

# DIEL FEEDING PATTERNS OF 16 SPECIES OF MESOPELAGIC FISHES FROM HAWAIIAN WATERS

THOMAS A. CLARKE<sup>1</sup>

## ABSTRACT

Diel patterns of stomach fullness, as percent of dry weight, were determined for 16 species of mesopelagic fishes. Nine species of myctophids and one melamphaid, all vertical migrators, appeared to feed solely or principally at night in the upper layers. These species encountered higher temperatures and prey concentrations at night. Four species of stomiatoid fishes appeared to feed during the day regardless of the extent of their migration or the absence thereof. Prey concentrations encountered by the stomiatoids during the daytime appeared to be higher than or similar to those encountered at night. One myctophid and one gonostomatid showed no diel pattern; diel changes in the environmental factors considered were relatively small in spite of the fact that both species undertook limited vertical migrations.

Crude estimates of instantaneous evacuation rate and daily ration were made from data for four species. These indicated that evacuation rate was increased at night in the upper layers and that daily rations of species which migrated into the upper layers were similar to values for shallow-living zooplanktivores, while rations of deeper living species were lower. Thus while the adaptive value of upward migration in the species which feed at night is obviously related to feeding activity, the upward ascent by the daytime feeders may allow processing of larger daily rations than if they remained at low temperature all day.

The extensive diel vertical migrations of certain mesopelagic fishes have been well documented in a variety of oceanographic situations. While a number of theories have been proposed to explain the adaptive value of the behavior—in both fishes and migrating invertebrates as well—data to support any of them are few. One of the most frequently proposed hypotheses (e.g., Marshall 1960) is that the organisms ascend at night to feed in the upper layers where food is presumably at higher concentrations and descend during the day to avoid predation while the upper layers are well lighted. Several studies of mesopelagic fishes (to be cited below) have considered the relationship between feeding chronology and vertical distribution in an effort to support at least one-half of the hypothesis, but the results have for the most part been rather equivocal. Apparent diel trends in stomach fullness or details thereof are often questionable owing to low numbers of specimens examined, insensitive methodology, or incomplete diel coverage. Furthermore, all such studies on mesopelagic fishes, with the exception of Merrett and Roe (1974), have been conducted in high

latitude or neritic situations and have dealt with only one or, at most, three species.

This study considered the feeding chronology of 16 species from 5 families of mesopelagic fishes from the north central Pacific Ocean. Vertical distribution and certain other aspects of the ecology of these fishes are covered in Clarke (1973, 1974) and Clarke and Wagner (1976); results from related investigations in the same study area are summarized in Maynard et al. (1975). Comparison of diel patterns of stomach fullness and diel changes in temperature and prey concentration allow consideration of adaptive value of the vertical migrations undertaken by most of these species. In four species, rough calculations of daily ration are possible using equations similar to those presented by Eggers (1977).

## MATERIALS AND METHODS

### Field Sampling

Specimens for this study were all collected with a 3-m Isaacs-Kidd midwater trawl ca. 20 km west of the island of Oahu, Hawaii (ca. lat. 21°20-30'N; long. 158°20-30'W) in waters 2,000-3,000 m deep. In order to reduce the concentration of zooplankton in the cod end of the net and thus

<sup>1</sup>University of Hawaii, Department of Oceanography and Hawaii Institute of Marine Biology, P.O. Box 1346, Kaneohe, HI 96744.

minimize bias due to fishes' feeding after capture, the net terminated in a 1-m diameter cone of ca. 3-mm ( $\frac{1}{8}$ -in) knitted nylon mesh instead of the "normal" plankton netting.

Specimens were taken in oblique tows which sampled vertically migrating species at nine different periods of the 24-h cycle. At night, cable was paid out in increments over a period of 1.5 h such that the trawl fished roughly equal amounts of time at all depths between the surface and ca. 350 m. The trawl was retrieved immediately afterwards for a total towing time of about 2 h. Four such tows were made between last light at dusk and first light at dawn. During the day, 1,200 m of wire were paid out initially. This placed the trawl at ca. 350-400 m. Subsequently, cable was paid out in increments such that the trawl fished between this depth and ca. 1,100-1,200 m over a period of 1.5 h and then retrieved for a total fishing time of ca. 2.5 h below 350-400 m. Three such tows were made during the day. At dusk, 1,500 m of cable were paid out initially, placing the trawl at ca. 500 m. Cable was then retrieved in increments such that the trawl fished between 500 m and the surface over 1.5 h. The trawl reached maximum depth just before sunset and was on deck shortly after last light. At dawn, the process was reversed, and the trawl shot before first light, and fished from the surface to ca. 500 m over 1.5 h such that it reached maximum depth ca. 1 h after sunrise. Ship speed was ca. 1 m/s (2 kn) for cable retrieval and ca. 2 m/s (4 kn) for all other phases.

In order to collect sufficient numbers of specimens for as many species as possible, three 24-h series of nine tows each (dusk, four at night, dawn, and three during the day) were made 27-30 August 1973. These dates were chosen to bracket new moon (August 28) and minimize avoidance of the trawl at night (Clarke 1973). One day tow of this series was fouled and could not be repeated until 13 September 1973. The total range of time fished by equivalent tows of each series (Table 1) overlapped—considerably so for the night series due to one night's fishing proceeding ahead of schedule. The overlap was effectively less than shown in Table 1 since most of the fishes analyzed were probably taken below 50 m (based on previously cited studies of vertical distribution) and not during the first 15 min or the last 5 min of each tow when the trawl was shallower than 50 m. Consequently, equivalent tows from each 24-h series were considered replicates and specimens were combined for data from each period. The nine

sampling periods will subsequently be designated as follows: SS for sunset and SR for sunrise; N1, N2, N3, N4 for the four night periods in chronological sequence; and D1, D2, D3 for the three daytime periods in sequence.

*Danaphos oculatus*, a nonmigrating species, was not taken in the shallow night tows described above. Nighttime data for this species were based on specimens from three night series of three tows each taken 30 August-1 September and 13-14 September 1973 (Table 1) using the same towing schedule described above for daytime (ca. 400-1,000 m). Thus only eight periods of the diel cycle were considered. The three nighttime periods for *D. oculatus* were designated dN1, dN2, and dN3.

In order to obtain more specimens of three species of stomiatoids, I utilized specimens taken 24-25 May 1974 in seven tows at the same location with the same net, and with the same procedure and timings as N1-4 and D1-3. The numbers of specimens used from this series will be noted in the results. All specimens of the other species came from 1973 collections.

The catch was immediately preserved in 4-5% formaldehyde in seawater. The specimens remained in this solution for up to 2 yr before processing, but since all specimens of a given species were processed within a period of 2-3 wk, any between-sample differences in weight loss due to leaching can be considered negligible.

### Laboratory Analyses

The ratio of the dry weight of the stomach contents to that of the fish as percent was used as an index of stomach fullness. Where sufficient specimens of a given species were available, 20 from each of the nine sampling periods were examined. If possible, the least damaged specimens (or perhaps more appropriately—equivalently damaged specimens) were selected from a narrow size range. For many species, however, it was necessary to use specimens damaged to various degrees and of all sizes between recently (but fully) metamorphosed juveniles and mature adults. In cases where a specimen was damaged beyond loss of scales or fin rays, i.e., where tissue was missing, I used the median dry weight of other specimens of the same standard length.

Each fish was briefly rinsed with tapwater and gently blotted; standard length was measured to the nearest millimeter. The stomach (anterior end of the esophagus to the pyloric valve) was removed

TABLE 1.—Towing times (Hawaiian Standard Time) for three 24-h series of oblique tows to sample vertically migrating mesopelagic fishes and three all night series for deep-living nonmigratory fishes. Times given for dusk (SS), dawn (SR), and shallow night (N1-4) are for the entire tow; those for day tows (D1-3) and deep night tows (dN1-3) are for the time the trawl fished below ca. 350-400 m.

Period	27-28 Aug.	28-29 Aug.	29-30 Aug.	Midpoint	Period	30-31 Aug.	31 Aug.-1 Sept.	13-14 Sept.	Midpoint
SS	1754-1956	1815-1955	1820-2023	1910	dN1	2040-2300	2005-2233	2000-2235	2130
N1	2045-2240	2001-2155	2040-2233	2120	dN2	2352-0215	2325-0154	2330-0155	0050
N2	2315-0110	2207-0005	2255-0045	2340	dN3	0308-0540	0250-0515	0255-0525	0415
N3	0120-0320	0015-0210	0113-0310	0150					
N4	0330-0520	0220-0420	0318-0515	0350					
SR	0535-0742	0515-0725	0533-0745	0630					
D1	0822-1047	0807-1034	0820-1045	0930					
D2	1143-1425	1125-1350	1135-1410	1300					
D3	1510-1740 <sup>1</sup>	1448-1710	1515-1740	1615					

<sup>1</sup>The D3 tow for 28 August was fouled; time given is for tow made on 13 September.

and its contents, if any, placed on a clean glass slide. The fish including the empty stomach was placed in a preweighed aluminum pan. After examination, the stomach contents were rinsed into a second preweighed pan using distilled water.

The stomach contents were examined only casually. A rough estimate of fullness was made and degree of digestion noted. Prosome length (PL) of copepods and total length (TL) of other prey were recorded from intact items. Intact prey items could usually be identified to genus, but no serious attempt was made to determine composition of the diet from these samples. The remarks below on types of prey include only the most frequently encountered items and are not meant to be taken as detailed analyses of diets.

Both fish and stomach contents were dried at 60°C for 24 h (somewhat longer for a few large fish) and allowed to cool under partial vacuum before weighing. The pans with stomach contents were weighed to the nearest 0.01 mg on a microbalance, and the content weight determined by subtraction. Both control pans and reweighing of several pans with dried stomach contents after a second period in the drying oven or desiccator indicated that the weighing and handling error was of the order of  $\pm 0.02$  mg. There was no indication that error was proportional to the amount of material in the pan. Pans with fish were weighed on a semimicro balance; the reading was recorded to 0.01 mg on small fish and to 0.1 mg on those over ca. 100 mg. Based on changes in weight of control pans and reweighing of fish after a second period of desiccation, the error was <1% of the fish weight.

While the weighing and handling error was such that estimates of stomach fullness were affected only to the fourth or possibly third decimal place, other errors or biases inherent in the material should be mentioned. As noted above, an unknown fraction of the material was lost due to leaching. Damage to the fish positively biased the

ratios since there was some loss of skin, scales, or fin rays in almost all specimens. Such errors were unrelated to the time of collection and were more likely to increase variability and thus to obscure rather than cause diel trends in the data. The intestinal contents, which were dried and weighed with the fish, may have varied with time and thus introduced a systematic error in fish weights. Based on visual examination, however, largest amounts of materials in the intestine were almost certainly <1% of the total fish weight, and, consequently, affected the stomach fullness index by <0.1%.

