

SOME ASPECTS OF THE ECOLOGY OF LANTERNFISHES (MYCTOPHIDAE) IN THE PACIFIC OCEAN NEAR HAWAII

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ABSTRACT

Most species of myctophids collected near Hawaii showed ontogenetic differences in vertical distribution and migration. Newly transformed juveniles of several species did not regularly migrate. Within both day and night depth ranges, the smaller fish tended to occur shallower than the adults. Few differences were related to sex or reproductive condition. Large fractions of populations of three species appeared not to migrate at certain seasons. Seasonal changes in size composition of populations and ripeness of mature females indicated that most abundant species spawn principally in the spring and summer and live about 1 year. The size-depth patterns of congeners and closely related species were quite different, while similar-sized individuals of dissimilar species tended to co-occur at the same depths.

Comparison of day and night estimates of abundance and size composition indicated that there was little differential avoidance by most species. There were differences between catches by a 10-ft Isaacs-Kidd trawl and a modified Cobb pelagic trawl related to both species and size with neither trawl showing a distinct advantage for all species. Comparison of catches at full and new moon indicated that at full moon most species occurred about 50 m deeper and avoided the Isaacs-Kidd trawl better than at new moon.

The average standing crop of myctophids was about 0.32 g(wet weight)/m², and the yearly turnover rate was estimated at roughly twice the standing crop. Myctophids and other vertically migrating micronekton appear to be very important in the trophic structure of the tropical open ocean and probably account for most of the consumption of zooplankton.

Myctophids or lanternfishes are one of the dominant families of mesopelagic fishes and are generally thought to be important in the open ocean ecosystem because of their frequent occurrence and apparently great abundances. The bulk of early work was concerned primarily with taxonomy and distribution. Most recent work has concentrated on one aspect of their ecology, diurnal vertical migration. Myctophids have been shown in a number of cases, e.g., Paxton (1967), Badcock (1970), to undertake substantial migrations from depths of several hundred meters during the day to the upper 100-200 m at night, but few studies have done more than describe the vertical distribution patterns and suggest possible relationships of these to gradients in temperature or light with depth or with the position of sonic scattering layers. There are numerous gaps in our knowl-

edge of other aspects of the ecology of this ubiquitous group of fishes. Moreover, previous work has not been equitably distributed in a geographic sense; most has been carried out at higher latitudes.

Among others, Badcock (1970) has indicated that there are size-specific differences in migration patterns of some species of myctophids, but ontogenetic changes in depth distribution have not been studied quantitatively. Similarly, Nafpaktitis (1968) has indicated that in some species of the genus *Diaphus* the mature females do not migrate. It is not known whether either of these patterns is typical or widespread within the family. Extensive life history data have been presented for some abundant northern species, *Benthosoma glaciale* (Halliday, 1970), *Stenobranchnus leucopsaurus* (Smoker and Percy, 1970), and *Myctophum affine* (Odate, 1966), but the life histories of most species, particularly tropical ones, remain unknown.

This paper presents and discusses data on myctophids collected in several series of mid-

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water trawl samples taken in the Central Pacific Ocean near Hawaii. The majority of the samples were collected during four series which attempted to cover the upper 1,000 m day and night at 3-mo intervals over a period of 1 year. The aims of the sampling were to determine the vertical migration patterns of the species present and to examine changes in abundance, size composition, and reproductive state with depth and season. In addition, changes in vertical distribution and avoidance with changing phases of the moon were investigated, and the catching ability of a 10-ft Isaacs-Kidd mid-water trawl was compared with that of a much larger anchovy trawl. The results allow detailed description of many aspects of the life history and ecology of myctophids. It is possible from these data to consider interspecific relationships with respect to time and space and to estimate the importance of myctophids and other micronekton in the tropical, open ocean ecosystem.

