	134	69	40	93
No. of intact prey													
Prey type	No. (Apparent search volume, m <sup>3</sup> )												
<i>Calanus tenuicornis</i>	—	—	—	1(0.05)	1(0.02)	3(0.02)	—	—	2(0.04)	—	—	—	1(0.05)
<i>Gaetanus</i> spp.	—	—	—	—	—	1(0.10)	—	—	—	—	—	—	3(0.49)
Aetideidae C <2.0 mm	—	1(0.26)	—	—	—	1(0.02)	—	—	—	—	—	—	1(0.11)
Aetideidae C 2.0-3.0 mm	1(0.20)	1(0.33)	—	—	3(0.12)	3(0.06)	—	—	1(0.05)	3(0.07)	2(0.05)	3(0.86)	11(1.44)
Aetideidae CV, CVI >3.0 mm	3(0.61)	3(0.99)	—	—	4(0.27)	6(0.19)	1(0.24)	—	3(0.29)	5(0.22)	9(0.40)	4(27.7)	10(3.49)
<i>Euchaeta media</i>	1(0.35)	—	—	1(0.66)	—	—	1(0.76)	—	—	1(0.04)	1(0.04)	1(6.94)	—
<i>Euchaeta</i> spp. C >2.0 mm	—	—	—	—	—	2(0.01)	—	—	—	—	1(0.08)	—	—
<i>Scolecithrixella</i> ≥1.0 mm	3(0.10)	—	—	—	—	1(0)	—	—	1(0)	2(0)	—	—	—
<i>Scotocalanus</i> spp. CV, CVI	—	—	—	—	—	—	—	—	—	1(0.11)	—	—	2(1.54)
<i>Pleuromamma xiphias</i>	10(0.43)	8(0.56)	6(0.77)	2(0.05)	3(0.02)	18(0.07)	—	2(0.12)	10(0.37)	45(0.75)	26(0.45)	10(1.45)	23(1.54)
<i>P. xiphias</i> CV	—	1(0.10)	—	2(0.39)	1(0.06)	6(0.17)	—	1(0.12)	1(0.08)	3(0.11)	—	—	—
<i>P. abdominalis</i>	1(0.16)	2(0.54)	2(0.98)	—	3(0.19)	12(0.35)	1(0.23)	2(0.33)	2(0.21)	9(0.44)	4(0.20)	8(5.56)	12(3.80)
<i>P. abdominalis</i> C	1(0.01)	—	—	—	—	—	—	—	—	—	—	1(0.07)	1(0.02)
<i>P. gracilis</i>	—	—	—	1(0.05)	1(0.02)	3(0.02)	2(0.12)	2(0.03)	2(0.02)	—	1(0)	—	—
<i>Lucicutia</i> spp.	—	—	—	1(0.36)	1(0.12)	—	—	—	—	—	—	—	—
<i>Heterorhabdus papilliger</i>	—	—	—	1(0.20)	—	—	—	—	—	1(0.03)	—	—	—
<i>Candacia longimana</i>	4(0.93)	5(1.89)	1(0.69)	—	3(0.50)	13(0.99)	2(1.19)	2(0.38)	5(0.61)	15(0.82)	2(0.11)	2(2.41)	5(2.74)
<i>Candacia</i> spp. CV, CVI	—	1(0.26)	—	—	1(0.04)	3(0.06)	—	2(0.33)	—	4(0.19)	2(0.10)	—	—
<i>Paracandacia</i> spp. CV, CVI	4(0.18)	—	—	2(0.14)	3(0.06)	5(0.05)	—	1(0.19)	—	3(0.16)	—	—	—
Unident. calanoid	1	—	—	1	2	2	—	1	—	1	—	—	4
<i>Oncaea</i> spp. >0.6 mm	3(0.31)	—	—	6(1.41)	4(0.30)	6(0.21)	1(0.27)	—	8(0.70)	5(0.20)	1(0.04)	3(0.19)	1(0.03)
<i>Corycaeus</i> spp.	—	—	—	—	1(0.04)	1(0.02)	—	—	—	—	—	—	1(0.06)
<i>Euphausia</i> spp.	5(0.04)	6(0.09)	6(0.16)	—	3(0.40)	2(0.12)	—	4(0.64)	5(0.51)	19(0.87)	9(0.42)	—	2(7.14)
<i>Stylocheiron</i> spp.	—	—	—	—	2(0.31)	6(0.45)	—	1(0.49)	3(0.92)	8(1.11)	—	—	7(0.19)
<i>Nematocelis</i> spp.	—	—	—	—	—	—	—	—	—	—	1(0.38)	—	3(0.07)
<i>Thysanopoda aequalis</i>	—	—	—	—	—	—	1(0.60)	—	—	—	2(1.32)	3(46.9)	2(14.3)
Euphausiid larva	2(0.26)	1(0.21)	1(0.38)	—	1(0.17)	—	—	—	—	3(0.66)	1(0.22)	—	—
Ostracod <1.0 mm	1(0.11)	—	—	—	—	—	—	—	2(0.92)	—	—	—	—
Ostracod 1.0-1.4 mm	—	—	—	—	1(0.02)	3(0.04)	1(0.09)	—	1(0.09)	—	1(0.04)	1(0.05)	1(0.02)
Ostracod 1.5-1.9 mm	—	1(0.10)	—	—	1(0.04)	2(0.03)	1(0.14)	—	—	5(0.33)	—	—	—
Ostracod 2.0-2.9 mm	—	—	—	—	—	1(0.10)	—	—	1(1.22)	—	—	—	—
Amphipod 1.0-1.9 mm	—	1(0.18)	—	—	—	—	—	—	—	—	—	—	—
Amphipod 2.0-2.9 mm	—	—	—	—	—	—	—	—	—	—	1(0.27)	3(1.10)	1(0.17)
Amphipod ≥3.0 mm	1(1.6)	—	—	—	—	—	—	—	—	—	—	—	—
Penaeidean larva	—	1(3.0)	—	—	—	—	—	—	—	—	—	—	1(∞)
Other prey:	70 m: 26-35 mm—2 <i>Clausocalanus</i> spp. (0.09), 1 <i>Neocalanus</i> spp. (1.2), 1 <i>Scolecithrix danae</i> (0.69)												
	36-45 mm—1 mysid (4.5)												
	90 m: 36-45 mm—1 <i>Euaetideus acutus</i> (0.05)												
	110 m: 36-45 mm—1 <i>Thysanopoda</i> spp. (1.4)												
	46-50 mm—2 megalopae (5.4), 1 <i>Undinula darwini</i> (1.73), 1 cyclopoid (0.09), 1 fish larva (0.31)												
	170 m: 36-45 mm—1 Penaeidean adult (8.94)												
	46-54 mm—1 <i>Nematobrachion sexspinosus</i> (9.51)												

TABLE 5.—Stomach contents of *Lampanyctus nobilis*. Format as in Table 4.

Depth	70 m			90 m		110 m			
	36-45	47-57	64-78	36-45	46-60	37-45	45-60	62-75	76-86
Standard length, mm	28	11	8	35	30	18	13	23	17
No. examined	19	8	5	22	19	12	10	16	13
No. with intact prey	56	18	9	45	33	32	28	61	25
No. of intact prey									
Prey type	No. (Apparent search volume, m <sup>3</sup> )								
Aetideidae 2.0-3.0 mm	1(0.19)	—	—	—	1(0.05)	—	—	2(0.12)	—
Aetideidae >3.0 mm	1(0.19)	—	—	—	2(0.15)	3(0.27)	2(0.31)	1(0.18)	4(0.46)
<i>Euchaeta media</i>	—	—	1(1.25)	—	1(0.24)	—	—	1(0.17)	—
<i>Pleuromamma xiphias</i>	13(0.53)	3(0.29)	—	—	2(0.02)	2(0.02)	6(0.35)	10(0.71)	18(0.79)
<i>P. xiphias</i> CV	—	—	—	—	1(0.07)	1(0.08)	2(0.25)	1(0.15)	—
<i>P. abdominalis</i>	1(0.15)	—	—	—	6(0.43)	2(0.17)	1(0.17)	—	2(0.25)
<i>P. gracilis</i>	3(0.06)	1(0.05)	—	—	4(0.08)	3(0.07)	2(0.03)	1(0.02)	—
<i>Candacia longimana</i>	2(0.47)	5(2.60)	—	—	1(0.19)	2(0.44)	1(0.19)	3(0.69)	—
<i>Candacia</i> spp. CV, CVI	—	—	—	—	4(0.20)	—	1(0.17)	—	—
<i>Paracandacia</i> spp. CV, CVI	1(0.04)	—	—	—	3(0.07)	2(0.06)	—	—	1(0.14)
<i>Oncaea</i> spp. >0.6 mm	2(0.19)	—	—	—	2(0.17)	—	—	—	—
<i>Corycaeus</i> spp.	2(0.04)	—	—	—	—	1(0.05)	—	—	1(0.04)
<i>Euphausia</i> spp.	11(0.09)	5(0.09)	5(0.16)	—	8(1.21)	4(0.70)	5(0.80)	6(1.15)	12(1.44)
<i>Stylocheiron</i> spp.	5(0.20)	—	—	—	2(0.38)	3(0.66)	4(1.95)	4(2.34)	3(1.09)
<i>Thysanopoda aequalis</i>	2(3.60)	1(4.30)	—	—	1(0.09)	1(0.22)	3(6.75)	—	5(8.44)
<i>Thysanopoda</i> spp.	1(5.80)	—	1(22.2)	—	1(∞)	1(∞)	1(4.9)	—	4(14.7)



TABLE 5.—Continued.