The 2-3 h durations of the tows were a possible source of bias and high variability. Bias in stomach fullness could result from evacuation of stomach contents between capture and death (Eggers 1977). It is likely that this was negligible since the fishes considered here were probably dead soon after capture by the net. The 2-3 h possible differences in capture time for fishes from the "same" period of the diel cycle almost certainly contributed to the variability in stomach fullness—particularly during periods when the latter was changing rapidly.

Stomach fullness could possibly be biased negatively by regurgitation after capture or positively by feeding in the net. (Either type of bias would tend to obscure rather than cause diel differences in stomach fullness.) Regurgitation apparently occurred infrequently in all species considered except *Lampanyctus nobilis*. Except for the latter (see below), specimens with partially digested food remains in the mouth or everted stomachs were not used. Hopkins and Baird (1975) showed that feeding in the net is an unimportant source of error even when a fine-mesh cod end is used, and there was little indication of net feeding in the present study. Zooplankton in good condition, usually crustaceans with appendages erect and extended, were infrequently found in the mouth. These were assumed to have lodged there during

capture and were not counted, but the fish and any other contents were used. Items part way down the esophagus with appendages flattened against the body or the body folded were assumed to have been eaten before capture and were included. I considered such "esophagus" items unlikely to have been eaten after capture because concurrent analyses of diet (Clarke in prep.) on the same species collected by the same net indicate that there is no difference in species composition between such items and items clearly in the stomach and partially digested.

Stomach fullness values for a single species and single time period were rarely distributed normally. Usually the values were skewed to the left, but variably so—the mean being sometimes close to the median and sometimes close to the 75th percentile. Consequently, the entire set of stomach fullness values for each species were ranked and tested for between-period differences by the Kruskal-Wallis nonparametric equivalent of analysis of variance (*H*-test). The test is mainly sensitive to differences in position (Tate and Clelland 1957), and significance implies differences among the medians for the separate time periods but does not single out which sets of data are different. Each adjacent (in time) pair of data sets was tested for differences in the median with the Mann-Whitney or Rank sum test (Tate and Clelland 1957); however, because of multiple testing on the same data, the significance levels from this cannot be taken rigorously.

Neither test used is sensitive to differences in variability, and no separate testing was done. Some idea of differences in frequency distribution can be gleaned from relative position of the mean and median. Other gross differences, e.g., bimodality vs. unimodality, will be pointed out in the results. Likewise, I did not test for possible correlations between sex or size of the fish and stomach fullness. The data from each period were, however, ranked and compared (by inspection) with sex and rank in length; no obvious correlations were found.

## RESULTS

A total of 15 vertically migrating species (10 myctophids, 4 stomiatoids, and 1 melamphaid) and 1 nonmigrating stomiatoid were investigated. These included species for which 20 individuals were collected at most of the nine periods sampled plus a few, less frequently taken species selected to

give broader coverage with respect to systematic position or vertical distribution pattern. In addition to graphical presentations (cited specifically below), ancillary data for all species are summarized in Table 2. In the subsequent presentation, stomachs were considered "empty" if stomach fullness was <0.1%. This included both visually empty stomachs and those with only a trace of digested remains in the pyloric end of the stomach. Types of prey organisms, state of digestion, and other aspects not obvious from the figures or Table 2 are considered in individual species accounts below.

Comments on vertical distribution of prey items are based on preliminary analyses of opening-closing plankton tows taken in the study area and their general agreement with data in the literature for the same or closely related species in other central water mass localities. The plankton tows—16 taken in September 1973 and 20 in November 1974—covered the depth ranges of the fishes considered both day and night. Euphausiids from all samples have been counted and identified, and copepods either counted (shallow night samples) or sufficiently examined to at least roughly determine the depth ranges of the important prey species. The apparent depth ranges agree generally with those given by Brinton (1967) and Roe (1972). These two important types of prey can, with a high degree of certainty, be classified as shallow nonmigrators (above 200-300 m both day and night), vertical migrators (above 200-300 m at night and below this depth by day), and deep living (below 300 m day and night). Similar statements cannot be made for ostracods, the other important crustacean group, nor for other taxa of zooplankton.

### Myctophidae

#### *Benthoosema suborbitale* (Figure 1)

The *H*-test indicated highly significant ( $P < 0.005$ ) differences in stomach fullness over the diel cycle. The data from SS and N1 were characterized by low averages, narrow percentile limits, and high proportions of empty stomachs. Subsequently stomach fullness generally increased until SR and decreased throughout the day. The most frequent prey items were copepods of the genera *Pleuromamma*, *Candacia*, and *Paracandacia*. *Euphausia* spp. and occasionally small decapods contributed significantly to the weight of

TABLE 2.—Summary of data for each of the 16 species of fishes examined from each of the periods of the diel cycle. In each species/time block, the first line gives the number of specimens examined and the number with stomach fullness <0.1% of fish dry weight in parentheses; the second line, the size range of the specimens in millimeters standard length; and the third, the range of stomach fullness values in percentage of fish dry weight. All values of stomach fullness are rounded to the nearest 0.1%.

Species	SS	N1	N2	N3	N4	SR	D1	D2	D3
<i>Benthosema suborbitale</i>	20(12)	20( 8)	20( 3)	20( 1)	20( 5)	19( 2)	20( 2)	20( 3)	20( 2)
	24-30	15-32	18-31	19-29	22-31	17-27	16-30	18-32	17-30
	0-0.9	0-2.8	0-6.0	0.1-2.7	0.1-2.8	0-2.6	0.1-3.6	0-3.8	0-2.2
<i>Bolinichthys longipes</i>	20( 7)	20( 2)	20( 2)	20( 0)	20( 1)	20( 0)	20( 0)	20( 0)	20( 0)
	24-46	21-46	20-51	17-49	18-43	21-32	16-50	17-46	19-48
	0-1.4	0.1-2.0	0.1-2.5	0.2-1.5	0.1-2.4	0.3-4.6	0.2-4.8	0.1-1.5	0.1-1.1
<i>Ceratoscopelus warmingi</i>	20( 9)	20( 1)	20( 2)	20( 2)	20( 0)	5( 0)	20( 1)	20( 0)	20( 2)
	22-53	18-45	24-45	23-50	25-47	18-23	19-48	19-59	18-52
	0-2.8	0.1-9.8	0-8.1	0-5.0	0.1-7.6	0.9-4.9	0.1-2.4	0.1-4.5	0.1-7.4
<i>Diaphus schmidti</i>	20( 2)	20( 2)	20( 0)	20( 0)	20( 0)	20( 0)	20( 0)	20( 0)	20( 2)
	25-39	20-41	19-41	19-40	17-38	20-38	14-37	15-38	19-38
	0.1-2.3	0.1-1.7	0.3-1.4	0.2-6.0	0.3-3.8	0.1-2.2	0.2-2.3	0.2-2.7	0-2.3
<i>Hypogomphus proximum</i>	20(14)	20( 0)	20( 2)	20( 1)	20( 0)	20(14)	20(16)	20(13)	18(11)
	26-33	19-32	18-38	18-42	18-37	19-43	19-42	19-40	18-46
	0-1.0	0.2-6.7	0-5.8	0.1-3.6	0.2-7.0	0-0.5	0-0.4	0-1.3	0-1.3
<i>Lampanyctus niger</i>	20(14)	20(11)	20( 7)	20( 8)	20( 4)	0	20(10)	20(11)	20(10)
	65-84	65-85	63-83	64-85	51-85	—	52-87	68-85	64-85
	0-1.9	0-1.0	0-1.7	0-1.3	0-1.5	—	0-4.0	0-3.7	0-3.9
<i>Lampanyctus nobilis</i>	9( 4)	20( 3)	20( 2)	20( 4)	20( 1)	0	14( 2)	14( 4)	18( 6)
	24-84	29-81	27-88	24-80	26-98	—	25-94	25-90	25-94
	0-6.2	0-3.3	0-7.5	0-8.5	0-5.5	—	0-3.6	0-10.3	0-2.0
<i>Lampanyctus steinbecki</i>	20( 2)	20( 4)	20( 3)	20( 1)	20( 0)	20( 2)	20( 0)	20( 4)	20( 2)
	25-39	22-48	22-41	21-39	22-42	18-36	22-42	23-44	27-42
	0-2.7	0-3.7	0-4.4	0-3.5	0.2-4.0	0.1-9.8	0.1-4.5	0-2.1	0-5.5
<i>Notolychnus valdiviae</i>	20( 0)	20( 1)	20( 3)	20( 0)	20( 0)	20( 0)	20( 2)	20( 1)	20( 0)
	19-24	20-23	19-23	19-23	18-23	19-24	20-23	17-22	19-24
	0.2-3.4	0.1-2.9	0-3.0	0.3-4.7	0.3-3.6	0.3-3.5	0-1.7	0-2.5	0.1-3.5
<i>Triphoturus nigrescens</i>	20( 3)	20( 6)	16( 3)	15( 3)	19( 0)	20( 0)	20( 4)	20( 3)	20( 4)
	18-34	17-31	15-34	15-35	16-33	15-36	16-34	18-33	18-34
	0-5.9	0-3.6	0-9.0	0-6.6	1.0-14.3	0.7-9.9	0-16.0	0-6.7	0-4.5
<i>Melamphaes danae</i>	3( 0)	12( 3)	14( 2)	12( 0)	9( 0)	0	3( 0)	2( 0)	14( 1)
	16-20	16-21	16-21	16-21	16-22	—	19-21	16	16-22
	0.4-0.6	0-3.2	0-3.0	0.4-3.5	0.5-4.0	—	0.3-1.5	1.1-1.5	0-1.6
<i>Gonostoma atlanticum</i>	4( 0)	20( 2)	20( 1)	20( 2)	17( 4)	7( 2)	9( 0)	20( 1)	8( 0)
	48-58	36-62	32-65	31-64	26-62	48-65	22-64	50-68	48-57
	1.1-3.3	0-6.3	0-4.5	0.1-4.3	0-3.5	0.1-1.6	0.3-2.4	0.1-4.6	0.4-11.2
<i>Gonostoma elongatum</i>	20( 2)	20( 2)	20( 1)	20( 9)	20( 3)	8( 0)	20( 4)	14( 3)	10( 1)
	26-112	31-126	30-135	30-132	32-79	30-150	24-125	30-149	29-87
	0.1-2.6	0-13.1	0.1-5.9	0-5.0	0-2.0	0.2-8.0	0-16.6	0-5.2	0.1-7.3
<i>Vinlguerria nimbaria</i>	20( 0)	20( 0)	20( 3)	20( 3)	20(13)	20(15)	20( 9)	20( 1)	20( 2)
	21-34	24-35	24-36	25-32	23-34	24-33	20-35	20-33	20-30
	0.7-8.9	0.2-8.9	0-7.9	0-3.1	0-0.6	0-1.8	0-12.7	0.1-6.3	0.1-14.2
<i>Danaphos oculatus</i>	15( 0)	9( 0)	11( 0)	11( 0)	—	15( 2)	20( 2)	4( 0)	10( 0)
	27-40	27-39	29-40	29-36	—	28-42	31-40	28-38	27-39
	0.5-2.5	0.6-2.3	0.3-1.0	0.3-1.8	—	0-0.8	0-1.0	0.6-1.7	0.2-2.3
<i>Valenciennellus tripunctulatus</i>	6( 0)	20( 0)	12( 0)	9( 2)	10( 1)	3( 2)	7( 2)	5( 0)	10( 0)
	25-30	22-32	23-32	21-32	21-32	21-31	25-30	21-30	22-33
	1.2-4.5	1.2-3.6	0.9-2.2	0-2.2	0.1-1.0	0-0.2	0-0.6	0.9-2.5	1.0-3.5