MATERIALS AND METHODS

A total of 221 mid-water trawl samples were taken for this study. Fifty-four were taken with a 6-ft Isaacs-Kidd (IK) mid-water trawl, 157 with a 10-ft IK trawl, and 10 with a modified Cobb pelagic trawl (CT). All trawls were fished without opening-closing devices. Thirty-seven IK tows were taken during September and November 1969 to provide preliminary data. The remaining tows consisted of four general types: a series of 31 6-ft IK tows taken in July 1970 to check various aspects of sampling, four series of 26-35 10-ft IK tows each taken at 3-mo intervals from September 1970 to June 1971, 17 10-ft IK tows taken in September and October 1971 to determine effects of moon phase on sampling, and 10 CT tows taken in conjunction with the 10-ft IK tows during February-March 1971.

All tows except those of November 1969 were taken west of the island of Oahu, Hawaii, roughly along a line between lat. 21°20'N; long. 158°20'W and lat. 21°35'N; long. 158°35'W. The depth of water for all tows was 1,800 m (1,000 fm) or more. BT casts to 300 m made during the study indicated that seasonal tem-

perature changes in the study area were nearly the same as for a nearby station (lat. 22°10'N; long. 158°W) studied more thoroughly by Gordon (1971). Presumably the depth profiles of other physical-chemical factors given by Gordon (1970, 1971) are also representative of the study area. The November 1969 tows were taken near Gordon's station.

The IK trawls were of standard dimensions and were lined with 6.35 mm (¼ inch) knotless nylon mesh anteriorly and 4.75 mm (3/16 inch) knotless nylon mesh posteriorly. The 10-ft IK terminated with a 1.0-m diameter plankton net of 333 μ nitex; the 6-ft, with a 0.5-m diameter net. The CT, described in detail by Higgins (1970), had 19-mm stretch mesh in the main body and a cod end lined with 6.35-mm mesh. Diver observations of the CT have indicated that the mouth opening under tow is about 12 m wide by 8 m high (Higgins, 1970).

IK trawls were fished from the University of Hawaii RV *Teritu*. Unless otherwise noted, the procedure was the same for all tows. The trawl was shot with the ship moving about 1.75 m/sec (ca. 3.5 knots), and the cable was paid out so that just enough tension was maintained to keep the net from fouling. For deeper (over 300 m) tows, the ship was slowed to ca. 1.0 m/sec for a few minutes after the cable was paid out to allow the trawl to sink farther. These procedures were designed to minimize forward motion while the trawl descended to towing depth. The trawl was towed at depth for 2-3 hr at a speed of about 1.75 m/sec. For retrieval, the ship was slowed to ca. 1.0 m/sec, again to minimize forward motion while the trawl was above sampling depth. Cable was retrieved as fast as possible; the average rate varied between 30 and 60 m/min. The rate was considerably faster than 60 m/min when there was more than 1,000 m of wire out. The CT was fished in a similar manner from the National Marine Fisheries Service (NMFS) RV *Townsend Cromwell*.

Depth of tow was determined by time-depth recorders (Benthos, Inc.)² attached to the trawl. For depths of less than 300 m the trawl reached

² Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

towing depth within a few minutes after cable was paid out and usually stayed within 5 m of this depth during the entire tow. For deeper tows, the trawl frequently took some time to descend to maximum depth and often moved up and/or down gradually during the tow. In all cases, however, a single, most frequently fished depth was assigned to each tow.

For some IK tows an acoustic telemeter (Benthos, Inc.) was used to determine depth while underway and to reach desired depth, but in most cases the amount of cable required to reach a given depth had to be estimated beforehand. This method required some practice, and, needless to say, depth coverage was more even for the later cruises.

Towing speed for the IK was, in some cases, measured by a TSK flowmeter attached to the trawl and rigged to signal, through the telemeter, every 500 revolutions. In all cases, position of the ship was determined by visual or radar fixes at ½- to 1-hr intervals during the tow and speed calculated from these data. The towing speed for the IK varied between 1.54 and 1.98 m/sec with most tows about 1.75 m/sec. The CT was towed at about 1.5 m/sec.