Depth	70 m			90 m		110 m			
	36-45	47-57	64-78	36-45	46-60	37-45	45-60	62-75	76-86
Standard length, mm									
Prey type	No. (Apparent search volume, m <sup>3</sup> )								
Euphausiid larva	1(0.12)	—	—	2(0.38)	—	—	—	—	—
Ostracod <1.0 mm	—	—	—	2(0.20)	—	—	—	—	—
Ostracod 1.0-1.4 mm	—	—	—	—	1(0.03)	—	—	—	—
Ostracod 1.5-1.9 mm	—	1(0.14)	1(0.22)	—	1(0.05)	3(0.70)	—	—	—
Ostracod 2.0-2.9 mm	—	—	—	—	—	—	—	—	2(3.60)
Amphipod 1.0-1.9 mm	1(0.11)	—	—	2(0.26)	—	—	—	—	1(0.60)
Amphipod 2.0-2.9 mm	5(1.75)	1(0.83)	—	—	—	—	—	—	—
Amphipod ≥3.0 mm	—	—	—	—	2(3.00)	—	—	2(1.76)	2(2.20)
Penaeidean juvenile + adult	—	—	—	—	—	1(3.5)	1(4.2)	4(10.4)	—
Other prey:	70 m: 36-45 mm—1 <i>Neocalanus</i> spp. (1.14), 1 <i>Scolecithrix danae</i> (0.65), 1 <i>Scottocalanus</i> spp. (0.25), 1 <i>Lucicutia</i> spp. (0.07)								
	47-57 mm—1 <i>Nannocalanus minor</i> (0.12)								
	64-78 mm—1 mysid (10.09)								
	90 m: 36-45 mm—1 <i>Eucalanus</i> spp. (2.30)								
	46-60 mm—1 <i>Heterorhabdus</i> spp. (∞), 1 Aetideidae C ≤2.0 mm (0.05), 1 megalopa (1.05)								
	110 m: 62-75 mm—1 <i>Euchaeta</i> spp. (1.6), 1 <i>Pleuromamma abdominalis</i> C (0.09), 1 <i>Nematoscelis</i> spp. (0.96)								
	76-86 mm—1 Caridean juvenile (19.2)								

TABLE 6.—Stomach contents of *Triphotorus nigrescens* and *Notolychnus valdiviae*.  
Format as in Table 4.

Species	<i>T. nigrescens</i>		90 m	<i>N. valdiviae</i>	
	70 m			110 m	170 m
Depth	19-25	26-37	16-24	19-24	20-23
Standard length, mm	19-25	26-37	16-24	19-24	20-23
No. examined	32	29	59	77	88
No. with intact prey	30	28	28	62	55
No. of intact prey	108	99	52	138	92
Prey type	No. (Apparent search volume, m <sup>3</sup> )				
<i>Calanus tenuicornis</i>	—	—	1(0.01)	2(0.01)	1(0.03)
<i>Nannocalanus minor</i>	2(0.07)	1(0.04)	—	—	—
<i>Undinula vulgaris</i>	2(0.83)	1(0.45)	—	—	—
<i>Undinula darwini</i>	1(0.28)	1(0.30)	—	—	—
<i>Clausocalanus</i> spp.	—	—	—	1(0.01)	1(0.04)
<i>Geetanus</i> spp.	—	—	1(0.10)	—	4(0.42)
Aetideidae C <2.0 mm	—	—	2(0.07)	2(0.03)	4(0.29)
Aetideidae C 2.0-3.0 mm	2(0.24)	1(0.13)	1(0.04)	—	10(0.83)
Aetideidae CV, CVI >3.0 mm	2(0.24)	2(0.26)	1(0.06)	2(0.06)	2(0.44)
<i>Euchaeta media</i>	1(0.21)	2(0.45)	1(0.19)	1(0.03)	1(2.00)
<i>Scolecithrix danae</i>	1(0.42)	1(0.45)	—	—	—
<i>Scolecithricella</i> spp. <1.0 mm	2(0.15)	2(0.16)	—	—	—
<i>Scolecithricella</i> spp. ≥1.0 mm	1(0.02)	2(0.04)	—	1(0)	2(0.03)
<i>Scottocalanus</i> spp. CV, CVI	—	1(0.17)	—	—	1(0.49)
<i>Pleuromamma xiphias</i>	14(0.36)	25(0.69)	3(0.02)	14(0.16)	25(1.10)
<i>P. xiphias</i> CV	—	1(0.04)	—	4(0.10)	4(0.09)
<i>P. abdominalis</i>	5(0.49)	3(0.31)	1(0.06)	9(0.30)	1(0.20)
<i>P. abdominalis</i> C	—	2(0.02)	—	—	2(0.20)
<i>P. gracilis</i>	6(0.08)	6(0.08)	2(0.03)	2(0.01)	—
<i>Lucicutia</i> spp.	—	1(0.05)	1(0.10)	1(0.05)	1(0.02)
<i>Heterorhabdus</i> spp.	—	—	—	2(0.40)	1(0.13)
<i>Candacia longimana</i>	3(0.42)	5(0.74)	5(0.74)	3(0.11)	5(1.75)
<i>Candacia</i> spp. CV, CVI	—	—	1(0.04)	1(0.03)	—
<i>Paracandacia</i> spp. CV, CVI	2(0.05)	4(0.12)	—	3(0.11)	2(∞)
Unident. calanoid	—	1	1	2	3
<i>Orcaea</i> spp. >0.6 mm	43(2.65)	12(0.79)	22(1.48)	74(1.99)	21(0.38)
<i>Corycaeus</i> spp.	2(0.02)	1(0.01)	—	—	—
<i>Euphausia</i> spp.	4(0.02)	12(0.07)	—	1(0.03)	—
Euphausiid larva	3(0.23)	2(0.16)	—	3(0.45)	—
Ostracod <1.0 mm	3(0.20)	—	4(0.31)	2(0.28)	—
Ostracod 1.0-1.4 mm	—	1(0.02)	3(0.06)	—	—
Ostracod 1.5-1.9 mm	1(0.04)	1(0.04)	1(0.03)	1(0.10)	—
Amphipod 1.0-1.9 mm	2(0.14)	1(0.07)	1(0.10)	—	—
Amphipod 2.0-2.9 mm	3(0.67)	1(0.24)	—	—	—
Amphipod ≥3.0 mm	2(2.22)	1(1.19)	—	3(0.23)	—
Other prey:	<i>T. nigrescens</i> — 70 m: 19-25 mm —1 <i>Neocalanus</i> spp. (0.72)				
	26-37 mm —1 megalopa (1.38), 1 <i>Stylocheiron</i> spp. (0.14)				
	1 <i>Euaetideus acutus</i> (0.08), 2 <i>Euchaeta</i> spp. C >2.0 mm (0.42)				
	<i>N. valdiviae</i> — 110 m: 19-25 mm —1 <i>Scolecithrix bradyi</i> (0.02), 1 <i>Pleuromamma gracilis</i> CV (0.02), 1 <i>Heterorhabdus papilliger</i> (0.02), 1 <i>Stylocheiron</i> spp. (0.09)				
	— 170 m: 20-23 mm —1 zoea (∞)				

small to medium copepods and euphausiids, the latter of which were taken frequently.

### *Notolychnus valdiviae* (Table 6)

*Notolychnus valdiviae* occurs throughout the depth range covered by the three deepest samples as evidenced by the high numbers of specimens available from each depth. With such large catches, it is unlikely that data from the deeper samples were seriously affected by catches in transit to and from towing depth.

Microzooplankton made up over half the diet at 90 and 110 m and about one-fourth at 170 m (Table 2). These were almost all *Oncaea*. If the ASV's are roughly corrected for undersampling, they are still relatively high at 90 and 110 m.

Most of the remaining prey were medium to large copepods; *P. xiphias*, *P. abdominalis*, *C. longimana*, and aetideids were important at one or more depths. Euphausiids were rarely taken. ASV's for items from 90 and 110 m were mostly rather low (Table 2). At 170 m ASV's for a large fraction of items and prey types were high (> 0.80 m<sup>3</sup>) mainly due to high values for *P. xiphias*, *C. longimana*, and 2-3 mm aetideids. This plus the lower proportion of microzooplankton in the diet at 170 m indicates increased preference for larger prey.

### *Ceratoscopelus warmingi* (Table 7)

*Ceratoscopelus warmingi* took a wide variety of sizes and taxa of prey. Small fractions of the diets of the large fish were microzooplankton—mostly *Oncaea* spp., but including several species of small calanoids, ostracods, and gastropod veligers. *Oncaea* and small ostracods made up over a third of the diet of the small fish from 90 m (Table 2). If the ASV's for *Oncaea* are decreased by a factor of 4 to roughly correct for undersampling, preference equivalent to that for larger prey is indicated. ASV's for other microzooplankton were very low. All sizes of calanoids and small to medium ostracods were taken, but ASV's were usually low.

Many prey items were large and most of these had high ASV's, resulting in large fractions of the prey from large fish at 70 and 110 m having high ASV's (Table 2). Euphausiids, decapods and their larvae, large amphipods, and ostracods were taken frequently, but fish, siphonophores, heteropods, and polychaetes (all >5 mm) were also

TABLE 7.—Stomach contents of *Ceratoscopelus warmingi*. Format as in Table 4.