food. The food from specimens taken by day samples was generally well digested; except for the thoracic spots or "buttons" from *Pleuromamma*, prey was rarely recognizable beyond general category.

#### *Bolinichthys longipes* (Figure 1)

Analyses of *B. longipes* were complicated by the frequent presence in the stomachs of digenetic trematodes. These were 1-10 mm long (most were 1-5 mm) and occurred in 41% of the stomachs examined. They were mingled with the food and

appeared to have been fixed while wrapping around or holding to items. As a probable consequence, whole prey were rarely found in *B. longipes*' stomachs. The parasites were, however, easily separated from the food; they were not included with either the fish or stomach content weight.

The number of trematodes was roughly a function of size of the fish. Fish < ca. 30 mm SL usually had 0-2 individuals while several > 40 mm contained 10-20. Since there was little between-period difference in size composition of the fish examined, there was no apparent correlation of trematode number with time of day. Also there

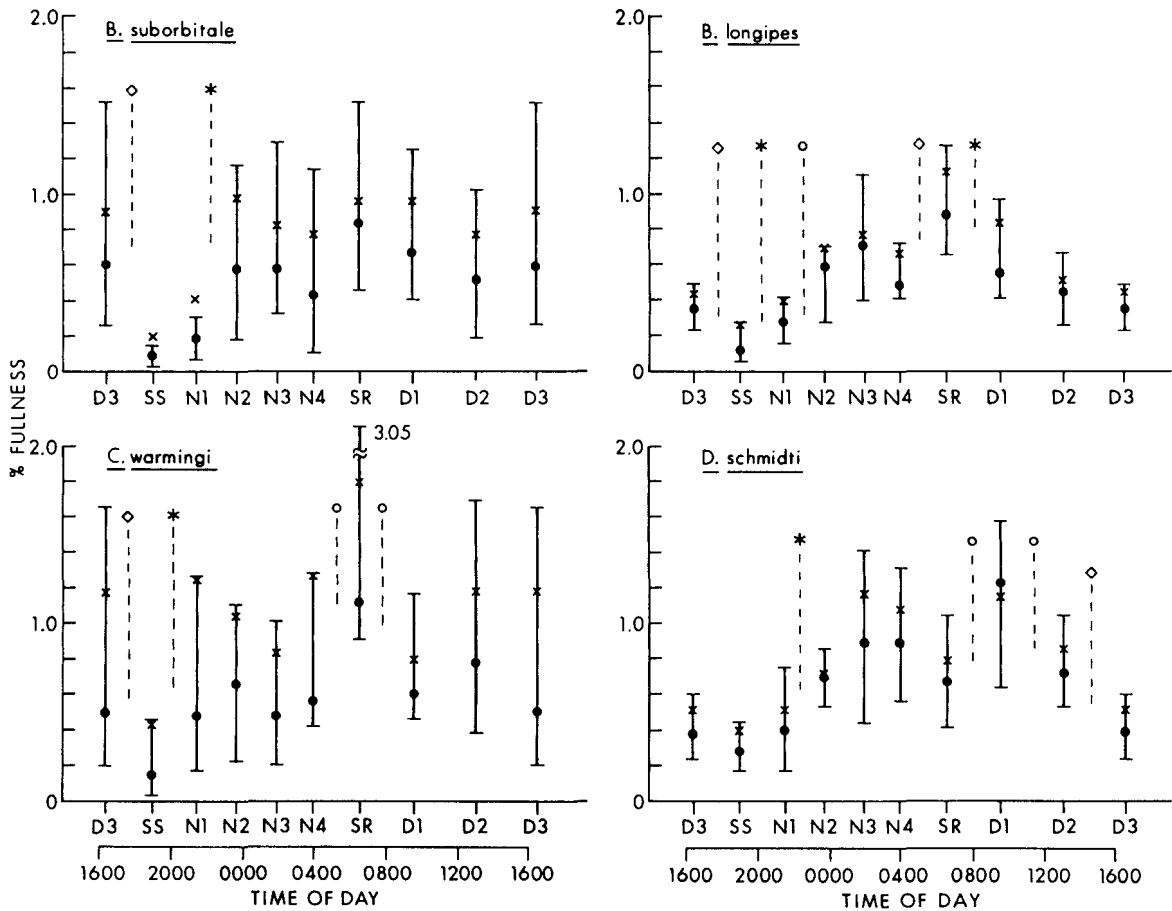


FIGURE 1.—Medians (dots), means (×'s), and ranges between 25th and 75th percentiles (solid vertical lines) of stomach fullness as percentage of body weight throughout the diel cycle for four species of myctophids: *Benthosema suborbitale*, *Bolinichthys longipes*, *Ceratoscopelus warmingi*, and *Diaphus schmidti*. Values are positioned at the midpoint of each sampling period (Hawaiian Standard Time). Dashed vertical lines indicate significant differences between adjacent pairs (circle— $0.05 < P < 0.10$ , \*— $0.01 < P < 0.05$ , diamond— $P < 0.01$ ; two-tailed probabilities, Rank Sum test).

was no apparent correlation between number of trematodes and amount of food in the gut.

There were highly significant differences ( $P < 0.005$ ) in stomach fullness over the diel cycle. The medians and means both showed a trend similar to that of *B. suborbitale* but more of the adjacent pairs showed significant differences and the changes in variability were not as great as with the latter species. The percentage of empty stomachs was  $< 10\%$  at all periods except SS (35%).

Small euphausiids, *Pleuromamma*, and a variety of small ( $< ca. 2$  mm PL) copepods occurred in the stomachs. Even though the stomach parasites apparently broke up the prey items soon after ingestion, there were identifiable pieces of prey in

the stomachs from night or dawn. In contrast, contents from day-caught specimens (particularly D2 and D3) were usually amorphous pink material; even the apparently resistant *Pleuromamma* buttons occurred infrequently.

#### *Ceratoscopelus warmingi* (Figure 1)

There were significant ( $P < 0.01$ ) diel differences in stomach fullness for *C. warmingi*. Similar to the above two species, median stomach fullness was lowest at SS and peaked at SR with an apparent decline in between. The peak at SR, based on only five specimens, differed marginally ( $P < 0.10$ ) from values before or afterwards. Day values were comparable with those at night and showed no clear

trend. Except for SS, the percentage of individuals with empty stomachs was low, and there were some fish with very full stomachs (>2%). Because of the latter, ranges and percentile limits were broad, and means were much higher than medians.

*Ceratoscopelus warmingi* fed on a wider variety of taxa and sizes of prey than did the other species covered here. The most frequent items were copepods, ostracods, and small euphausiids, but heteropods, siphonophores, and other zooplankton also occurred. Intact items of such relatively small prey were recorded mostly from specimens collected at night; remains from day-collected specimens were usually well digested. *Ceratoscopelus warmingi* also took items up to 10% of bodily weight; squid, other fishes, and large euphausiids or decapods occurred in specimens >35-40 mm. Such single large items accounted for nearly all the fish with high values of stomach fullness, and intact prey of this size occurred at all times of the day. Most such items were vertically migrating species that could have been taken at night, but remains of nonmigrating *Cyclothone* spp., which could have only been encountered between dawn and dusk, were found in 11 specimens. Thus, while the overall trend of the data indicates that *C. warmingi* feeds principally on small zooplankton in the upper layers at night, it probably takes large prey whenever encountered.

#### *Diaphus schmidti* (Figure 1)

Diel differences in stomach fullness for *D. schmidti* were highly significant ( $P < 0.005$ ), and the trend was similar to that of the preceding myctophids except for timing; the maximum value occurred at D1 instead of SR. Empty stomachs occurred only in a few specimens from D3, SS, and N1. *Diaphus schmidti* took a large variety of prey items; the dominant taxa were small crustaceans (ca. 0.5-3.0 mm PL or TL): ostracods, copepods, and larval and juvenile malacostracans. Heteropods, pteropods, polychaetes, and chaetognaths were also noted. Excepting chaetognaths, few items were >4-5 mm. Frequency of intact items was highest at SR, and lowest at D3 and SS.

#### *Hygophum proximum* (Figure 2)

Diel differences in stomach fullness for *H. proximum* were highly significant ( $P < 0.005$ ), and the trend quite different from those of the other

species examined here. Most stomachs were empty, and even 75th percentile values were zero or nearly so between SR and SS; the peak value occurred at N2. *Hygophum proximum* fed principally on medium-sized copepods (1-3 mm PL) and occasionally other crustaceans. Less than 10% of the stomachs were empty for any of the night periods, but intact items were found frequently only in stomachs from N1. By N2 most of the prey were unrecognizable, and only six items were recognizable to even general category in all the other samples.

#### *Lampanyctus niger* (Figure 2)

This species, one of three forms of the *L. niger*-complex which occur near Hawaii, has minute pectoral fins and lower AO counts than the others; it was designated as "Form B" in Clarke (1973). Zahuranec<sup>2</sup> has recently identified the form as *L. niger* (sensu stricto). There was evidence from deep night tows taken during the same sampling period that a fraction of the population of *L. niger* did not vertically migrate; consequently, some of the day-caught specimens may not have ascended to the upper layers the previous night. (Such "non-migration" was also recorded in previous studies, see Clarke 1973.)