Assuming 100% filtering efficiency and a speed of 1.75 m/sec, the 10-ft IK sampled about 9.4×10^4 m³ per 2-hr tow. At 1.5 m/sec, the CT sampled just over 10^6 m³ per 2-hr tow or about 11 times the IK tows. Only fish over 10-mm long were considered sampled quantitatively by the IK since smaller individuals could pass through the meshes. Larger fish, up to 25-30 mm long, appeared to escape through the CT meshes.

The July 1970 (5-10 July 1970) series of tows with the 6-ft IK were designed primarily to determine whether significant changes in vertical distribution occurred in the upper layers during the course of night and to obtain an estimate of sample variability. At depths of 50 m and 100 m, five 2-hr tows were taken from dusk to dawn on a single night, and one replicate tow was made during the following night. Dusk, dawn, and night tows were taken at other depths in the upper 400 m. In addition, day tows were taken between 500 and 1,125 m.

The four quarterly series of 10-ft IK tows were designed to sample for seasonal changes

and were intended to be replicate surveys of the upper 1,000 m both day and night. Since preliminary day tows caught no nonlarval myctophids above 300 m, no attempt was made to cover the upper layers during the day. The dates of the cruises were 14-17 and 20-24 September 1970; 8-10 and 13-17 December 1970; 26 February-3 March and 19 March 1971; and 8-11 and 15-19 June 1971. The series will subsequently be called September 1970, December 1970, March 1971, and June 1971. Depths sampled for these series and the July 1970 series are given in Figure 1.

In addition to some gaps in depth coverage during September 1970, the shallow night tows were made at both full and new moon. Subsequent analyses showed that the depth distribution and avoidance for many species changed considerably with moon phase, and as a consequence, some populations were sampled

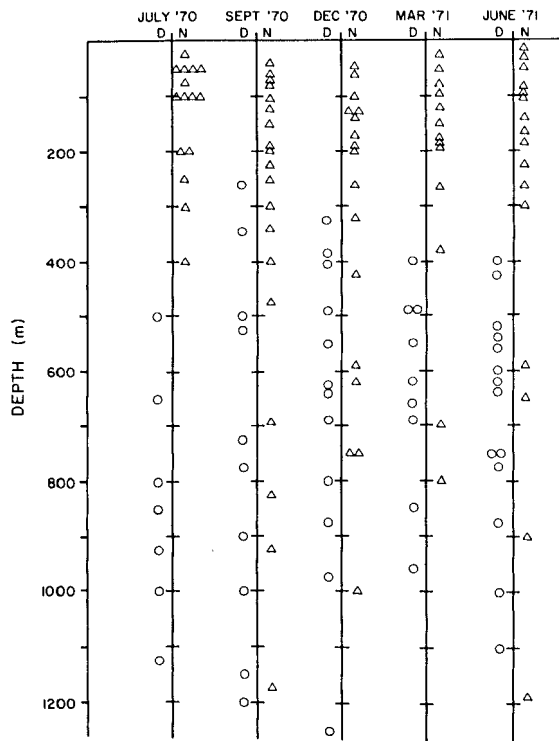


FIGURE 1.—Depths of Isaacs-Kidd trawl samples taken during July 1970, September 1970, December 1970, March 1971, and June 1971. Day samples are designated by circles, night samples by triangles.

twice and others not at all during the September 1970 series. This also occurred to a lesser extent during the December 1970 series. All night tows above 200 m were made during new moon for the March 1971 and June 1971 series. The March 1971 series was incomplete due to a storm, and the 400-700 m zone was not sampled at night. Such limitations are taken into account in interpreting the data.

The CT tows were taken in conjunction with the March 1971 IK series. Eight night tows were taken at 25-m intervals between 25 and 200 m during the same three nights that IK tows were taken at or near these depths. The IK-CT pairs were unfortunately not all taken simultaneously. All tows but one were 2 hr at depth; the 25-m CT tow was only 15 min long, but catches of some species were sufficient for useful analyses. Two day tows at 300 and 400 m were also taken with the CT during this period.