Depth	70 m	90 m	110 m
Standard length, mm	46-69	38-45	46-62
No. examined	23	16	90
No. with intact prey	12	12	61
No. of intact prey	57	34	179
Prey type	No. (Apparent search volume, m <sup>3</sup> )		
<i>Nannocalanus minor</i>	1(0.08)	1(0.18)	—
Aetideidae C 2.0-3.0 mm	1(0.30)	—	1(0.02)
Aetideidae CV, CVI >3.0 mm	1(0.30)	2(0.28)	3(0.08)
<i>Pleuromamma xiphias</i>	2(0.13)	3(0.05)	9(0.03)
<i>P. abdominalis</i>	—	2(0.27)	6(0.16)
<i>P. abdominalis</i> C	1(0.02)	1(0.22)	1(0.04)
<i>P. gracilis</i>	2(0.06)	2(0.07)	1(0.01)
<i>Lucicutia</i> spp.	1(0.11)	—	4(0.09)
<i>Paracandacia</i> spp. CV, CVI	—	—	1(0.01)
Unident. calanoid	—	2	—
<i>Oncaea</i> spp. >0.6 mm	7(1.08)	10(1.57)	20(0.62)
<i>Corycaeus</i> spp.	—	1(0.07)	2(0.03)
<i>Euphausia</i> spp.	6(0.08)	3(0.83)	8(0.44)
<i>Stylochelron</i> spp.	—	—	4(0.27)
<i>Thysanopoda aequalis</i>	3(8.60)	2(0.69)	6(0.41)
Euphausiid larva	3(0.58)	1(0.35)	3(0.20)
Ostracod <1.0 mm	3(0.09)	2(0.36)	3(0.11)
Ostracod 1.0-1.4 mm	1(0.06)	—	12(0.12)
Ostracod 1.5-1.9 mm	2(0.18)	1(0.08)	9(0.72)
Ostracod ≥2.0 mm	5(4.50)	—	5(0.34)
Amphipod 1.0-1.9 mm	—	—	5(0.05)
Amphipod 2.0-2.9 mm	—	—	3(0.53)
Amphipod ≥3.0 mm	6(14.2)	1(2.40)	4(1.90)
Penaeidean juvenile + adult	—	—	1(0.55)
Mysid	1(4.20)	—	—
Polychaete	—	—	1(0.08)
Siphonophore	1(0.12)	—	5(0.06)
Fish larva	2(0.79)	—	8(0.94)
<i>Cyclothone</i> spp.	1(∞)	—	26(∞)
Other prey:			
70 m—	1 <i>Undinula darwini</i> (0.69), 1 <i>Heterorhabdus papilliger</i> (0.10),		
	— 1 Augaptilidae (0.52), 1 megalopa (3.20), 2 stomatopod larvae		
	— (∞), 1 Ctenophore (∞).		
90 m—	46-62 mm—1 <i>Calanus tenuicornis</i> (0.01), 2 <i>Clausocalanus</i> spp.		
	(0.03), 1 <i>Pseudocalanidae</i> (0.55), 1 <i>Ischnocalanus</i> sp. (∞),		
	1 Aetideidae C <2.0 mm (0.02), 1 <i>Euchaeta media</i> (0.09),		
	1 <i>Scolecithrix bradyi</i> (0.04), 2 <i>Candacia longimana</i> (0.14),		
	5 <i>Candacia</i> spp. CV, CVI (0.09), 1 Caridean larva (0.23),		
	1 Penaeidean larva (0.33), 2 Anomuran larvae (∞), 1 Chaetognath		
	(0), 6 Heteropods (1.14), 2 Gastropods (0.16).		
110 m—	2 <i>Nematocellus</i> spp. (2.20), 1 <i>Nematobranchion sexspinosus</i> (23.8).		

present. Items listed as "fish" (Table 7) were all epipelagic larvae or juveniles, but *C. warmingi* also frequently eats *Cyclothone*, which it encounters only during the day. Results of studies of feeding chronology (Clarke 1978) indicate that *Ceratoscopelus warmingi* takes such large items both day and night. While it is possible that the other large items mentioned above could have been taken at depths other than those sampled and thus that the high ASV's are artifacts, these items do cooccur with *C. warmingi* at the depths sampled and those recorded were relatively fresh and intact in stomachs of fish collected in the latter half of the night. (*Cyclothone* were, however, eliminated for calculations in Table 2.) Even allowing for the probability that ASV's of some of the largest prey types were overestimated due to avoidance of the plankton nets (see Methods sec-

tion), the high ASV's observed probably indicate a real preference for large prey.

A 48 mm *Ceratoscopelus warmingi* female from 90 m had no lenses in the eyes. The outer eye cover was intact and the space normally occupied by the lens was filled with gelatinous material similar to the humor in the rest of the eye. Thus the lenses were not missing due to damage during capture or even a recent injury. This fish had not only managed to reach adult size, but had three fresh copepods and remains of others and a euphausiid in the stomach.

*Bolinichthys longipes* (Table 8)

Trematode parasites were frequently present in the stomachs of *B. longipes*: The large fish from 110 m averaged over six parasites/stomach (Table 8). Parasite load and frequency was much lower in the small fish from 70 m. It was not possible, due to

insufficient numbers, to rigorously compare stomach contents of fish with and without parasites from any given depth-size group; however, while some of the unparasitized fish had more intact prey than most parasitized specimens, there were no obvious differences in prey type or frequency. Thus the parasites did not appear to bias the diet directly or by effectively increasing digestion rate and causing more resistant prey types to appear as intact in disproportionate frequencies.

Microzooplankton, 90% of which were *Oncaea* spp., made up the great majority of food items in all groups (Table 2). A large fraction of the *Oncaea* spp. eaten were very small ( $\leq 0.6$  mm); such sizes were rarely eaten by most of the other fishes considered. The ASV's for these small forms were absurdly high; data from very fine mesh plankton nets would be needed to estimate preference. If the ASV's for the large *Oncaea* are reduced by a factor of 4 (see Methods section), the values are still quite

TABLE 8.—Stomach contents of *Bolinichthys longipes* and *Diogenichthys atlanticus*. Format as in Table 4. Also given are incidence and number per fish of trematode parasites in *B. longipes*.

Species Depth	70 m	<i>B. longipes</i> 90 m		110 m		<i>D. atlanticus</i> 70 m
		27-35	36-47	26-35	36-49	17-21
Standard length, mm	17-26	27-35	36-47	26-35	36-49	17-21
No. examined	11	25	35	38	35	9
No. with intact prey	11	25	35	38	35	6
No. of intact prey	78	127	168	238	323	43
No. with trematodes	3	19	35	36	32	—
Average (range) no./fish	0.36(0-2)	1.84(0-6)	3.48(1-9)	2.74(0-8)	6.03(0-12)	—
Prey type		No. (Apparent search volume, m <sup>3</sup> )				
<i>Calanus tenuicornis</i>	—	2(0.03)	1(0.01)	—	1(0.01)	—
<i>Acrocalanus</i> spp.	—	—	—	—	—	3(5.40)
<i>Clausocalanus</i> spp.	1(0.07)	—	—	—	1(0.01)	—
<i>Euaetideus acutus</i>	—	1(0.10)	2(0.15)	—	2(0.06)	—
Aetideidae CV, CVI >3.0 mm	1(0.33)	1(0.07)	1(0.05)	—	1(0.05)	—
<i>Scolecithrix bradyi</i>	1(0.12)	2(0.21)	2(0.15)	2(0.06)	4(0.14)	2(0.45)
<i>Scolecithricella</i> spp. <1.0 mm	—	1(0.12)	1(0.09)	—	—	—
<i>Scolecithricella</i> spp. $\geq 1.0$ mm	—	—	—	1(0)	—	1(0.10)
<i>Pleuromamma xiphias</i>	1(0.07)	1(0.01)	2(0.01)	4(0.07)	10(0.20)	—
<i>P. abdominalis</i>	—	1(0.06)	—	2(0.11)	2(0.11)	—
<i>P. gracilis</i>	—	2(0.03)	1(0.01)	4(0.02)	2(0.01)	1(0.06)
<i>Lucicutia</i> spp.	—	—	1(0.08)	1(0.08)	—	2(0.45)
<i>Heterorhabdus papilliger</i>	—	—	1(0.05)	1(0.03)	—	—
<i>Candacia longimana</i>	1(0.38)	1(0.17)	2(0.24)	2(0.12)	10(0.66)	—
<i>Candacia</i> spp CV, CVI	—	1(0.04)	2(0.06)	8(0.41)	26(1.46)	—
<i>Paracandacia</i> spp. CV, CVI	1(0.07)	2(0.04)	5(0.15)	1(0.06)	15(0.97)	1(0.14)
Unident. calanoid	1	2	2	2	6	3
<i>Oithona</i> spp.	—	1(0.05)	1(0.04)	—	—	—
<i>Oncaea</i> spp. >0.6 mm	17(2.86)	45(3.40)	86(4.64)	125(5.48)	150(7.14)	11(3.40)
<i>Oncaea</i> spp. $\leq 0.6$ mm	42(95)	52( $\infty$ )	42( $\infty$ )	78(205)	84(240)	11(45.8)
<i>Corycaeus</i> spp.	1(0.03)	2(0.07)	1(0.03)	—	2(0.04)	—
<i>Microsetella</i> spp.	2( $\infty$ )	1( $\infty$ )	1( $\infty$ )	2( $\infty$ )	—	4( $\infty$ )
<i>Euphausia</i> spp.	—	—	—	—	1(0.05)	1(0.03)
Euphausiid larva	2(0.42)	—	—	—	1(0.27)	—
Ostracod <1.0 mm	1(0.18)	5(0.44)	3(0.19)	—	2(0.50)	—
Ostracod 1.0-1.4 mm	—	—	2(0.03)	2(0.09)	1(0.05)	—
Ostracod 1.5-1.9 mm	3(0.31)	—	2(0.05)	1(0.07)	1(0.08)	1(0.18)
Amphipod 1.0-1.9 mm	1(0.18)	1(0.11)	1(0.08)	—	—	1(0.33)
Chaetognath	—	—	—	1(0.02)	—	1(0.05)
Gastropod larva	1(0.03)	—	1(0.14)	—	—	—
Other prey: <i>B. longipes</i> — 70 m: 17-26 mm—1 <i>Pontella</i> sp. ( $\infty$ )						
90 m: 26-35 mm—2 Aetideidae C <2.0 mm (0.08), 1 <i>Euchaeta media</i> (0.21)						
36-47 mm—2 <i>Lophothrix</i> spp. (0.14), 1 <i>Gaetanus</i> sp. (0.08),						
1 <i>Pareuchaeta</i> sp. ( $\infty$ ), 1 zoea (9.50)						
110 m: 26-35—1 Amphipod <1.0 mm ( $\infty$ )						
36-49—1 <i>Stylocheiron</i> sp. (0.17)						

high, indicating a real preference for *Oncaea*. Except for three prey types not taken by the plankton tows, the ASV's for other microzooplankton are low even without any adjustment for undersampling.