The *H*-test indicated no significant diel differences in stomach fullness ( $P > 0.10$ ), and none of the adjacent pairs differed significantly. The medians from nighttime show a trend similar to that of other myctophids, but the means were highest during the day. No specimens were available from SR. Values of stomach fullness were overall much lower than observed in other species. Stomach fullness exceeded 1% in only 21 of the 160 specimens, and over 50% of the stomachs were empty at all periods except N2, N3, and N4.

The most frequent food items were large copepods of the families Metridiidae, Euchaetidae, and Aetideidae and small (<10-15 mm TL) euphausiids. Occasionally small fishes were found. Intact prey items were found in stomachs from all periods. Deep-living copepods such as *Metridia* and *Pseudochirella* were noted in day-caught specimens indicating that at least some feeding occurs during the day.

<sup>2</sup>B. J. Zahuranec. Oceanic Biology Program, Office of Naval Research, Arlington, VA 22217. Personal communications, June 1977.

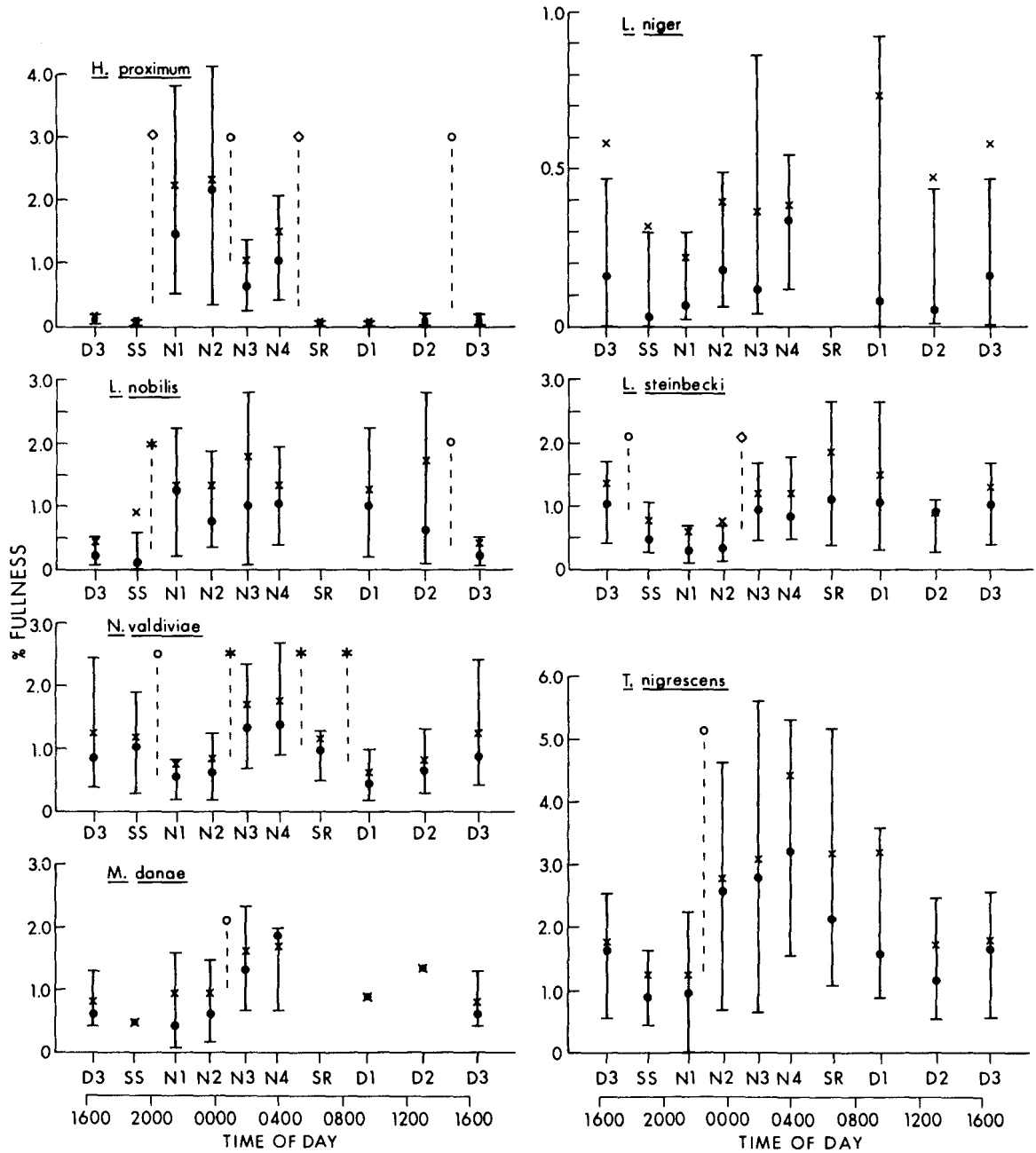


FIGURE 2.—Stomach fullness throughout the diel cycle for six species of myctophids and one species of melamphaid: *Hygophum proximum*, *Lampanyctus niger*, *Lampanyctus nobilis*, *Lampanyctus steinbecki*, *Notolychnus valdiviae*, *Triphoturus nigrescens*, and *Melamphaes danae*. Symbols and format as in Figure 1.

*Lampanyctus nobilis* (Figure 2)

*Lampanyctus nobilis* appeared to regurgitate food more frequently than other species examined.

Because few specimens of *L. nobilis* were collected (none from SR and <20 from four other periods), I included in the analyses data from 19 specimens that had some partially digested food in the mouth



or esophagus. In all of these specimens, the stomach also contained food and was not everted; the remains from the esophagus or mouth were picked out as carefully as possible and added to the stomach contents. (No specimens with everted stomachs were included.) Use of these 19 specimens had the desirable effect of increasing the numbers upon which statistical estimates were based, but, as pointed out earlier, possibly biased the data because some of the regurgitated food may not have been recovered. The data were treated with and without these 19 specimens. Inclusion of the latter either had no effect or increased the significance of differences indicated without them. Thus bias, if any, that was introduced was insufficient to obscure between-period differences in stomach fullness.

Diel differences in stomach fullness were significant ( $P < 0.05$ ) and resembled the trends of other myctophids. There was, however, no clear indication of a peak value at dawn; no specimens from SR were available and the medians for N3, N4, and D1 were similar to each other. The percentage of empty stomachs was low throughout most of the night and increased steadily between D1 and SS.

The size-frequency distribution of the specimens was bimodal; 45% were  $< 40$  mm SL and 47%  $> 60$  mm. The small specimens had eaten mostly copepods and amphipods 1-3 mm and *Euphausia* spp.  $< 10$  mm, while the large ones had taken large copepods ( $> 3$  mm PL) and euphausiids, mysids, sergestiids, and fishes 10-30 mm long. Intact prey were found frequently in night specimens and occasionally in those caught by day. The latter were, with the exception of a single *Lophothrix humilifrons* (apparently a deep-living copepod), migrating species that could have been taken at night. One specimen from N4 contained; among the remains of a euphausiid, crab megalopa, and copepods; a partially digested insect (probably a hymenopteran).

#### *Lampanyctus steinbecki* (Figure 2)

Stomach fullness values for *L. steinbecki* differed significantly ( $P < 0.005$ ) over the diel cycle. The medians generally increased from SS to SR and thereafter stayed at about 1% until a sharp decrease between D3 and N1. The percentage of fish with empty stomachs was low for all periods. The principal prey of *L. steinbecki* were copepods  $> ca. 2$  mm PL—mostly aetideids, *Pleuromamma*,

and *Candacia*—and euphausiids. A few intact items were found in specimens from D1 and D2 but all were shallow-living or migrating species that could have been taken the previous night. With the exception of a single *Pareuchaeta* sp. (probably a deep-living nonmigrator), the prey from D3 and SS were all well digested.

#### *Notolychnus valdiviae* (Figure 2)

The *H*-test indicated highly significant ( $P < 0.005$ ) diel differences in stomach fullness for *N. valdiviae*. Median values were low early in the night and increased to a peak at N4. The minimum value at D1 was slightly below the early night values. Stomach fullness increased slightly until SS and then decreased at SS-N1. The percentage of fish with empty stomachs was low at all periods. The positions of the 75th percentiles indicated higher percentages of fish with relatively full stomachs at N3, N4, SS, and D3.

*Notolychnus valdiviae* had taken a wide variety of sizes (ca. 0.5-4.0 mm PL) and species of copepods, but the bulk of the food in terms of weight was made up by large (relative to the weight of *N. valdiviae*) items such as *Pleuromamma xiphias*, *Candacia longimana*, and 2-4 mm aetideids. Intact prey were more frequently noted in specimens from N3 and N4 than in those from the apparent "secondary peak" in stomach fullness at D3 and SS. Considering only those specimens with stomach fullness  $> 2\%$  (whose numbers distinguish the peak periods from others), only three of the nine from D3 and SS contained intact or partially intact *Pleuromamma*. The other six contained remains that were either unrecognizable or barely so. In contrast, of the 15 specimens from N3 and N4, 12 contained 1-3 intact items, while only 3 contained unrecognizable remains. This plus the absence of any apparent significant differences associated with the D3/SS peak indicate that the latter was due to a chance collection of a few more specimens that had taken large meals the previous night rather than to extensive daytime feeding.

#### *Tripoturus nigrescens* (Figure 2)

Overall diel differences in stomach fullness were highly significant ( $P < 0.005$ ). Both medians and means rose from low values at SS and N1 to a peak at N4 and then, except for a slight increase at D3, declined until SS. Due to the broad overlap in

ranges and percentiles for most pairs, only the large increase between N1 and N2 was even marginally significant. The percentage of empty stomachs was highest at N1 and zero at and just after the peak at N4.

*Triphoturus nigrescens* fed principally on *Pleuromamma* and *Euphausia* spp. Intact prey were recorded more frequently during N2-N4 than in other periods. As in the case of *N. valdiviae*, the apparent peak at D3 was due to a few fishes' containing large amounts of well-digested material rather than freshly taken items.

## Melamphaidae

### *Melamphaes danae* (Figure 2)

Few *M. danae* were taken at any period. None were taken at SR, and only two or three were taken at SS, D1, and D2. The data indicate a diel trend similar to that of several myctophids, but the *H*-test indicated that diel differences were only marginally significant ( $P = \text{ca. } 0.10$ ). If the data from SS, D1, and D2 were not included, the *H*-test indicated significance at  $P = \text{ca. } 0.05$  and the N4 and D3 values differed at  $P < 0.05$ . This latter, and statistically dubious, manipulation indicates that the apparent trend in the data is real, but that more specimens would be needed to confirm it properly.