To determine effects of moon phase on vertical distribution and avoidance at night, 10-ft IK tows of 1½ hr each were made at depths of 15, 45, 65, 80, 100, 125, 145, and 165 m on 17-19 September 1971 (new moon) and at 20, 50, 75, 100, 130, 170, and 190 m on 4-6 October 1971 (full moon). This series, designated September 1971, also provided useful data on other aspects.

During December 1970 and June 1971, three and four, respectively, short oblique tows were made to depths of 250-300 m at night in order to roughly estimate the catch due to ascent and descent through the upper layers. The cable was paid out as described above, but the ship was slowed and the trawl retrieved immediately. A longer oblique tow was made in June 1971 to 330 m at night. Fifty meters of cable was paid out every 15 min in an attempt to sample all depths equally.

The dusk and dawn tows taken during July 1970 indicated that myctophids had completed their upward migration by 2000 hr and had begun to descend by 0400-0500 hr. All subsequent night tows were taken between these times. Differences between tows taken in sequence at 50 and 100 m through the night were not markedly greater than differences between tows taken at the same hour on two successive nights. There was no trend among the species which indicated that anything

analogous to a "mid-night dispersal" occurred. Therefore, all night tows were considered together regardless of what period of the night they were taken. No comparable study was made to check on possible changes in depth distribution during the day. It was assumed that no changes took place during the day between 0800 and 1600 hr.

Specimens were preserved in Formalin. Standard length was measured to the nearest mm for all collected by IK. For some CT collections of over 1,000 individuals per species, a subsample of several hundred was measured. Wet weights of blotted specimens were determined to the nearest mg for small individuals and to the nearest 10 mg for larger fish or whole samples.

Insufficient replicate samples were taken to reliably specify the variance associated with the estimate of abundance from a single tow. There was considerable variability in the catches of the two series of four tows each taken at 50 and 100 m in July 1970. (Appendix Table 1.) In particular, one tow in the 100 m series caught much higher numbers of several species. This variability, probably related to patchiness in the organisms sampled and differences in avoidance due to differences in ship's speed, cloud cover (light), etc., limits interpretation of some of the data. Where I have drawn conclusions without statements of statistical significance, I have attempted to be conservative. Features not consistently evident from a series of tows should be regarded as tentative.

The significance of differences between two samples in size composition was determined using the Kolmogorov-Smirnov test (Tate and Clelland, 1957). Two samples were considered significantly different if the probability (one-tailed) associated with the maximum difference between the cumulative size-frequency curves was less than 0.05. The overall significance of the differences is somewhat altered because multiple tests were often made with the same data. In most cases, the trends observed were obvious and consistent, and it is doubtful that large errors resulted from the procedure.

There were relatively few significant differences in size composition between replicates at the same depth. For 10 sets of data for eight

species caught in abundance in the replicates at 50 and 100 m during July 1970, there were no significant differences between size-frequency curves in seven and only one sample in each of the other three sets differed significantly from one or more of the other replicates.

Not all individuals were sexed and no detailed gonad studies were done. Size at maturity was taken as the minimum size at which females were found with obviously ripened ova. A variable number of each species were examined. For abundant species, sex was determined for about 50 juveniles, and sex ratio of mature fish and ripeness of mature females were determined for samples from several depths and seasons. If significant or nearly significant differences between samples were noted, a larger series was examined to determine trends. It was assumed that the percentage of females among mature fish and the percentage of ripe out of total mature females were distributed as a binomial and that the differences in percentages were considered significant if the 95% confidence limits did not cross zero.

For species collected in low numbers, the data from each series were simply pooled to estimate overall size composition and relative abundances. For abundant species, total numbers and overall size composition for the entire water column were computed by a rectangular integration of the depth-abundance curves. Numbers collected were adjusted to a 2-hr towing time. It was assumed that abundance and size composition from the depth sampled were the same for the layer between the mid-points between that depth and the next shallower and next deeper depth sampled; i.e., abundance estimated from a sample at depth z_i was assumed constant throughout $(z_{i-1} + z_i)/2$ to $(z_i + z_{i+1})/2$ where z_{i-1} was the next shallower depth sampled and z_{i+1} the next deeper. The number of individuals of each size in each sample was weighted accordingly.