Except for the large fish from 110 m, macrozooplankton were taken very infrequently and mostly had low ASV's. The large fish from 110 m had eaten *Pleuromamma* and candaciids frequently, and this was the only group from which euphausiids were recorded. The data indicate some preference for candaciids. ASV's for these copepods were high for the large fish from 110 m and sometimes fairly high in other groups.

### *Diogenichthys atlanticus* (Table 8)

About three-fourths of the items eaten by *D. atlanticus* were microzooplankton—mostly *Oncaea* spp. The ASV for the grossly undersampled small *Oncaea* is meaningless, but if ASV's for the other microzooplankton are reduced by a factor of 4, there is reasonable indication of preference for the large *Oncaea* spp. and *Acrocalanus* spp. Most of the macrozooplankton were small to medium copepods, and ASV's of most types were low.

### *Benthoosema suborbitale* (Table 9)

*Benthoosema suborbitale* usually does not occur as deep as 110 m, but the number collected at that depth was considerably larger than that expected from catches in transit. Thus the data are probably not seriously affected by fish caught at shallower depths. The sample from 90 m, which was taken at a different time of the year, had too few *B. suborbitale* to merit analysis.

Microzooplankton were important fractions of the diet of *B. suborbitale*; they made up over half the items from the small fish and slightly less for the larger ones. Almost all were *Oncaea* spp.—mostly the larger forms. Macrozooplankton were mostly medium to large copepods, but also included euphausiids and large amphipods. Such prey, especially *P. xiphias* and candaciids, were eaten more frequently by the large fish from both depths. ASV's for most macrozooplankton prey types were 0.40 m<sup>3</sup> or less. If the ASV's for the large *Oncaea* spp. are reduced by a factor of 4, they are commensurate with those of the macrozooplankton.

TABLE 9.—Stomach contents of *Benthoosema suborbitale*. Format as in Table 4.

Depth	70 m		110 m
	18-25	26-30	26-32
Standard length, mm	20	48	38
No. examined	11	32	26
No. with intact prey	29	69	47
Prey type	No. (Apparent search volume, m <sup>3</sup> )		
<i>Nannocalanus minor</i>	—	—	1(0.98)
<i>Undinula darwini</i>	1(0.75)	2(0.52)	—
<i>Clausocalanus</i> spp.	1(0.07)	—	1(0.02)
Aetideidae C 2.0-3.0 mm	—	—	3(0.12)
Aetideidae CV, CVI >3.0 mm	1(0.33)	1(0.11)	2(0.14)
<i>Euchaeta media</i>	—	1(0.20)	—
<i>Scolecithrix danae</i>	1(1.14)	—	—
<i>Pleuromamma xiphias</i>	1(0.07)	11(0.27)	8(0.22)
<i>P. xiphias</i> CV	1(0.10)	1(0.03)	—
<i>P. abdominalis</i>	1(0.27)	2(0.18)	2(0.15)
<i>P. gracilis</i>	1(0.04)	2(0.02)	3(0.02)
<i>Heterorhabdus papilliger</i>	1(0.11)	—	—
<i>Candacia longimana</i>	1(0.38)	3(0.39)	—
<i>Candacia</i> spp. CV, CVI	—	1(0.09)	1(0.08)
<i>Paracandacia</i> spp. CV, CVI	—	5(0.13)	3(0.26)
Unident. calanoid	1	—	—
<i>Oncaea</i> spp. >0.6 mm	10(1.68)	21(1.22)	19(1.22)
<i>Oncaea</i> spp. ≤0.6 mm	4(9.09)	8(6.25)	1(3.85)
<i>Corycaeus</i> spp.	—	2(0.02)	1(0.03)
<i>Euphausia</i> spp.	—	3(0.01)	1(0.07)
<i>Thysanopoda aequalis</i>	—	2(2.20)	—
Euphausiid larva	3(0.63)	1(0.07)	—
Ostracod 1.5-1.9 mm	1(0.10)	1(0.03)	—
Amphipod 1.0-1.9 mm	—	1(0.06)	—
Amphipod 2.0-2.9 mm	—	—	1(0.42)
Zoea	—	1(0.04)	—

### *Diaphus schmidti* (Table 10)

The numbers of prey per fish and diversity of prey were relatively high for *D. schmidti*; several small copepods and noncrustacean prey that were either rare or absent in the diets of other species were taken relatively frequently.

Microzooplankton made up 30-50% of the items (Table 2); half to two-thirds of these were *Oncaea*. If ASV's for *Oncaea* are roughly corrected, they are still quite high. ASV's for other types of microzooplankton were variable.

Although the composition of macrozooplankton prey was generally similar for all groups, there were some differences between sizes or depths. *Pleuromamma* and *Euphausia* spp. were eaten more frequently at 70 m than at 90 m. Overall, *Corycaeus* spp. were the most frequently eaten prey, but at both depths, frequency and ASV's were higher for the small fish. About half the prey of the small fish from 70 m had high ASV's. These were mostly *Corycaeus* spp., but also included several medium to large prey types. Among the large fish from 70 m, a few types of large prey had high ASV's, but most prey from both these and both groups from 90 m had low ASV's. The generally higher ASV's associated with the small fish from 70 m appear to have resulted mostly from higher

TABLE 10.—Stomach contents of four *Diaphus* species. Format as in Table 4.

Species Depth	<i>D. schmidti</i>		<i>D. perspicillatus</i>		<i>D. fragilis</i>	<i>D. trachops</i>	
	70 m	90 m	70 m	90 m	170 m	170 m	
Standard length, mm	31-35	36-40	27-35	36-41	46-56	34-44	36-50
No. examined	12	15	30	21	20	6	15
No. with intact items	11	14	30	19	17	5	12
No. of intact items	162	124	188	81	457	29	32
Prey type	No. (Apparent search volume, m <sup>3</sup> )						
<i>Neocalanus</i> spp.	2(3.90)	—	—	—	2(2.60)	—	—
<i>Calanus tenuicornis</i>	—	—	2(0.03)	—	—	1(0.08)	—
<i>Nannocalanus minor</i>	2(0.18)	2(0.14)	3(0.22)	—	8(0.48)	—	—
<i>Undinula vulgaris</i>	1(1.10)	1(0.89)	—	—	6(0.44)	—	—
<i>U. garwini</i>	5(3.80)	2(1.20)	1(0.09)	—	4(2.00)	—	—
<i>Acrocalanus</i> spp.	—	1(0.76)	1(×)	—	2(1.30)	1(×)	—
<i>Clausocalanus</i> spp.	1(0.07)	—	2(0.06)	1(0.05)	—	—	—
<i>Gaetanus</i> + <i>Chiridius</i> spp.	—	—	—	1(0.15)	—	—	7(3.30)
Aetideidae C <2.0 mm	—	—	—	—	—	1(0.21)	4(1.30)
Aetideidae C 2.0-3.0 mm	—	—	3(0.10)	—	—	1(0.21)	1(0.38)
Aetideidae CV, CVI >3.0 mm	—	1(0.26)	—	1(0.09)	9(1.90)	—	2(2.00)
<i>Euchaeta media</i>	1(0.57)	—	—	—	5(1.80)	—	—
<i>Scolecithrix danae</i>	2(2.30)	1(0.89)	—	—	—	—	—
<i>Scottocalanus</i> spp. CV, CVI	—	—	—	—	1(2.80)	—	2(4.50)
<i>Pleuromamma xiphias</i>	2(0.14)	6(0.33)	4(0.03)	5(0.05)	29(1.30)	5(0.20)	1(0.19)
<i>P. xiphias</i> CV	2(0.20)	—	—	—	1(0.06)	—	—
<i>P. abdominalis</i>	6(1.60)	7(1.50)	2(0.11)	3(0.25)	23(4.00)	1(0.32)	1(0.93)
<i>P. abdominalis</i> C	—	1(0.02)	—	1(0.14)	3(0.05)	—	—
<i>P. gracilis</i>	10(0.35)	4(0.14)	3(0.04)	3(0.07)	51(1.16)	1(0.08)	—
<i>Centropages</i> spp.	—	—	—	—	2(1.40)	—	—
<i>Lucicutia</i> spp.	4(0.49)	5(0.48)	5(0.48)	1(0.15)	18(1.40)	—	2(0.17)
<i>Heterorhabdus papilliger</i>	1(0.11)	1(0.09)	—	—	—	—	1(0.47)
<i>Candacia longimana</i>	—	1(0.30)	1(0.14)	—	5(1.20)	1(0.83)	—
<i>Candacia</i> spp. CV, CVI	—	1(0.21)	3(0.11)	2(0.11)	1(0.17)	—	—
<i>Paracandacia</i> spp. CV, CVI	2(0.15)	2(0.11)	1(0.06)	2(0.06)	20(0.96)	1(0.11)	—
<i>Acartia</i> spp.	1(0.24)	1(0.19)	1(0.15)	—	2(0.31)	1(0.90)	—
Unident. calanoid	8	4	8	3	38	—	3
<i>Oithona</i> spp.	—	—	1(0.04)	—	1(0.07)	—	—
<i>Oncaea</i> spp. >0.6 mm	32(5.39)	35(4.63)	46(2.89)	24(2.38)	121(13.20)	9(3.39)	2(0.17)
<i>Corycaeus</i> spp.	40(1.25)	16(0.39)	23(0.69)	6(0.28)	34(0.69)	—	2(0.34)
Other cyclopoids	1(0.61)	2(0.95)	1(0.04)	—	2(0.78)	—	—
<i>Euphausia</i> spp.	7(0.10)	5(0.06)	4(0.44)	—	13(0.12)	—	—
<i>Stylocheiron</i> spp.	2(0.69)	1(0.27)	—	—	4(0.09)	—	—
<i>Thysanopoda aequalis</i>	—	—	—	—	1(0.22)	—	1(20.80)
Euphausiid larva	2(0.42)	—	11(1.50)	3(0.66)	6(0.81)	—	—
Ostracod <1.0 mm	5(0.91)	4(0.57)	10(0.72)	3(0.34)	2(0.24)	4(1.70)	1(0.22)
Ostracod 1.0-1.4 mm	5(0.33)	2(0.10)	3(0.06)	1(0.03)	6(0.25)	1(0.12)	—
Ostracod 1.5-1.9 mm	2(0.20)	3(0.24)	7(0.22)	6(0.31)	4(0.26)	—	—
Amphipod 1.0-1.9 mm	—	1(0.14)	1(0.09)	1(0.15)	—	—	—
Amphipod 2.0-2.9 mm	—	2(0.95)	3(1.07)	—	—	—	—
Amphipod ≥3.0 mm	—	1(2.0)	—	—	1(1.70)	—	—
Caridean larva	1(0.18)	2(0.29)	—	1(0.75)	16(1.90)	—	—
Penaeidean larva	—	—	1(0.67)	—	—	1(4.00)	—
Zoea	—	—	1(11.1)	—	—	—	1(×)
Megalopa	3(10.50)	—	1(0.67)	—	1(2.30)	—	—
Chaetognath	—	—	2(0.02)	—	2(0.04)	—	—
Larvacean	2(1.30)	1(0.52)	—	—	—	—	—
Gastropod larva	4(0.13)	3(0.08)	11(1.70)	1(0.25)	3(0.06)	—	—
Pelecypod larva	3(2.30)	—	14(20.30)	6(13.70)	2(0.98)	—	—
Other prey: <i>D. schmidti</i> —70 m: 31-35 mm—1 <i>Eucalanus</i> sp. (1.60), 2 isopods (×)							
36-40 mm—1 <i>Neocalanus</i> CV (0.11), 1 Unident. Harpactacoid (×), 1 <i>Thysanopoda</i> sp. (7.90), 2 pteropods >1.0 mm (×)							
90 m: 27-35 mm—1 <i>Scolecithrix bradyi</i> (0.09), 1 <i>Calocalanus</i> sp. (×), 2 heteropods (0.95), 1 Penaeidean juvenile/adult (1.10), 1 polychaete (0.17), 1 fish larva (0.24)							
36-41 mm—1 <i>Ischnocalanus</i> sp. (×), 1 amphipod <1.0 mm (×), 1 ostracod >3.0 mm (1.10)							
<i>D. perspicillatus</i> —3 <i>Euchaeta rimana</i> (×), 1 <i>Euchaeta</i> sp. (0.63), 1 <i>Scolecithricella</i> sp. <1.0 mm (0.13), 1 <i>Nematoscelis</i> sp. (2.70), 1 Caridean juvenile/adult (0.84), 1 polychaete larva (×), 1 insect (×)							
<i>D. trachops</i> —1 Siphonophore (11.90)							