*Melamphaes danae* fed on a wide variety of zooplankton including polychaetes and chaetognaths as well as crustaceans—mostly small copepods and ostracods. The copepods identified were all either vertical migrators or shallow-living, non-migrating species. Intact items were present in nighttime specimens; those from daytime contained remains barely identifiable to general taxon.

## Gonostomatidae

### *Gonostoma atlanticum* (Figure 3)

Relatively few *G. atlanticum* were available from four periods even though 23 additional specimens from the May 1974 collections were included. Still there were significant ( $P < 0.05$ ) differences in stomach fullness over the diel cycle. Median values rose steadily from SR to D3, remained at ca. 2% between D3 and N2, and then dropped sharply between N2 and N3. Though the median for N4 was slightly higher than that for

either N3 or SR, the percentage of empty stomachs was highest at N4 and SR, indicating an overall trend for decrease during the late night.

*Gonostoma atlanticum* fed on large copepods—mostly *Pleuromamma xiphias*, *Candacia longimana*, and aetideids and scolecithricids of several genera—and small (<10-15 mm) euphausiids. Intact prey were found in stomachs from all periods, but were mostly from the period between D1 and N2. The majority of the contents from N3 and N4 were well digested.

### *Gonostoma elongatum* (Figure 3)

Relatively few *G. elongatum* were available from three periods and the size range of individuals used was extremely broad (26-150 mm). There is evidence from past studies that fractions of the population occasionally do not migrate (Clarke 1974), but catches from deep night tows taken during the same sampling period did not clearly indicate whether or not this occurred during this study.

The *H*-test indicated marginally significant differences ( $0.05 < P < 0.10$ ) in stomach fullness over the diel cycle, and there was no clear trend in any of the parameters. Medians for all periods except SR (only 8 specimens) and D3 (10 specimens) were <1%. The means were well above the medians for several periods due to a few fishes' having very full stomachs. *Gonostoma elongatum* fed on the same copepods and euphausiids noted for *G. atlanticum* and on ostracods, amphipods, small sergestiid shrimps, and fish as well. Fresh or intact items were noted most frequently in specimens from SR, D1, D3, and N1.

## Photichthyidae

### *Vinciguerria nimbaria* (Figure 3)

Although previous evidence (Clarke 1974) indicated that a fraction of the population of *V. nimbaria* does not always migrate, catches of deep night tows from the same cruise indicated that only an insubstantial fraction, if any, remained at depth during the shallow night sampling periods.

Diel differences in stomach fullness were highly significant ( $P < 0.005$ ). The median was highest at SS and decreased steadily throughout the night to nearly zero at N4 and SR. The values were only slightly higher during the day, but increased sharply between D3 and SS. A clearer picture of changes between D2 and SS is given by the means

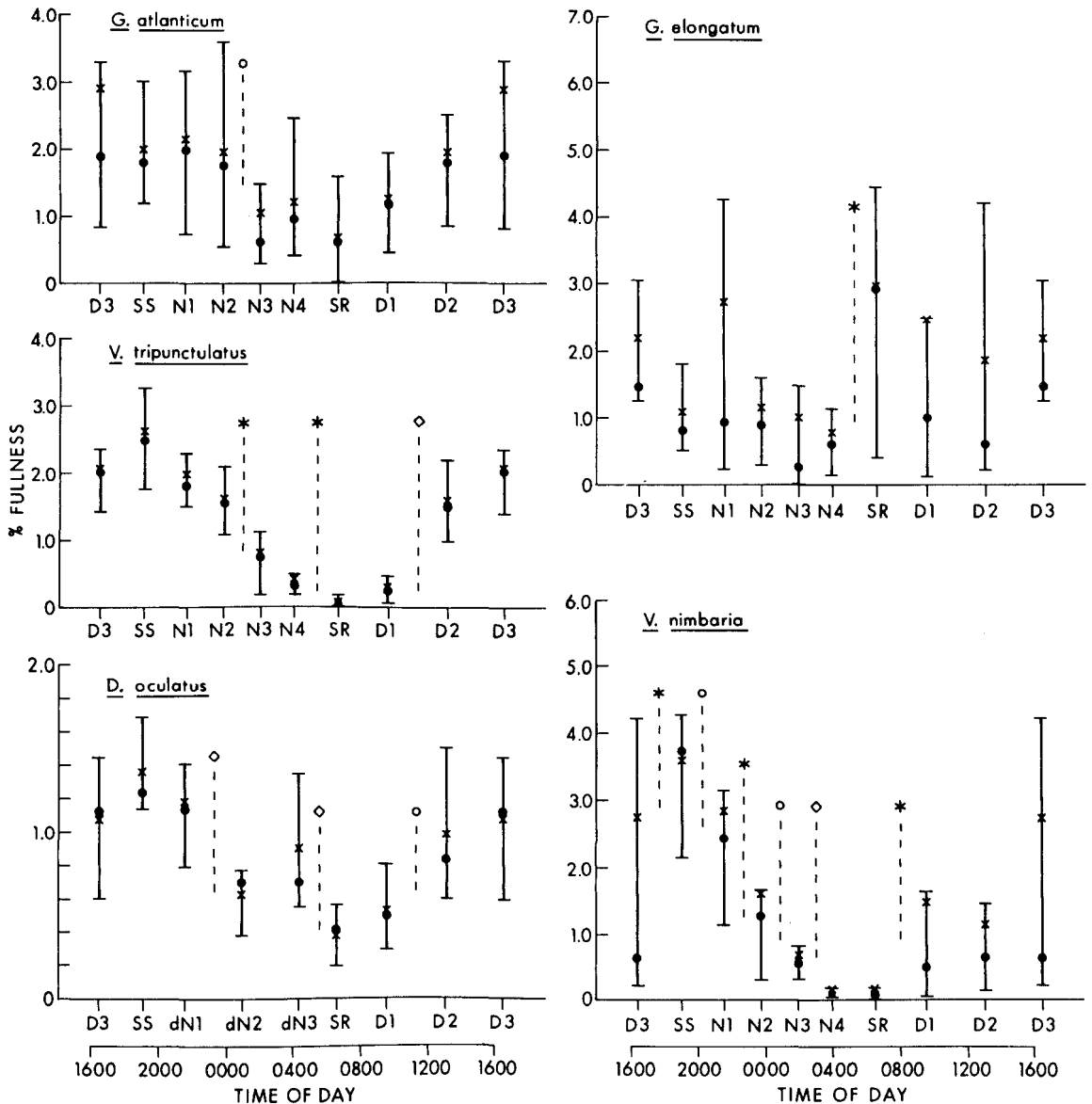


FIGURE 3.—Stomach fullness throughout the diel cycle for five species of stomiatoids: *Gonostoma atlanticum*, *Gonostoma elongatum*, *Valenciennellus tripunctulatus*, *Danaphos ocellatus*, and *Vinciguerrria nimbaria*. Symbols and format as in Figure 1.

rather than the medians, because there were marked differences in frequency distribution for these periods—differences to which the median is not sensitive. At D2 the data were skewed to the left with most values <1% and very few full stomachs. At D3 the data were bimodal; 7 values were higher than the mean of ca. 2.75% and 11 <1%. By SS, the data were again unimodal and skewed slightly to the right with 16 values >2%

and only 2 <1%. Thus the trend between D2 and SS was one of a gradual change in percentages of the fish with very full stomachs, and the abrupt increase in median values between D3 and SS occurred as the high values became the dominant mode. The percentages of empty stomachs showed a trend opposite to that of the average values, i.e., an increase during the night and a decrease between SR and D2.

*Vinciguerria nimbaria* fed upon a wide variety of sizes and taxa of prey. Small (< ca. 2 mm PL) copepods and ostracods were most frequent, but larger copepods and small euphausiids occurred regularly. Both the number of prey items and absolute values of stomach fullness for the peak period were higher than for most of the other species examined here; in several instances the remains of 20-40 prey items were found in a single stomach. Intact items were most frequent at SS and common in specimens from day samples. Some intact items were noted from N1 and a few from N2, but stomachs from N3, N4, and SR contained practically nothing but well-digested remains.

### Sternoptychidae

#### *Danaphos oculus* (Figure 3)

Few *D. oculus* were available for any period except D1, and numbers were particularly low for D2. Nine of the specimens used came from the May 1974 series. In spite of this, there was an evident and highly significant ( $P < 0.005$ ) diel trend in stomach fullness. Median values rose steadily from a minimum at SR to a maximum at SS and declined nearly constantly throughout the night. There were a few empty stomachs at SR and D1 and none at other periods. *Danaphos oculus* fed almost exclusively on *Pleuromamma xiphias*, *Euchaeta media*, and similar-sized juveniles and adults of several aetideid species. Intact items were most frequently noted in D3 and SS specimens; some were found in those from D1 and D2. Almost none of the night specimens contained any but well-digested remains.

#### *Valenciennellus tripunctulatus* (Figure 3)

Few *V. tripunctulatus* were available from any period except N1; 31 of the total examined came from the May 1974 collections. Still, like *D. oculus*, *V. tripunctulatus* showed a clear and highly significant ( $P < 0.005$ ) diel trend in stomach fullness. Medians rose from zero at SR to a maximum at SS and declined throughout the night. The principal prey items were *P. xiphias*, *P. abdominalis*, *E. media*, and similar-sized aetideids. The stomachs from D2 to SS were nearly uniformly packed with intact prey while those from late night and SR were either empty or contained only traces of well-digested remains.

## DISCUSSION

### Feeding Chronology

Interpretation of data on stomach fullness is limited because observed fullness is a function of two rate processes—feeding rate and stomach evacuation rate. Diel changes in stomach fullness indicate that one or both rates vary over the diel cycle, but without independent estimates of one or the other, the only certain statements that can be made are that feeding exceeds evacuation during periods when fullness increases, the opposite when fullness decreases, and that both rates are zero when the stomach is empty. Notes on state of digestion of stomach contents are helpful, but must be interpreted with caution. Absence of intact items indicates that feeding rate is zero, but presence of intact items does not necessarily mean feeding rate was positive during a given period since some items may remain intact for an unknown time after feeding ceases. Still, it is possible within these limits to qualitatively consider changes in the two rates and to relate them to environmental changes which the fishes encounter over the diel cycle.