Differences in the numbers and size composition of these calculated totals could not be compared statistically since no estimate of the variances of the data were available, but where depth coverage was adequate, calculated totals and size-frequency curves were used to roughly compare whole series for day and night, sea-

sonal, full and new moon, and IK and CT differences. The calculated size-frequency curves for December 1970 and June 1971 could be compared with those of the oblique tows when sufficient specimens of a given species were taken in the latter. Unless there were obvious deficiencies in depth coverage, etc., the calculated curves agreed closely with those from the oblique tows.

RESULTS

A total of 47 species of myctophids were collected. The number collected, size range, size at maturity for females, and day and night depth ranges are given in Table 1. Unless noted under individual species headings (below), the individuals caught did not deviate from species descriptions in Wisner (1971, *manuscr.*³), Nafpaktitis (1968), or Nafpaktitis and Nafpaktitis (1969).⁴ The percentage of ripe females among total mature females examined for each of the four quarterly cruises is given for several abundant species in Table 2.

The depth ranges given in Table 1 are the best estimates based on all available data. Because the trawl was open during descent and ascent, some individuals were caught in tows made below the levels where they occurred. For abundant species, catches below the depth ranges given were low and consistently close to those of short oblique tows (see Appendix Table 2). A few cases where substantial numbers were caught near the day depth at night are discussed below under the species headings. For rarer species, where the chances of being caught in a tow at their actual depth were not much greater than the chances of being caught in transit by deeper tows, catches due to contamination could not be readily distinguished and the lower depth limits in Table 1 may be erroneous. In most cases, the values given are conservative.

³ Wisner, R. L. Unpubl. *manuscr.* Annotated and illustrated key to the identification of fishes of the family Myctophidae of the eastern Pacific Ocean, eastward of 160° West Longitude.

⁴ Specimens of most species will be deposited at the U.S. National Museum, Los Angeles County Museum, Scripps Institution of Oceanography, and the Bernice P. Bishop Museum in Honolulu.

TABLE 1.—List of myctophid species collected, the number collected, size range, size at maturity, night and day depth ranges, and seasons when juveniles were present or present in markedly higher abundances. Under "Number collected" the figures given are the totals from the four quarterly series of samples; where few or none were caught in these series, the total number caught in all other samples is given in parentheses. Figures in parentheses under "Size range" are for dipnetted specimens.