numbers of prey per fish rather than from any obvious differences in diet composition or relative preference.

### *Diaphus perspicillatus* (Table 10)

The number of prey per fish for *D. perspicillatus* was the highest of any species included and, possi-

bly because of this, so was the diversity of prey. Almost a third of the prey were microzooplankton (Table 2)—the great majority of these, *Oncaea* spp. The ASV for *Oncaea*, if corrected, is still high, as were the ASV's for about half the macrozooplankton prey types. The most frequent macrozooplankton were small copepods: *P. gracilis*, *Lucicutia*, *Paracandacia*; but several medium to

large prey: *Pleuromamma xiphias*, *P. abdominalis*, and large aetideids, were eaten frequently. Several small to medium copepods, the most frequent of which was *Corycaeus*, had intermediate ASV's (0.41-0.70 m<sup>3</sup>). Very few prey had low ASV's; half of these were ostracods and euphausiids.

### *Diaphus fragilis* (Table 10)

Few *D. fragilis* were available, and number of prey items was low. The data are most similar to those for *D. schmidti*. Microzooplankton accounted for about one-half the diet. The corrected ASV for *Oncaea* spp., the dominant microzooplankton, and those of most macrozooplankton were low. Only two prey types—each taken only once—had ASV's over 0.40 m<sup>3</sup>.

### *Diaphus trachops* (Table 10)

Data for *D. trachops* are few, but indicate that its diet is quite different from those of the other

*Diaphus* spp. in that few microzooplankton were eaten. Most prey items were medium to large forms and had high ASV's.

### *Melamphaes danae* (Table 11)

Microzooplankton made up minor fractions of the diet of *M. danae*; most were either small ostracods or gastropods. Among the other prey only chaetognaths and euphausiid larvae were consistently important. At 70 and 90 m, 22 and 26% of the prey had high ASV's; most other types had low values (Table 2). At 110 m, the great majority of prey types and items had high ASV's. For most prey types, the ASV's at different depths were either consistently high (euphausiid larvae, *Neocalanus*, amphipods) or low (ostracods), but the value for chaetognaths at 110 m was much higher than shallower.

### *Bregmaceros japonicus* (Table 11)

*Bregmaceros japonicus* ate few microzooplankton; small macrozooplankton were also taken infrequently and usually with low ASV. Most prey were medium to large and, except for chaetognaths and *Euphausia* spp., ASV's were moderate to high.

TABLE 11.—Stomach contents of *Melamphaes danae* and *Bregmaceros japonicus*. Format as in Table 4.

Species Depth	<i>M. danae</i>			<i>B. japonicus</i>
	70 m	90 m	110 m	70 m
Standard length, mm	17-22	19-22	19-22	38-51
No. examined	26	15	10	23
No. with intact prey	18	10	8	18
No. of intact prey	54	32	34	41
Prey type	No. (Apparent search volume, m <sup>3</sup> )			
<i>Neocalanus</i> spp.	3(3.60)	—	1(0.96)	—
<i>Calanus tenuicornis</i>	—	—	1(0.05)	—
<i>Nannocalanus minor</i>	2(0.11)	—	3(9.60)	1(0.06)
<i>Undinula darwini</i>	1(0.46)	—	1(8.90)	—
<i>Clausocalanus</i> spp.	—	—	1(0.05)	—
Aetideidae C 2.0-3.0 mm	—	1(0.10)	—	—
Aetideidae CV, CVI > 3.0 mm	1(0.20)	—	1(0.23)	—
<i>Euchaeta rimana</i>	3(∞)	—	2(∞)	1(∞)
<i>Scolecithricella</i> spp. < 1.0 mm	—	1(0.31)	—	—
<i>Pleuromamma xiphias</i>	—	—	—	12(0.52)
<i>P. xiphias</i> CV	—	—	—	2(0.12)
<i>P. abdominalis</i>	—	—	—	5(0.82)
<i>P. gracilis</i>	—	—	—	1(0.02)
<i>Heterorhabdus papilliger</i>	—	—	—	1(0.07)
<i>Candacia longimana</i>	—	—	—	2(0.46)
<i>Paracandacia</i> spp.	1(0.04)	—	1(0.29)	—
Unident. calanoid	—	1	—	—
<i>Oncaea</i> spp. > 0.6 mm	—	1(0.19)	—	—
<i>Oncaea</i> spp. ≤ 0.6 mm	—	—	—	1(1.38)
<i>Corycaeus</i> spp.	4(0.07)	5(0.45)	2(0.18)	—
<i>Euphausia</i> spp.	1(0.01)	—	1(0.24)	2(0.02)
Euphausiid larva	4(0.51)	4(1.67)	6(6.95)	4(0.51)
Ostracod < 1.0 mm	4(0.44)	3(0.65)	1(1.10)	—
Ostracod 1.0-1.4 mm	2(0.08)	5(0.30)	—	—
Ostracod 1.5-1.9 mm	2(0.12)	2(0.19)	—	—
Amphipod 1.0-1.9 mm	5(0.57)	—	—	—
Amphipod 2.0-2.9 mm	5(1.85)	—	2(2.70)	—
Caridean larva	1(0.11)	—	2(3.20)	4(0.44)
Penaeidean larva	1(1.80)	—	—	—
Mysid	—	—	1(17.90)	—
Chaetognath	6(0.11)	6(0.18)	7(0.81)	5(0.09)
Heteropod	—	1(1.43)	—	—
Gastropod larva	8(0.16)	2(0.95)	1(0.72)	—

## DISCUSSION

The fishes considered here clearly showed preference in a broad sense, i.e., some abundant zooplankton were rarely or never taken, and the ASV's of types regularly eaten were variable. Though there were exceptions, these fishes generally grazed on relatively large, visible crustaceans. Other taxa were rarely taken and then usually with low ASV's. Most other taxa in the plankton were either translucent forms, e.g., chaetognaths and tunicates, or quite small, e.g., gastropod veligers. Among the crustacean microzooplankton, the densely pigmented and relatively opaque *Oncaea* spp. were the only types that were taken regularly and had high ASV's. Some apparently less visible forms such as *Clausocalanus* and small *Scolecithricella* spp. were abundant in the plankton samples (in spite of mesh escapement), but rarely eaten, and the undoubtedly more numerous smaller types which mostly passed through the plankton net mesh were absent from almost all the fishes' diets. Among the crustacean macrozooplankton, several translucent or weakly

pigmented types, e.g., *Calanus tenuicornis* and *Neocalanus* and *Pleuromamma* spp. copepodites, were abundant but mostly ignored by the fishes.