The species considered here undergo diel changes in numerous environmental factors, some of which are likely to affect either feeding or stomach evacuation rate in a qualitatively predictable manner. The migrating species encounter higher temperatures at night. Diel temperature changes for each species (Table 3) were determined using temperature-depth profiles from the study area (Maynard et al. 1975 give profiles from several seasons of three different years) and depth ranges of the fishes (Clarke 1973, 1974; Clarke and Wagner 1976). Because all species considered occur below the steepest part of the thermocline during the day, the magnitude of the diel temperature change is mostly a function of nighttime depth range and not day depth or absolute range of migration. For the same reason, juveniles, which occur shallower than adults in most species (Clarke 1973), incur greater temperature change than adults of the same species. The migrating species also encounter lower pressures and higher oxygen concentrations at night (oxygen-depth profiles for a site near the study area are given in Gordon 1970).

Unless the fishes are able to regulate metabolism over the range of diel changes, the day-night

TABLE 3.—Depth ranges, estimated diel changes in temperature, and probable day-night differences in prey concentration for the 16 species of fishes considered. (See text for sources of estimates.)

Species	Depth range (m)		Temperature change (°C) Night-day	Prey density Night vs. day
	Night	Day		
<i>Benthosema suborbitale</i>	0-100	500-600	18-19	N>D
<i>Bolinichthys longipes</i>	50-150	500-700	16-19	N>D
<i>Ceratoscopelus warmingi</i>	0-150	600-1,000	16-20	N>>D
<i>Diaphus schmidti</i>	0-75	500-600	17-19	N>D
<i>Hygophum proximum</i>	0-150	500-700	15-19	N>D
<i>Lampanyctus steinbecki</i>	75-200	600-1,000	10-17	N>>D
<i>Lampanyctus nobilis</i>	50-150	600-1,200	16-20	N>>D
<i>Notolychnus valdiviae</i>	80-150	500-650	15-16	N>D
<i>Triphoturus nigrescens</i>	25-100	550-750	17-19	N>D
<i>Melamphaes danae</i>	75-200	750-1,200	10-18	N>>D
<i>Danaphos oculatus</i>	450-650	450-650	0	N<<D
<i>Valenciennellus tripunctulatus</i>	200-330	400-500	5-6	N<D
<i>Gonostoma atlanticum</i>	150-300	500-550	6-14	N≤D
<i>Vinciguerria nimbaria</i>	0-125	400-560	13-17	N≥D
<i>Gonostoma elongatum</i>	60-265	550-725	10-19	N≥D
<i>Lampanyctus niger</i>	100-300	650-900	7-15	N>D

differences in temperature and oxygen concentration both predict lower rates of metabolic processes in general and in particular lower feeding or stomach evacuation rate during the day. Childress (1975) and Childress and Nygaard (1973) indicated that mesopelagic organisms can regulate over a wider range of oxygen partial pressures than these fishes encounter off Hawaii. Thus temperature changes are more likely to affect rate processes. Teal (1971) showed that increased pressure can stimulate metabolic rates and thus mediate or cancel effects of temperature; however, it seems likely that temperature effects are predominant for the species considered here since these fishes migrate through a much stronger thermocline than did the shrimps studied by Teal.

As a consequence of vertical migration—by the fishes and by many of their prey—the fishes encounter diel differences in prey concentration, with which feeding rate is likely to be positively correlated. As noted above, the depth distributions

of all prey species in the study area are not known in detail; however, general, qualitative features were evident from the available plankton samples (see above). Most of the important prey species were either shallow-living nonmigrators that occurred above ca. 200 m day and night or were vertical migrators with maximal concentrations at ca. 300-450 m by day. Some important genera, e.g. *Euphausia*, *Pleuromamma*, and *Euchaeta*, occurred as deep as 600 m during the day but not at high densities. At night, most copepods and many of the euphausiids occurred at highest densities above ca. 150-200 m. Many prey species occurred between 200 and 300 m at night, but except for a few euphausiid species, concentrations were much lower than in the upper 200 m. Below ca. 600 m by day and below ca. 300 m at night, total zooplankton concentration was low and that of important prey species nearly zero. Based on the above features and the fishes' depth ranges, qualitative estimates of day-night differences in prey concentration were made for each species (Table 3).

Nine species of myctophids and probably *Melamphaes danae* had similar diel patterns in that median values of stomach fullness were minimal at or near dusk and increased only at night, but details of the patterns were variable. Six species, *Benthosema suborbitale*, *Bolinichthys longipes*, *Ceratoscopelus warmingi*, *Diaphus schmidti*, *Lampanyctus steinbecki*, and *L. nobilis* (Figures 1, 2), had two periods of increasing stomach fullness during the night separated by a decline. Maximum stomach fullness occurred at or near dawn, and the fish reached day depth with relatively full stomachs. Stomach fullness appeared to decrease during the day in some species and showed no clear trend in others, but in most there was a significant decrease at or near dusk. In *Notolychnus valdiviae*, *Triphoturus nigrescens*, and possibly *Melamphaes danae* (Figure 2), median stomach fullness appeared to increase steadily throughout the night to a peak value just before dawn. In the first two of these species, stomachs were partially evacuated by the time they reached day depth. In *Hygophum proximum* (Figure 2) median fullness reached a peak value early in the night, and stomachs were completely evacuated by dawn.

For most of the above species there was no evidence of significant feeding at depth during the day. Intact items were more frequent at night, and stomach contents of day-caught fish were usually

well digested. *Lampanyctus nobilis* and *L. steinbecki* occasionally take deep-living copepods during the day, and *C. warmingi* apparently takes large items whenever it encounters them. Still, the instances of definite day feeding were so few in even the latter three species that the medians and, therefore the diel patterns, were only marginally affected.

All of these myctophids undergo diel changes in temperature and prey concentration (Table 3) that correlate with the observed pattern of feeding solely or mostly at night while in the upper 200 m. All are at much higher temperatures at night. Although some species occur as shallow as ca. 500-600 m during the day and thus partially overlap the daytime depth ranges of certain of their prey, all occur below daytime maxima of prey concentrations and almost certainly encounter higher concentrations at night. Certain details of the patterns of stomach fullness indirectly indicate that stomach evacuation rate may be lower during the day as predicted by temperature differences. In many species, stomach fullness did not clearly decrease during the day; since feeding rate was apparently zero then, the evacuation rates must have been low or zero. The sharpest declines in stomach fullness occurred at or near dusk in most species, near dawn in *N. valdiviae* and *T. nigrescens*, and during the night in *H. proximum*—not during periods when the fishes remained within their day depth ranges. In all cases except *H. proximum*, however, something related to vertical migration itself, e.g., activity, could be responsible for the apparent increases in evacuation rates.

Four species of stomiatoids, *Gonostoma atlanticum*, *Danaphos oculatus*, *Valenciennellus tripunctulatus*, and *Vinciguerrria nimbaria*, fed only during the day. The last three species occur somewhat shallower by day then do the myctophids and are consequently at or near depths of maximum concentration of their prey then. The upward migration of *V. nimbaria* is similar in extent to that of its prey. Thus this species encounters little or no diel change. *Danaphos oculatus* does not migrate, and *Valenciennellus tripunctulatus* migrates less than do its prey. Consequently, both species occur below high concentrations of prey at night. The adults of *G. atlanticum* (as were most specimens used here) occur near the lower depth limits of most prey species both day and night, and the day-night difference is probably minor. Thus in these species, the day depth ranges, rather than the occurrence or up-

ward extent of migration, seem more related to observed feeding pattern.

All four species feed at nearly the same, low temperature. Diel temperature change is zero for *D. oculatus*, and relatively small for *V. tripunctulatus* and large *G. atlanticum* because they penetrate only part way through the thermocline. *Vinciguerrria nimbaria* undergoes a change similar to that of the myctophids. The temperature changes or lack thereof obviously have no effect on feeding periodicity; however, the steepness of the nighttime decline in stomach fullness seems roughly correlated with nighttime temperature indicating an effect on stomach evacuation rates. This trend is considered in more detail below.

*Lampanyctus niger* and *G. elongatum*, the two species which showed no diel pattern in stomach fullness, do not undergo large diel changes in either temperature or prey concentration in spite of the fact that they migrate. The large individuals of both species (as were all the *L. niger* and most *G. elongatum*) undergo a relatively small temperature change. Likewise, only the smallest juveniles of either species encounter markedly higher prey concentrations at night. The relatively low values of stomach fullness in both species and the presence of deep-living, nonmigrating zooplankton in *L. niger* indicate that these two species feed at a low rate whenever and wherever they encounter prey.

### Relationship to Previous Studies

Comparison of the present results with those of previous studies is restricted because methodology in all cases was different from that of the present study and in many cases equivocal or probably not sensitive enough to discern diel trends or lack thereof. With the exception of the study by DeWitt and Cailliet (1972), appropriate statistical testing was not done, and it is impossible to do so from the published data.

The most directly comparable study is that by Holton (1967) on *Lampanyctus* (= *Triphoturus*) *mexicanus*. Using 10 fish from each of eight periods of the day, he determined dry weights, but for some unknown reason weighed the entire alimentary canal with the food. The minimal values observed, presumably from empty stomachs, indicate that his "% nutrition" values should be decreased by about 2.5-3 to make them roughly comparable to those of the present study. Though

the ranges and standard deviations of the data are broad relative to the differences in means, the diel trend in the latter is similar to that observed here for *H. proximum*, i.e., peak value was reached early in the evening and then dropped to low values and probably zero before the dawn descent.

Most previous studies have used visual estimates of fullness with a scale of 3-5 ranks. Because of the lack of "intercalibration" between investigators, only the rank for "empty" can be compared unequivocally, and it is not certain in what manner the ranks might correlate with percentages of the fishes' dry bodily weight. Finally the validity or absence of trends and details thereof are questionable because scales of only 0-3 or 0-4 are rather insensitive. (Had only visual estimates of fullness been used for the present study, only in a few cases, e.g., *H. proximum* or *Valenciennellus tripunctulatus*, would the diel trends have been obvious.)

Anderson's (1967) data on *T. mexicanus* indicate a peak in stomach fullness just before sunrise, but his data on degree of digestion indicate that fresh food items were most frequent between sunset and midnight. His data for *Bathylagus stilbius* (cardiac portion of the stomach only) indicate two separate periods of increasing fullness at night and the sharpest decrease prior to ascent at dusk. This pattern correlates with frequency of less-digested prey items and is very similar to that observed for several myctophids in this study.