Species	Number collected	Size range (mm)	Size at maturity (mm)	Night depth (m)	Day depth (m)	Juveniles
<i>Protomyctophum beckeri</i>	0 (3)	34-38	—	400 ?	400 ?	—
<i>Benthoosema suborbitale</i>	1,157	9-38	25	15-75	490-620	June (Mar.)
<i>Benthoosema fibulatum</i>	14 (30)	10-72	—	15-165	500-550	—
<i>Diogenichthys atlanticus</i>	27	12-22	17	15-100	400-600	—
<i>Hygophum proximum</i>	696	12-51	38	25-150	500-700	June, July
<i>Hygophum reinhardti</i>	413	12-48	33	50-175	550-900	all ?
<i>Myctophum nitidulum</i>	18 (34)	13-54 (65)	57	0-15?	600-800	—
<i>Myctophum obtusirostrum</i>	15 (59)	12-63 (77)	58	0-15?	500-700	—
<i>Myctophum spinosum</i>	5 (32)	34-93 (115)	110 ?	0-15?	600 ?	—
<i>Myctophum selenoides</i>	14 (24)	9-67	62	25-150	300-500	Mar., June
<i>Symbolophorus evermanni</i>	186	15-86	70	0-125	600-900	—
<i>Loweina laurae</i>	2 (3)	22-43	—	250 ?	690 ?	—
<i>Loweina terminata</i>	1	22	—	—	825	—
<i>Centrobranchus choerocephalus</i>	22	12-37	29	0-150	490-650	—
<i>Centrobranchus andreae</i>	4 (6)	14-47	—	100-165	640-650	—
<i>Lobianchia gemellari</i>	177	9-59	41	25-360	410-560	June, July, Sept.
<i>Lobianchia urolampa</i>	1 (1)	25-26	—	100 ?	—	—
<i>Diaphus bertelseni</i>	6 (79)	17-38	—	100-150	300 ?	—
<i>Diaphus "glandulifer"</i>	37	12-73	55	95-225	425-600	—
<i>Diaphus schmidti</i>	823	9-47	31	15-80	490-625	June, July, Sept.
<i>Diaphus fragilis</i>	56	10-83	61	15-120	520-600	Sept.
<i>Diaphus rolfbolini</i>	104	9-76	65	50-200	490-690	June, July, Sept.
<i>Diaphus elucens</i>	132	7-65	48	15-100	490-600	Sept.
<i>Diaphus adenomus</i>	7	71-126	—	—	495-550	—
<i>Diaphus chrysothynchus</i>	7 (27)	11-84	—	75-125	550	—
<i>Diaphus metopoclampus</i>	1	49	—	185	—	—
<i>Diaphus theta</i>	0 (1)	23	—	145	—	—
<i>Diaphus sp. A</i>	253	9-36	25	25-85	490-525	July, Sept.
<i>Diaphus sp. B</i>	165	9-64	42	30-190	490-560	June
<i>Diaphus anderseni</i>	261	10-29	20	95-260	300-560?	June, July, Sept., Dec.
<i>Diaphus brachycephalus</i>	100	9-61	28	30-200	300-600?	June, July, Sept.
<i>Notolychnus valdiviae</i>	1,267	9-25	20	80-150	525-640	Sept. (Mar., June)
<i>Lampadena luminosa</i>	77	15-77	—	75-250	525-725	June, July, Sept.
<i>Lampadena urophaos</i>	44	17-115	100 ?	95-140	620-775	—
<i>Lampadena anomala</i>	1 (2)	30-49	—	300-400	800	—
<i>Taaningichthys bathyphilus</i>	55	20-72	51	590-930	620-800	—
<i>Taaningichthys minimum</i>	71	20-64	53	150-475	640-775	Mar.
<i>Taaningichthys paurolychnus</i>	2	20-22	—	1,175	1,000	—
<i>Lampanyctus niger</i>	1,946	12-135	60	100-310	640-900	Dec. (Sept.)
<i>Lampanyctus nobilis</i>	384	15-114	98	40-140	590-1,200	all ?
<i>Lampanyctus steinbecki</i>	2,362	14-56	43	80-275	625-1,000	July, Sept.
<i>Lampanyctus tenuiformis</i>	14	28-136	125	250-300	640-775	—
<i>Triphoturus nigrescens</i>	2,120	9-38	30	25-75	540-775	June, July
<i>Bolinichthys longipes</i>	1,458	11-56	37	50-150	525-725	June, July, Sept.
<i>Bolinichthys supralateralis</i>	85	12-90	88 ?	95-225	490-690	Sept., Dec.
<i>Ceratoscopelus warmingi</i>	3,911	11-79	45	15-140	620-1,000	Mar., June, July
<i>Notoscopelus caudispinosus</i>	6 (17)	20-125	111 ?	75-125	590-680	—

Eight species—*Protomyctophum beckeri*, *Loweina laurae*, *L. terminata*, *Centrobranchus andreae*, *Diaphus metopoclampus*, *D. theta*, *Lampadena anomala*, and *Taaningichthys paurolychnus*—were taken so rarely that little other than their capture in the area can be noted. For 39 species, the individual accounts

below include where possible the following aspects: deviations from depth ranges given in Table 1; changes in size composition and sex ratio with depth; differential avoidance between day and night, IK and CT, and full and new moon; and changes in size composition, abundance, and reproductive state with season.

TABLE 2.—Proportion of females with developed ova among total mature females (figures in parentheses) examined for 10 species from September 1970 and 1971, December 1970, March 1971, and June 1971 samples. Significant differences between values are noted in text.