Difference between species' diets were often correlated with differences in one or more of the morphological features examined (Figures 1-4). The

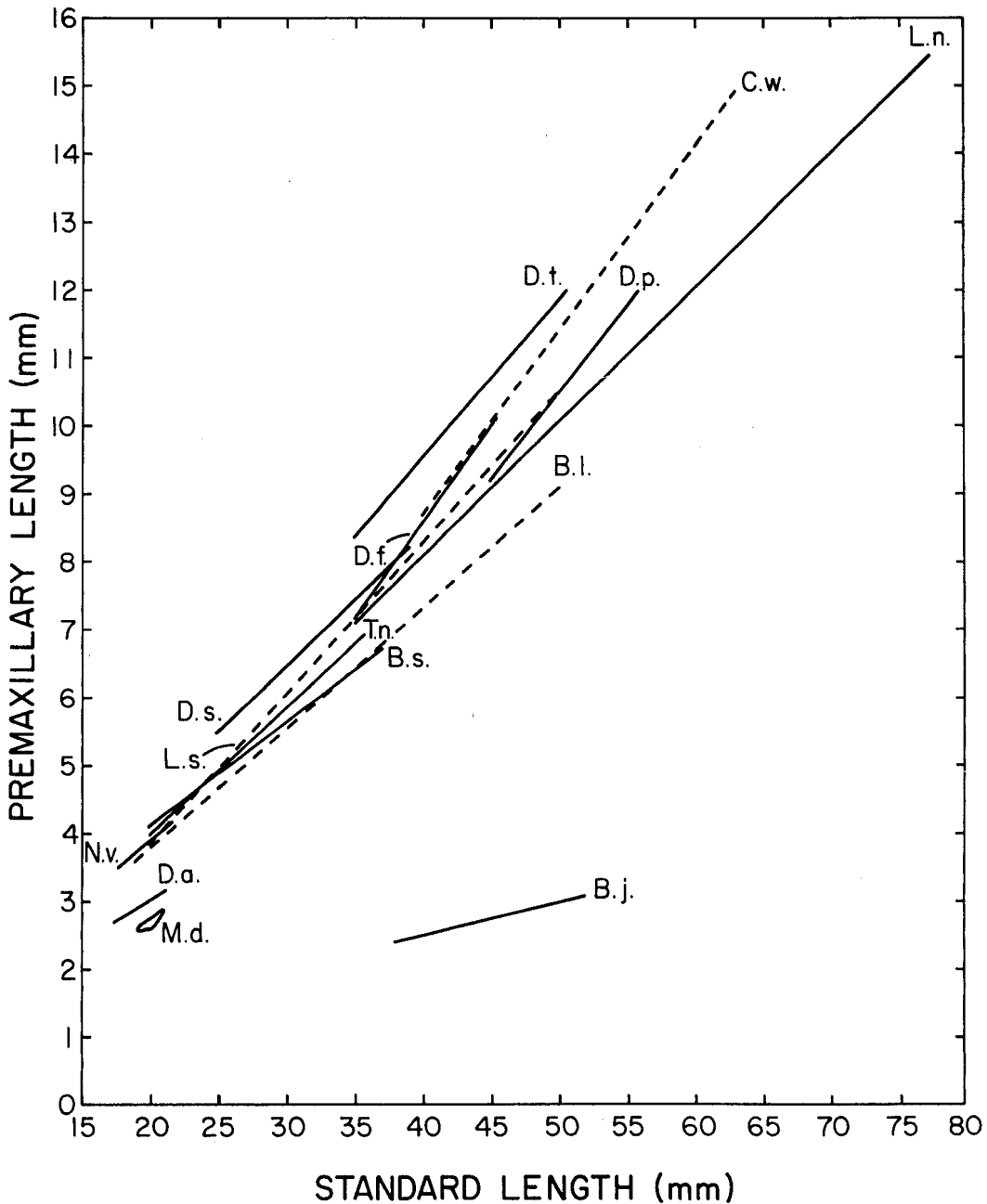


FIGURE 1.—Relationships between standard length and premaxillary length for 14 species of mesopelagic fishes designated by initials of genus and species names. Lines for *Lampanyctus nobilis*, *Triphoturus nigrescens*, *Notolychnus valdiviae*, *Benthosema suborbitale*, *Diogenichthys atlanticus*, *Diaphus schmidti*, *D. perspicillatus*, *D. fragilis*, *D. trachops*, and *Bregmaceros japonicus* and (dashed lines) for *Lampanyctus steinbecki*, *Ceratoscopelus warmingi*, and *Bolinichthys longipes* are drawn from equations determined by least squares regression on measurements from five or more specimens of each species over the size ranges plotted; coefficients of determination ( $r^2$ ) exceeded 0.80 for all. *Melamphaes danae* ( $r^2 = 0.48$ ) is represented by the area enclosed by points from five specimens.

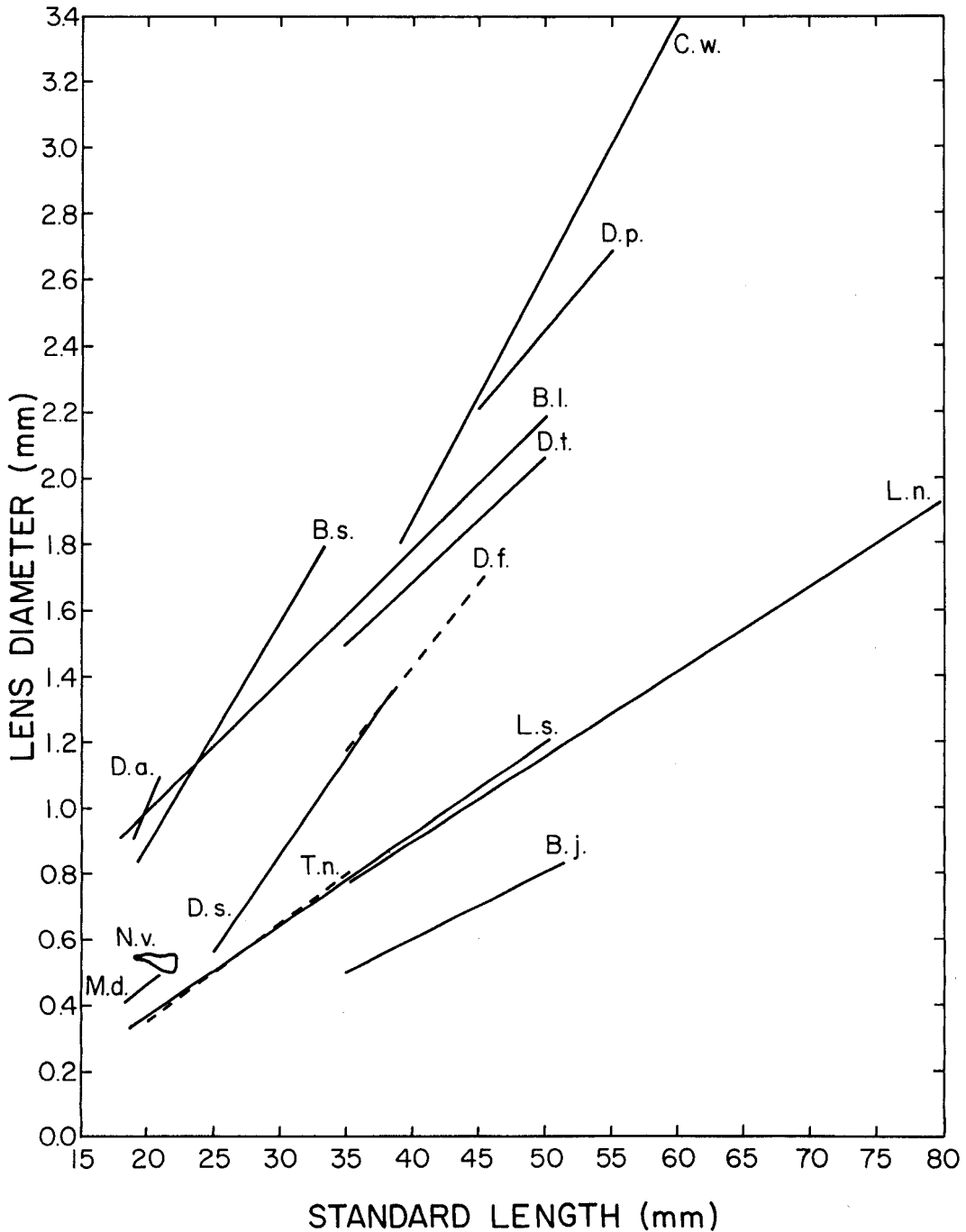


FIGURE 2.—Relationships between standard length and lens diameter for 14 species of mesopelagic fishes designated by initials of genus and species names. Lines for *Lampanyctus steinbecki*, *L. nobilis*, *Ceratoscopelus warmingi*, *Benthoosema suborbitale*, *Diogenichthys atlanticus*, *Bolinichthys longipes*, *Diaphus schmidti*, *D. perspicillatus*, *D. trachops*, *Melamphaes danae*, and *Bregmaceros japonicus* and dashed lines for *Triphoturus nigrescens* and *D. fragilis* are drawn from equations determined by least squares regression on measurements from five or more specimens of each species over the size ranges plotted; coefficients of determination ( $r^2$ ) exceeded 0.80 for all except *Diogenichthys atlanticus* ( $r^2 = 0.62$ ). *Notolychnus valdiviae* ( $r^2 = 0.23$ ) is represented by the area enclosed by points from five specimens.