Similar indices were used in the studies of four species of high latitude myctophids: *Benthoosema glaciale* (Gjösæter 1973) and *Stenobrachius leucopsarus*, *Diaphus theta*, and *Tarletonbeania crenularis* (Tyler and Percy 1975). Both studies examined large numbers of specimens from each of a few, very broad time periods. Their data indicated highest percentages of full or nearly full stomachs at night and highest percentages of low values during the day. The occurrence of some full stomachs during the day led Gjösæter to conclude that diel variation in feeding was not great and Tyler and Percy to conclude that there was no evidence against diurnal feeding. Both studies noted a higher degree of digestion during the day. These results are, however, consistent with the possibility that like many of the myctophids in the present study, their species descended at dawn with full stomachs and did not evacuate them completely until the dusk ascent. The latter may well have not been detected in these studies due to the broad time periods used.

Data on myctophids from recent studies by Merrett and Roe (1974) and Baird et al. (1975) are consistent with nocturnal feeding but are equivocal to varying degrees due to low numbers of specimens, incomplete diel coverage, or methodology. Both studies based stomach fullness estimates on counts of identifiable prey items. Apparently, the presence of a single resistant part, e.g., a *Pleuromamma* button, was counted the same as an intact, whole individual of the same taxon. Because of this and the likelihood that some prey taxa or parts of prey are digested—and concomitantly rendered unrecognizable—at different rates (e.g., Pandian 1967; Gannon 1976), such counts seem to be insensitive or possibly biased estimates of gut fullness—especially so when the counts are used to back-calculate dry weight as done by Baird et al. Furthermore, neither study corrected the fullness estimate for fish weight, which (using standard length ranges given by these authors and assuming that weight is roughly proportional to the cube of the length) varied by factors of ca. 7-15 in the myctophids covered by Merrett and Roe and ca. 2.75 in *D. taaningi*, the species studied by Baird et al.

Merrett and Roe's data for *L. cuprarius* indicated peak fullness in the middle of the night and a decrease before the dawn descent—a pattern similar to that of *H. proximum*. Their data for *Lobianchia dolfeini* and *N. valdiviae* include no samples between dusk and near dawn, but show fuller stomachs at dawn. Data of Baird et al. for *D. taaningi* are also similar to that for *H. proximum*. The rise in fullness from empty or nearly empty stomachs in the afternoon to fairly high values in early evening is evident and based on 39 and 9 specimens, respectively; however, the subsequent decline is based on a single specimen from late night and 4 from just after dawn (1 which contained a fair amount of food).

Fewer stomiatoids have been examined elsewhere, but much of the data available is consistent with diurnal feeding. Perhaps the most convincing data (because of good diel coverage and numerous specimens) presented by Merrett and Roe (1974) is that for *Valenciennellus tripunctulatus*, which does not migrate in their study area. The pattern is clearly similar to that observed for the Hawaiian specimens. Hopkins and Baird (1977) cited their own unpublished data also indicating diurnal feeding for the same species. Merrett and Roe (1974) interpreted dusk peaks of numbers of items/nonempty stomach as

an indication of dusk feeding activity in two species of *Argyropelecus*; however, the data for *A. hemigymnus* seem to me more consistent with increasing stomach fullness throughout the day and a nighttime decline. Except for high dawn values (based on only three specimens from two tows), *A. aculeatus* shows a similar trend.

DeWitt and Cailliet (1972) found no diel trend in feeding of *Cyclothone signata*, but, based on fewer empty stomachs in fish caught in the upper part of the depth range, proposed that this species, although it does not undertake diel vertical migrations, may ascend irregularly to levels of higher prey concentration to feed. Their data also indicated that a deeper living species *C. acclinidens*, had a higher percentage of empty stomachs by day; as noted by the authors, the latter seems to defy any reasonable explanation.

Legand et al. (1972) considered feeding chronology of 14 species of mesopelagic fishes from the South Pacific. Though trends in stomach fullness of some species are similar to those noted here, e.g., that for *Triphoturus microchir* (which almost certainly = *T. nigrescens*) is very similar to that for *T. nigrescens* near Hawaii, a number of species show patterns quite different from those reported by either the present or other studies. Interpretation of the validity of such "exceptions" is difficult owing to the sparse presentation of Legand et al. Though total numbers of specimens are fairly high, it is not clear that they were equitably distributed among diel periods, from the same area, or from the same season, etc. The percent fullness values are obviously based on wet weights—an imprecise measurement, particularly for stomach contents—and it is not clear whether all fish and stomach contents were weighed or some sort of averaging or regression procedure was employed.

The feeding patterns shown by previous studies cannot be compared in detail with those presented here; however, there is general agreement in data on the two dominant groups of mesopelagic fishes. Myctophids feed mostly at night, while stomiatoids tend to feed by day. My interpretations indicate that near Hawaii, the differences are at least partially related to different diel relationships of the fishes to vertical distributions of their prey. Other interpretations are obviously possible, e.g., the feeding patterns may prove to be characteristic of the two taxa regardless of relationship to prey distribution. It would be of particular interest to investigate myctophids with vertical dis-

tribution patterns similar to those of the stomiatoids, i.e., with shallow day depth ranges at or near high daytime concentrations of zooplankton. (Certain *Myctophym* and *Diaphus* spp. from Hawaii meet this criterion [Clarke 1973], but were not captured in sufficient numbers to be included in this study.)

The diel feeding patterns of mesopelagic fishes could well be related to light rather than (or in addition to) temperature and prey concentration. No data on diel light changes near Hawaii are available; however, data of Kampa (1970) from a similar area of clear oceanic water in the North Atlantic show that during full moon the diel change in depths of relevant isolumes is of the order of 300-350 m. Even allowing for considerable differences in extinction coefficients between Hawaii and Kampa's study area, the diel change in isolumes at new moon (when the present samples were taken) off Hawaii is probably at least 300-350 m and could be as great as 500 m. The absolute diel change in depth for most of the myctophids is over 500 m while that for the 4 day-feeding stomiatoids is ca. 400 m or less (Table 3). Thus it is possible that feeding in both groups occurs when higher light levels are encountered—at night for the myctophids and by day for the stomiatoids.

### Estimation of Rates

As mentioned previously, neither feeding rate nor stomach evacuation rate can be considered quantitatively without an independent estimate of the other. Because of the difficulty in keeping mesopelagic fishes alive for grazing or evacuation experiments, it will likely be a long time before independent estimates are available. For a few species considered here it is, however, possible to derive "quasi-independent" estimates of evacuation rate given certain plausible assumptions. These allow, with further assumptions, rough estimates of feeding rate and daily ration.

For any period where feeding rate is zero, changes in stomach fullness are due to evacuation alone, and, if temperature, pressure, etc., remain essentially constant during that period, the rate of evacuation can be assumed to be proportional to the amount of food in the stomach (Kjelson and Johnson 1976; Eggers 1977). The change in stomach fullness would then be described by:

$$dS/dt = -kS \text{ or } S_t = S_0 e^{-kt} \quad (1)$$



where  $S$  is stomach fullness as percentage of fish weight;  $S_0$  and  $S_t$ , the values at the beginning and end of a period of  $t$  hours; and  $k$ , the instantaneous evacuation rate in per hour.

For most of the species considered here, there is no extended period of decline in stomach fullness where the above assumptions are met, but a rough estimate of  $k$  is possible for *H. proximum* and three species of stomiatoids. *Hygophum proximum* apparently ceases feeding early in the night, and stomach fullness declines from N2 to SR under essentially constant conditions, i.e., the fish remain in the upper layers. Stomach fullness declines from SS to SR in *Vinciguerria nimbaria*, *Valenciennellus tripunctulatus*, and *Danaphos oculatus*, and except for relatively brief periods of migration in the first two species, they remain at the same temperature, etc., for this period.

The values of  $k$  for these four species were calculated by simply using the integral form of Equation (1) and the median values of  $S$  for the beginning and end of the periods mentioned above (Table 4). (Other fitting procedures, such as least square methods, require that a number of questionable statistical assumptions be made.) The values of  $k$  are inversely correlated with night depth and thus positively with temperature being lowest for *D. oculatus*, highest for *Vinciguerria nimbaria* and *H. proximum*, and intermediate for *Valenciennellus tripunctulatus*.

For each of the four species, prey concentration and temperature, pressure, etc., were essentially constant throughout the period when feeding occurred (SS to N2 for *H. proximum* and SR to SS for the stomiatoids). It is not unreasonable to assume, as a first approximation, that feeding rate was constant during the periods of increasing stomach fullness. Changes in fullness would then be described by:

$$dS/dt = F - k'S \quad (2)$$

where  $k'$  is the instantaneous evacuation rate during the period of feeding, and  $F$  is the feeding rate in percentage bodily weight per hour. Integrating and rearranging gives an equation for  $F$  in terms of  $k'$ , the duration of the feeding period  $t'$  in hours, and median fullness at the beginning ( $S_0'$ ) and end ( $S_t'$ ) of the feeding period:

$$F = \frac{k'(S_t' \times S_0' e^{-k't'})}{1 - e^{-k't'}} \quad (3)$$

(In some cases, there were a few relatively high values of stomach fullness among the data for a given period; consequently, the feeding rate of some individuals may have been lowered due to satiation. Such values had little effect on the median, and thus the assumption of constant feeding rate is probably not seriously violated as long as medians are used in the calculations.)

Estimates of feeding rate and daily ration (=  $Ft'$ ) were calculated (Table 4) using median values of stomach fullness at SR and SS as  $S_0'$  and  $S_t'$ , respectively, for the stomiatoids and, similarly, SS and N2 for *H. proximum*. Since both *D. oculatus* and *H. proximum* feed at the same temperatures as those under which the instantaneous evacuation rates were estimated above,  $k'$  in Equation (3) was assumed equal to  $k$  calculated from Equation (1). The daytime or "feeding" temperatures of *Vinciguerria nimbaria* and *Valenciennellus tripunctulatus* are lower than those under which  $k$  was estimated from Equation (1). During the day both species occur at nearly the same temperature as does *D. oculatus* both day and night. Consequently, for each of the two migrating stomiatoids, two values of feeding rate and daily ration are given in Table 4—one calculated using

TABLE 4.—Estimates of instantaneous stomach evacuation rates, feeding rates, and daily rations for four species of mesopelagic fishes based on changes in median stomach fullness over the diel cycle. The first three columns give the sampling periods (Table 1) between which feeding rate was assumed to be zero, the duration of this interval ( $t$ ), and the calculated instantaneous stomach evacuation rate ( $k$ ). The last five columns give the sampling periods between which feeding rate was assumed constant and positive, the duration of this interval ( $t'$ ), the instantaneous stomach evacuation rate assumed for the feeding periods ( $k'$ ), and calculated feeding rate ( $F$  in % of bodily weight per hour) and daily ration ( $R = Ft'$  in % of bodily weight per day). For both *Valenciennellus tripunctulatus* and *Vinciguerria nimbaria*, two values of  $k'$ ,  $F$ , and  $R$  are given: the higher values under the assumption of constant stomach evacuation rate night and day ( $k' = k$ ), the lower under the assumption that stomach evacuation rate during the feeding period was lower and equal to that estimated for the nonmigrating, deep-living, *Danaphos oculatus*. See text for formulae and further explanation.