Species	September	December	March	June
<i>Benthoosema suborbitale</i>	0.39 (18)	0.98 (62)	1.00 (38)	— (0)
<i>Hygophum proximum</i>	.78 (37)	.72 (7)	0.91 (22)	0.86 (22)
<i>Diaphus schmidti</i>	.375 (8)	— (0)	.88 (59)	1.00 (11)
<i>Diaphus</i> sp. A	.96 (46)	1.00 (8)	.89 (9)	1.00 (14)
<i>Notolychnus valdiviae</i>	.70 (54)	.71 (69)	.91 (11)	.89 (38)
<i>Lampanyctus niger</i>	.35 (51)	.76 (95)	.88 (69)	.53 (47)
<i>Lampanyctus steinbecki</i>	.64 (42)	.44 (22)	.81 (103)	.78 (122)
<i>Triphoturus nigrescens</i>	.54 (13)	.39 (142)	1.00 (41)	.94 (36)
<i>Bolinichthys longipes</i>	.67 (12)	.12 (17)	.81 (70)	.88 (17)
<i>Ceratoscopelus warmingi</i>	.60 (102)	.62 (124)	.52 (48)	.70 (27)

Differences in sex ratio with size and season are of somewhat dubious significance and will be treated in the discussion.

Benthoosema suborbitale

Small (10-12 mm) *B. suborbitale* tended to remain at depth both day and night. On all three cruises where night samples were taken near the day depth, low but probably significant numbers of small fish were taken. In June 1971, the number caught at about 550 m was nearly equal to that caught at 25 m at night and at the same depth during the day. In all cases except the June 1971 series the size-frequency curves of the deep night catches differed significantly from those of most other tows, the differences being due to much greater proportions of 10- to 12-mm fish in the deep night tows. There was no evidence that larger fish did not migrate regularly.

The depth ranges for this species were rather narrow relative to the sample spacing, and populations at a given time were usually made up of one size class. There were, however, significant differences between the size-frequency curve at 25 m and those at 50 and 80 m in March 1971. The difference was due to the absence of fish <25 mm at 50 and 80 m rather than a decrease of larger fish at 25 m. Other night series also showed a trend for smaller fish to occur higher in the water column.

There was no indication of differential day-night avoidance. The calculated size-frequency curves for day and night samples from each series agreed quite well with each other, except

for June 1971. The total calculated numbers agreed well in June 1971, but for the other series, the day totals were 1.5–2× higher than the night totals. This difference was probably a result of the weighting factors assigned to the day tows being too large, i.e., the depth range was probably narrower than the relatively wide-spaced samples indicated.

The IK appears to sample *B. suborbitale* as well or better than the CT. The calculated total for the CT series was 7× that for the IK; factors for individual pairs varied between 4.2 and 8.8×. There were no significant differences between size-frequency curves of IK-CT pairs at the same depths, and the calculated curves for the two series agreed well. The fact that the CT size-frequency curves did not differ from those of the IK suggests that the lower CT estimates of abundance were not due to escape-ment through the meshes. If the latter had been substantial, the smaller fish would have escaped more frequently, and size composition of the catches would have differed from those of the IK.

At new moon, *B. suborbitale* occurred mostly above 50 m at night; at full moon the population was centered at about 75 m with practically none above 50 m (Figure 2). The size-frequency curves of both the individual samples and those calculated from the new and full moon series agreed closely. The numbers at peak depths were similar, and the calculated total for new moon was only 1.25× that for full moon. Thus the change in depth distribution apparent in the full moon samples was mainly if not totally due to a depression of the night depth by about 50 m.

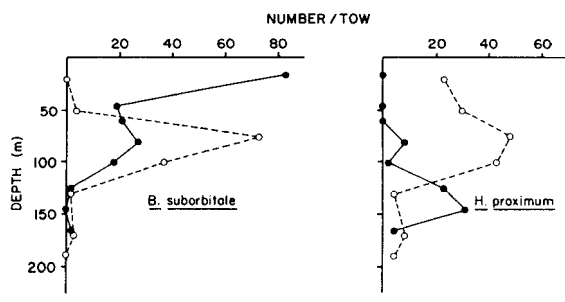


FIGURE 2.—Number of individuals of *Benthosema suborbitale* (left) and *Hygophum proximum* (right) caught per tow at several depths in the upper layers at night during new moon (solid circles and lines) and full moon (open circles, dashed lines) during September 1971.