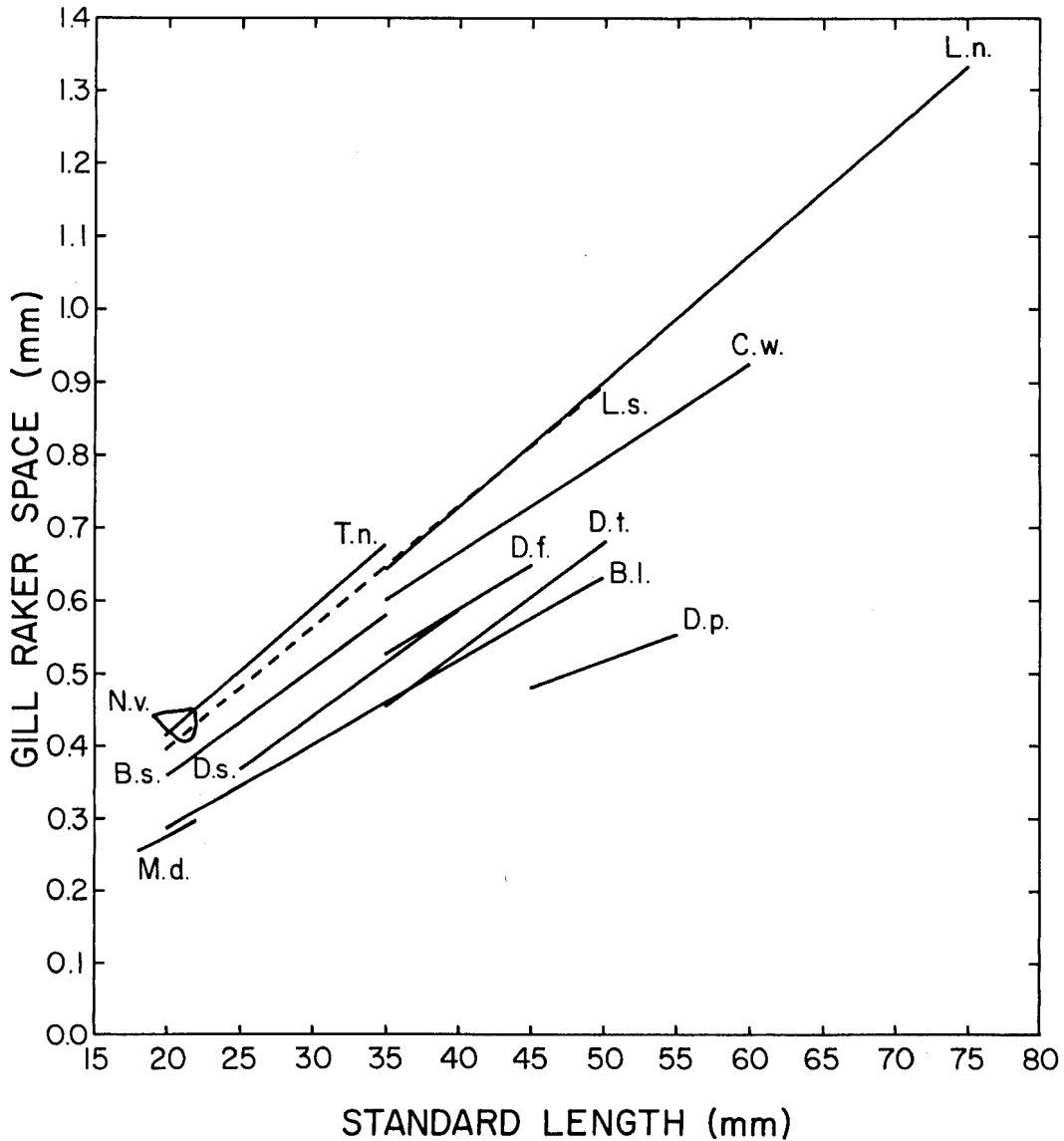


FIGURE 3.—Relationships between standard length and average space between gill rakers on the lower branch of the first gill arch for 12 species of mesopelagic fishes designated by initials of genus and species names. Lines for *Lampanyctus nobilis*, *Triphoturus nigrescens*, *Ceratoscopelus warmingi*, *Bentosema suborbitale*, *Bolinichthys longipes*, *Diaphus schmidti*, *D. perspicillatus*, *D. fragilis*, *D. trachops*, and *Melamphaes danae* and dashed line for *Lampanyctus steinbecki* are drawn from equations determined by least squares regression on measurements from five or more specimens of each species over the size ranges plotted; coefficients of determination ( $r^2$ ) exceeded 0.80 for all except *M. danae* ( $r^2 = 0.78$ ). The equation for *Diogenichthys atlanticus* ( $r^2 = 0.60$ ) was almost identical with that for *M. danae* and was omitted for clarity. *Notolychnus valdiviae* ( $r^2 = 0.04$ ) is represented by the area enclosed by points from five specimens.

most similar species were *Lampanyctus steinbecki*, *L. nobilis*, *T. nigrescens*, and *Notolychnus valdiviae*. All ate relatively large and opaque or pigmented prey. Both within and between species, the sizes of the most frequent and most preferred prey were roughly correlated with standard length, i.e.,

the large *L. nobilis* favored euphausiids and large copepods, while *N. valdiviae* and the small *L. steinbecki* and *T. nigrescens* preferred some types as small as *Oncaea*. All four species had relatively small eyes and relatively large gill raker gaps, and three had relatively low gill raker "areas." The gill

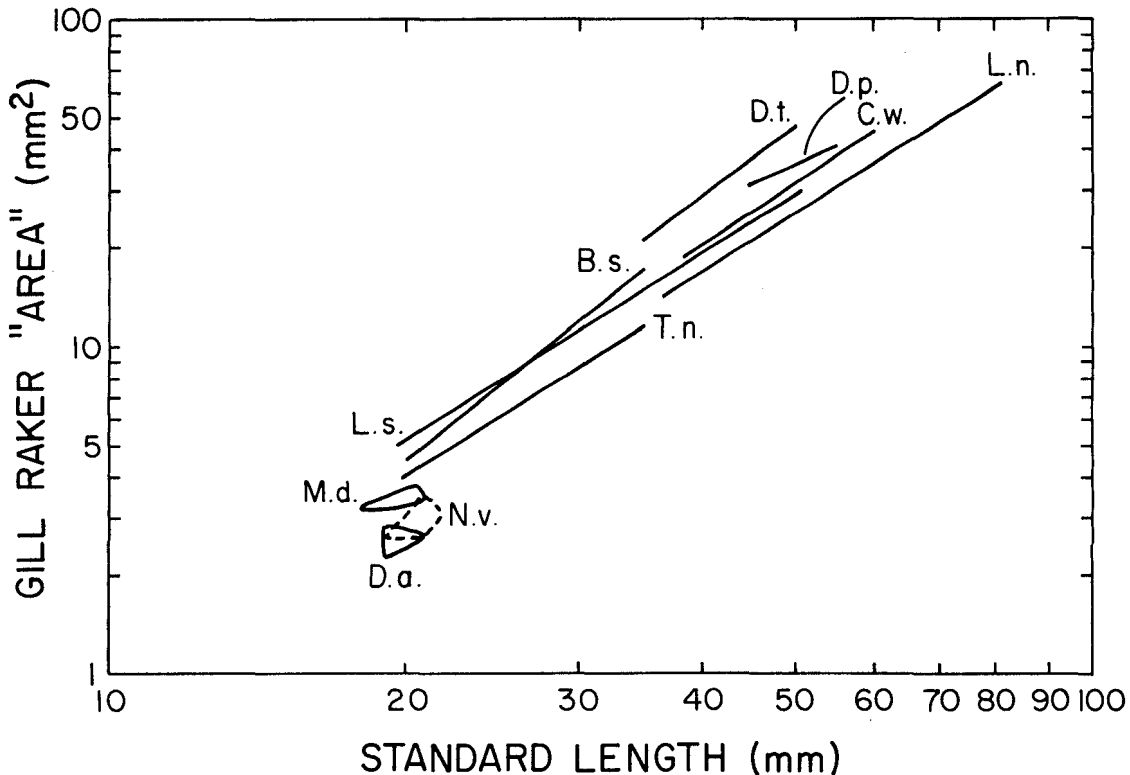


FIGURE 4.—Relationships (on logarithmic scales) between standard length and gill raker "area" (see text) for 10 species of mesopelagic fishes designated by initials of genus and species names. Lines for *Lampanyctus steinbecki*, *L. nobilis*, *Triphoturus nigrescens*, *Ceratoscopelus warmingi*, *Benthoosema suborbitale*, *Diaphus perspicillatus*, and *D. trachops* are drawn from equations determined by least squares linear regression on the logarithms of the data from five or more specimens of each species over the size ranges plotted; coefficients of determination ( $r^2$ ) exceeded 0.89 for all shown and also for *Bolinichthys longipes*, *D. schmidti*, and *D. fragilis* whose relationships were so similar to those of one or more species illustrated that they were omitted for clarity. *Notolychnus valdiviae* ( $r^2 = 0.26$ , dashed lines) and *Diogenichthys atlanticus* ( $r^2 = 0.09$ ) and *Melamphaes danae* ( $r^2 = 0.23$ ) are represented by the areas enclosed by points from five specimens each.

rakers of all four were thin, cylindrical in cross section, and covered with short rasplike teeth; while those of the other species were flattened usually with sawlike teeth on the leading edge. Thus these species seem best adapted for detecting the more visible prey and for retaining only relatively large items.

*Ceratoscopelus warmingi* and *D. perspicillatus* had the largest lenses of any species and sizes considered. For both species the ASV's of many types of prey were high, indicating that they are capable of searching greater volumes than species with smaller lenses. *Ceratoscopelus warmingi*, however, preferred relatively large prey while *D. perspicillatus* showed high ASV's for small as well as large types. Consonant with these differences in diet, *C. warmingi* had a relatively larger gape

and less closely spaced gill rakers than did *D. perspicillatus*.