Species	Nonfeeding period	$t$ (h)	$k$ ( $h^{-1}$ )	Feeding period	$t'$ (h)	$k'$ ( $h^{-1}$ )	$F$ (%/h)	$R$ (%/d)
<i>Hygophum proximum</i>	N2-SR	6.8	-0.52	SS-N2	4.5	-0.52	1.26	5.7
<i>Danaphos oculatus</i>	SS-SR	11.3	-0.10	SR-SS	12.7	-0.10	0.15	1.9
<i>Valenciennellus tripunctulatus</i>	SS-N4	8.7	-0.22	SR-SS	12.7	-0.22	0.57	7.3
						-0.10	0.34	4.3
<i>Vinciguerria nimbaria</i>	SS-SR	11.3	-0.38	SR-SS	12.7	-0.38	1.42	18.1
						-0.10	0.51	6.5

$k' = k$  from Equation (1) and the other using  $k' = 0.10$ , the value for *D. oculatus*.

The estimated ration for *Vinciguerria nimbaria* seems inordinately high (18%) if  $k'$  is assumed equal to  $k$ , the nighttime estimate of evacuation rate. Such values have been estimated for very young, rapidly growing zooplanktonivorous fishes, e.g., *Alosa aestivalis* (Burbidge 1974) and *Oncorhynchus gorbuscha* (Parsons and LeBrasseur 1970). Data from Kjelson and Johnson's (1976) study of postlarval *Lagodon rhomboides* and *Leiostomus xanthurus* feeding rates on zooplankton yield estimates of daily ration of only 9.4 and 8.6%, respectively, in terms of wet weight (my calculations from their data). The estimated ration for *V. nimbaria* using the low value for  $k'$  and that for *H. proximum* lie within the range of values observed for larger individuals in the first two studies cited above and for *Morone chrysops* juveniles feeding on zooplankton (Wissing 1974). The daily ration of the California sardine, *Sardinops caerulea*, which is a larger zooplanktonivore, is apparently slightly lower; judged from Lasker's (1970) estimates of metabolic and growth requirements, the daily ration is probably about 3-4% (in terms of calories) for the sizes considered.

The above comparisons are admittedly stretched and ignore, among other things, possible differences due to environmental temperature, but the similarity of estimated daily rations of *H. proximum* and *V. nimbaria* to those of shallow-living planktonivores is not entirely unexpected. Childress and Nygaard (1973) have shown that the chemical composition of mesopelagic fishes which migrate to the upper layers at night is more similar to that of epipelagic species than to non-migrating, deep-living forms.

Differences between estimates for the three stomiatoids are correlated with the extent of vertical migration. Nighttime stomach evacuation rate is highest in *V. nimbaria*, lowest in *D. oculatus*, and intermediate in *Valenciennellus tripunctulatus*. Feeding rate and daily ration estimates show the same trend regardless of whether or not daytime stomach evacuation rates are assumed lower. The absolute values of stomach fullness at the end of the feeding period (Figure 3) are also highest in *Vinciguerria nimbaria* and lowest in *D. oculatus*. These trends indicate a possible adaptive value for the upward migrations of some stomiatoids. The higher temperatures encountered at night by migrators could allow processing of larger meals and presumably

faster growth, turnover, etc., rates than for species which remain at depth day and night.

## ACKNOWLEDGMENTS

I thank the captain and crew of the RV *Teritu* for their cooperation on their vessel's final cruise; the many people who assisted in collection of the samples; P. J. Wagner and G. L. Hoff for careful and competent sorting of the fishes and dry weight determinations, respectively; and K. Gopalakrishnan for identification of euphausiids and decapods. This research was supported by NSF GA-38423 and the State of Hawaii, Hawaii Institute of Marine Biology.

## LITERATURE CITED

- ANDERSON, R.  
1967. Feeding chronology in two deep-sea fishes off California. M.S. thesis, Univ. South. Calif., Los Ang., 11 p.
- BAIRD, R. C., T. L. HOPKINS, AND D. F. WILSON.  
1975. Diet and feeding chronology of *Diaphus taaningi* (Myctophidae) in the Cariaco Trench. *Copeia* 1975:356-365.
- BRINTON, E.  
1967. Vertical migration and avoidance capability of euphausiids in the California Current. *Limnol. Oceanogr.* 12:451-483.
- BURBIDGE, R. G.  
1974. Distribution, growth, selective feeding, and energy transformations of young-of-the-year blueback herring, *Alosa aestivalis* (Mitchill), in the James River, Virginia. *Trans. Am. Fish. Soc.* 103:297-311.
- CHILDRESS, J. J.  
1975. The respiratory rates of midwater crustaceans as a function of depth of occurrence and relation to the oxygen minimum layer off Southern California. *Comp. Biochem. Physiol.* 50A:787-799.
- CHILDRESS, J. J., AND M. H. NYGAARD.  
1973. The chemical composition of midwater fishes as a function of depth of occurrence off southern California. *Deep-Sea Res.* 20:1093-1109.
- CLARKE, T. A.  
1973. Some aspects of the ecology of lanternfishes (Myctophidae) in the Pacific Ocean near Hawaii. *Fish. Bull., U.S.* 71:401-434.  
1974. Some aspects of the ecology of stomiatoid fishes in the Pacific Ocean near Hawaii. *Fish. Bull., U.S.* 72:337-351.
- CLARKE, T. A., AND P. J. WAGNER.  
1976. Vertical distribution and other aspects of the ecology of certain mesopelagic fishes taken near Hawaii. *Fish. Bull., U.S.* 74:635-645.
- DEWITT, F. A., JR., AND G. M. CAILLIET.  
1972. Feeding habits of two bristlemouth fishes, *Cyclothone acclinidens* and *C. signata* (Gonostomatidae). *Copeia* 1972:868-871.
- EGGERS, D. M.  
1977. Factors in interpreting data obtained by diel sam-

- pling of fish stomachs. *J. Fish. Res. Board Can.* 34:290-294.
- GANNON, J. E.  
1976. The effects of differential digestion rates of zooplankton by alewife, *Alosa pseudoharengus*, on determinations of selective feeding. *Trans. Am. Fish. Soc.* 105:89-95.
- GJØSAETER, J.  
1973. The food of the myctophid fish, *Benthosema glaciale* (Reinhardt), from western Norway. *Sarsia* 52:53-58.
- GORDON, D. C.  
1970. Chemical and biological observations at Sta. Golum, an oceanic station near Hawaii, January 1969 to June 1970. *Rep. Hawaii Inst. Geophys., Univ. Hawaii, H.I.G.-70-22*, 44 p.
- HOLTON, A. A.  
1969. Feeding behavior of a vertically migrating lanternfish. *Pac. Sci.* 23:325-331.
- HOPKINS, T. L., AND R. C. BAIRD.  
1975. Net feeding in mesopelagic fishes. *Fish. Bull., U.S.* 73:908-914.  
1977. Aspects of the feeding ecology of oceanic midwater fishes. In N. R. Andersen and B. J. Zahuranec (editors), *Oceanic sound scattering prediction*, p. 325-360. Plenum, N.Y.
- KAMPA, E. M.  
1970. Underwater daylight and moonlight measurements in the eastern North Atlantic. *J. Mar. Biol. Assoc. U. K.* 50:397-420.
- KJELSON, M. A., AND G. N. JOHNSON.  
1976. Further observations of the feeding ecology of postlarval pinfish, *Lagodon rhomboides*, and spot, *Leiostomus xanthurus*. *Fish. Bull., U.S.* 74:423-432.
- LASKER, R.  
1970. Utilization of zooplankton energy by a Pacific sardine population in the California current. In J. H. Steele (editor), *Marine food chains*, p. 265-284. Univ. Calif. Press, Berkeley.
- LEGAND, M., P. BOURRET, P. FOURMANOIR, R. GRANDPERRIN, J. A. GUÉRÉDRAT, A. MICHEL, P. RANCUREL, R. REPELIN, AND C. ROGER.  
1972. Relations trophiques et distributions verticales en milieu pélagique dans l'Océan Pacifique intertropical. *Cah. O.R.S.T.O.M., sér. Océanogr.* 10:303-393.
- MARSHALL, N. B.  
1960. Swimbladder structure of deep-sea fishes in relation to their systematics and biology. *Discovery Rep.* 31:1-122.
- MAYNARD, S. D., F. V. RIGGS, AND J. F. WALTERS.  
1975. Mesopelagic micronekton in Hawaiian waters: Faunal composition, standing stock, and diel vertical migration. *Fish. Bull., U.S.* 73:726-736.
- MERRETT, N. R., AND H. S. J. ROE.  
1974. Patterns and selectivity in the feeding of certain mesopelagic fishes. *Mar. Biol. (Berl.)* 28:115-126.
- PANDIAN, T. J.  
1967. Transformation of food in the fish *Megalops cyprinoides*. I. Influence of the quality of food. *Mar. Biol. (Berl.)* 1:60-64.
- PARSONS, T. R., AND R. J. LEBRASSEUR.  
1970. The availability of food to different trophic levels in the marine food chain. In J. H. Steele (editor), *Marine food chains*, p. 325-343. Univ. Calif. Press, Berkeley.
- ROE, H. S. J.  
1972. The vertical distributions and diurnal migrations of calanoid copepods collected on the SONDR Cruise, 1965. I. The total population and general discussion. *J. Mar. Biol. Assoc. U.K.* 52:277-314.
- TATE, M. W., AND R. C. CLELLAND.  
1957. *Nonparametric and shortcut statistics in the social, biological, and medical sciences*. Interstate Printers and Publishers, Danville, Ill., 171 p.
- TEAL, J. M.  
1971. Pressure effects on the respiration of vertically migrating decapod crustacea. *Am. Zool.* 11:571-576.
- TYLER, H. R., JR., AND W. G. PEARCY.  
1975. The feeding habits of three species of lanternfishes (family Myctophidae) off Oregon, USA. *Mar. Biol. (Berl.)* 32:7-11.
- WISSING, T. E.  
1974. Energy transformations by young-of-the-year white bass *Morone chrysops* (Rafinesque) in Lake Mendota, Wisconsin. *Trans. Am. Fish. Soc.* 103:32-37.