*Diogenichthys atlanticus*, *Benthoosema suborbitale*, *Bolinichthys longipes*, and *Diaphus trachops* also had relatively large lenses; if *Diogenichthys atlanticus* or *Benthoosema suborbitale* grew as large as *C. warmingi* or *Diaphus perspicillatus*, their lenses would be larger. The first three species' diets included high fractions of microzooplankton. *Diogenichthys atlanticus*, which had the largest relative lens size and smallest gape, had eaten the widest variety of microzooplankton including many forms probably less visible than the *Oncaea* spp., which dominated the microzooplankton eaten by *B. suborbitale* and *Bolinichthys longipes*. *Bolinichthys longipes*, which was the only species which ate the small

*Oncaea* spp. ( $\leq 0.6$  mm) frequently and had the lowest fractions of macrozooplankton, had much finer gill rakers and somewhat larger lenses than similar-sized *Benthosema suborbitale*, which took a wider variety of sizes. *Diaphus trachops*, in contrast to the other three, ate mostly large prey. ASV's of most of its prey were also much higher than those of the other species. Its gape was the largest of all species examined, consonant with large prey size, but its relatively finely spaced gill rakers and high raker area indicate it is equipped to retain small prey as well. *Diaphus trachops* was the only species caught only at 170 m where zooplankton densities and particularly microzooplankton were much lower. While the large lenses of the other three species seem related to increased ability to detect small prey, *D. trachops*' seem related to detection of relatively large, less dense prey from greater distances. Lower light levels in its depth range would also favor large lenses.

*Diaphus schmidti* and *D. fragilis* were similar to each other and intermediate to other myctophids in all four features. Diet of *D. schmidti* was generally similar to that of *D. perspicillatus*, i.e., very general, but it differed in that high ASV's were not associated with many types of small copepods preferred by *D. perspicillatus*. This is consonant with *D. perspicillatus*' much finer gill rakers and larger lenses. Although data are few, the diet of *D. fragilis* seems most similar to that of *D. schmidti*. *Diaphus fragilis* is uncommon near Hawaii but very abundant in more productive waters near the Equator (Hartmann and Clarke 1975). It is also larger than *D. schmidti*. Ebeling (1962) has suggested that "dwarf" species of melamphoids are adapted to the less productive central water masses. The above indicates that similarly the larger of two otherwise similar myctophids is less successful in the central water mass.

*Bregmaceros japonicus* was the most distinct morphologically of all species considered. It had no gill rakers and the smallest lenses and gape of all species. Though it ate chaetognaths fairly frequently, the ASV's indicated that it prefers large crustaceans. Apparently the small mouth of this species does not inhibit it from ingesting large prey, and in spite of its small lenses, it is able to detect and capture at least a fraction of the translucent chaetognaths encountered.

Diet of *M. danae* was quite distinct from that of the others. The most frequent and preferred items included large and small forms and taxa other

than crustaceans—many of which were rarely eaten by other fishes. Also, certain prey such as *Pleuromamma* and *Oncaea* spp., which appeared in diets of almost all other fishes, were absent or nearly so from that of *M. danae*. Not a great deal can be gleaned from its morphological features; in spite of its small mouth and lens, *M. danae* is obviously capable of ingesting fairly large items and detecting small or translucent prey, but there is no clear indication of why certain prey types were not eaten.

Among the myctophids, differences in lens size and gill raker space were most obviously and frequently correlated with differences in diet and preference. These indicate that ability to visually detect and to retain prey in the mouth are important factors affecting frequency and preference. The general lack of correlation of dietary features with differences in gill raker area indicates these fish are probably not simply filtering. Morphological relationships within the myctophids, however, do not seem to extend to the sole representatives of the other two families considered here. *Bregmaceros japonicus* and *M. danae* appear basically different; whether their morphological features are in any way related to diet must await data on other species of these families.

Aside from the correlations of lens size with diet and lack thereof for gill raker area, the preferences observed and absolute values of ASV's also indicate that these fishes feed in a particulate, visually oriented mode (O'Connell 1972) as opposed to filtering. That the fishes are selective precludes simple filtration unless it is assumed that the differences between diet and available prey are due entirely to differential escape capabilities of the prey, and the general absence of small or translucent prey from the diets implicates vision. In many cases, the ASV's, which are minimal estimates of the volume searched, seem too high to have resulted from filtering alone. Even assuming that the area filtered is as large as the square of the premaxillary and that the fish swam at 2.5 body lengths/s (Ware 1978) for 5 h, a 50 mm *D. trachops*, *C. warmingi*, *D. perspicillatus*, or *L. steinbecki* would search only 0.25-0.32 m<sup>3</sup> (depending on premaxillary length). Yet ASV's were as high as 1.0 m<sup>3</sup> for several prey of these species. To search 1.0 m<sup>3</sup> visually would require that the fish detect prey within only about 12 mm. Similarly, a 20 mm *Diogenichthys atlanticus* could at best filter only about 0.008 m<sup>3</sup>, while ASV's of at least five times this were associated with several of

its prey. Even the smaller and therefore slower *D. atlanticus* would have to detect prey only within about 19 mm to search 1.0 m<sup>3</sup> in the same time.

Comparison of my results with those of other studies is limited to generalizations due to different methodologies. In most other studies, prey items have been identified only to major taxa, bias due to differential digestion has not been considered, and diets have not been compared with appropriate estimates of available prey densities.

Legend and Rivaton (1969) gave diets of nine comparable species from the tropical Indian Ocean. As near Hawaii, crustaceans dominated the diets, and except for higher proportions of amphipods and lower proportions of ostracods, the diets of the myctophids were similar to those of congeners from Hawaii. *Ceratoscopelus townsendi* (which is probably really *C. warmingi*) had a wide variety of prey and with the two *Lampanyctus* spp. had the highest frequency of euphausiids. The diet of *Benthoosema simile*, the only species for which copepod genera were given, was quite similar to that of *B. suborbitale*. *Bregmaceros maclellandi*, unlike *B. japonicus* from Hawaii, had eaten no chaetognaths. Merrett and Roe's (1974) data on three myctophid species from the subtropical Atlantic also indicate that crustaceans were the most important prey. Diets of the individual species appear generally similar to those of the most closely related species considered from Hawaii.

Gorelova (1978) found that migratory crustaceans dominated the diets of both *C. warmingi* and *Bolinichthys longipes* in the western equatorial Pacific. The diet of small *C. warmingi* was dominated by copepods, and most items were <4 mm long, but specimens of sizes comparable to those examined in my study (40-90 mm total length) had eaten a wider variety of prey, over 50% of which (by weight) were >4 mm. The dominant euphausiids were the large *Thysanopoda* and *Nematobrachion* spp. The diet of all sizes of *B. longipes* was dominated by copepods, and the euphausiids eaten were mostly the smaller *Euphausia* and *Stylocheiron* spp. *Oncaea* spp. were much less important than near Hawaii. Among the large copepods, however, candaciids were the dominant type in both areas. Gorelova (1977) noted that *Lampanyctus* and *Triphoturus* (species not given) in the equatorial Pacific eat euphausiids almost exclusively.

Baird et al. (1975) showed that *Diaphus taaningi* in the Cariaco Trench, like two Hawaiian

*Diaphus* spp., ate a wide variety of prey, but in contrast to all other species considered here or elsewhere, the diet was heavily dominated by *Oikopleura*. Since *Oikopleura* is probably rendered unrecognizable in the stomach faster than most of the other prey types, its importance in the diet is probably even greater than Baird et al.'s data indicate. Its frequency in the plankton from the cod end of the trawl was much lower than in the diet; however, it was probably under-represented relative to larger forms in such a sample. Whether the dominance of *Oikopleura* reflects a real preference or simply very high densities at the depths where the fish were feeding cannot be determined.

Tyler and Percy (1975) investigated three species of myctophids from off Oregon. The diets of all three were heavily dominated by euphausiids, mostly *E. pacifica* which was the most abundant species in the area, and medium to large copepods, the most frequently identified of which were *Calanus* and *Metridia* spp. There was little indication of differences between fish species. Gjøsæter (1973) showed similar results for another high latitude myctophid, *Benthoosema glaciale*; in this case *Thysanoessa* spp. were the dominant euphausiids.

The results of most studies generally agree that, with the obvious exception of *D. taaningi*, vertically migrating fishes feed primarily upon relatively large, probably more visible crustacean zooplankton; however, the data for some species considered here and by Gorelova (1978) indicate that small juveniles graze the microzooplankton more heavily than sizes considered by most studies. In contrast to the neustonic myctophids, e.g., *Centrobranchus* and certain *Myctophum* spp., which feed primarily on shallow-living zooplankton (Gorelova 1977), the principal prey of the species considered here and by most other studies undertake substantial diel vertical migrations themselves (Brinton 1967; Roe 1972)—some almost as extensive as those of the fishes—and are not present in the epipelagic by day.

Though the diets of the 14 species considered here show some general similarities, differences in frequency of and preference for different prey types indicate that most species are at least somewhat specialized. The discussion of diet and morphology above points out unique features for most species. *Lampanyctus steinbecki*, *L. nobilis*, *Triphoturus nigrescens*, and *Notolychnus valdiviae* were the only species which were very simi-

lar to each other, but quite distinct from the others. Differences in size and depth distribution at night probably reduce diet overlap among these species. *Triphoturus nigrescens* and *L. nobilis* occur shallower than do *N. valdiviae* and *L. steinbecki*, and within each pair, one species is considerably larger than the other. Other multispecies studies in the tropical or subtropical open ocean also indicate some degree of specialization among cooccurring species.

In contrast, Tyler and Percy's (1975) results indicate that high latitude species have little or no separation or specialization in diet. Confirmation and further documentation of the apparent difference are certainly merited. If true, it could indicate that tropical species are less likely to be competing against each other for food or that species in the highly productive waters off Oregon are not food limited. The apparent difference in degree of dietary specialization also has obvious implications relevant to differences in diversity—both of the fish faunas and of their prey—between tropical and temperate oceanic communities.

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