Size composition and abundance showed a definite seasonal pattern. In June 1971, about 70% were 10-15 mm; there were a few adults and practically no intermediate sizes. The calculated size-frequency curves (Figure 3) shifted to the right from June to March indicating changes in size-composition due to growth. Though calculated day totals were higher than night totals for all but the June 1971 series, the rank order was the same for both, abundances being highest in December, lowest in June, and intermediate and nearly equal in September and March.

It appears that *B. suborbitale* spawns principally in the spring and summer. A few young (10-15 mm) are present by March and many by June. A substantial portion are 20-25 mm long

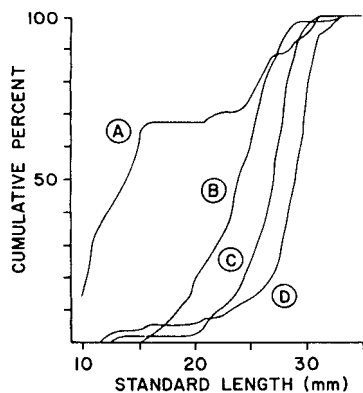


FIGURE 3.—Cumulative size-frequency curves for *Benthosema suborbitale* at four seasons. Size composition was calculated (see text) from samples taken throughout the water column in June 1971 (A), September 1970 (B), December 1970 (C), and March 1971 (D).

by September, but apparently not all have reached the minimum size caught by the trawl until later. Most fish are mature by December when maximum abundance occurs. There is apparently little growth in size between December and March and a decrease in total numbers. By June, most of the adults are gone and the next generation has begun to reach trawlable size. The percentages of mature females with ripe ova (Table 2) correlate with these trends; they were significantly higher in December and March, before the periods when juveniles appeared.

Benthosema fibulatum

B. fibulatum is apparently epibenthic or restricted to nearshore areas. In Hawaii, large individuals (45-95 mm) are regularly taken in bottom trawls at depths of 100-190 m at night (P. J. Struhsaker, pers. comm.), and large catches have been made by NMFS in CT tows at 25-100 m over areas where the bottom depth is about 600 m. Only eight of the individuals taken during this study were of the size taken by inshore trawls, 40-72 mm. The rest were 15-27 mm and mostly taken in the upper 100 m at night.

Diogenichthys atlanticus

D. atlanticus, although quite abundant in the Equatorial Pacific (Hartmann, 1971), was captured rarely in Hawaiian waters. About 80% of the individuals collected were adults, but the presence of 11- to 15-mm fish several times of the year suggests some spawning may occur in this area.

Hygophum proximum

In June 1971, nine small *H. proximum* (12-14 mm) were caught at about 650 m at night. As low as this catch was, it was higher than any shallow night catch and unlikely due to contamination. Similar numbers of this size were caught near this depth during the day and none in the shallow night tows, suggesting that the smallest *H. proximum* caught by the trawl do not regularly migrate. Individuals of this

size were, however, taken in shallow night tows during July 1970 and March 1971.

H. proximum appeared to avoid the IK at night more during new moon (see below) and was sampled best by the CT and by the full moon IK series. Both of these series indicated similar depth distribution but different trends in size composition with depth (Figure 4). In the CT series the curves for 75, 100, and 125 m were all similar and differed significantly from those at 25 and 50 m. Over 50% of the deeper catches were less than 30 mm. Over 50% of the deeper catches were less than 30 mm, most about 20 mm. In the 25- and 50-m catches, which also differed significantly from each other, only 30% and 10% individuals were under 30 mm. Comparison of curves from IK catches at new moon during December and March 1971 also showed significant differences, with only the larger fish occurring above 50-60 m and smaller ones predominating deeper.

In the September 1971 series, the size-frequency curves for full moon tows at 25 and 50 m differed significantly from each other and

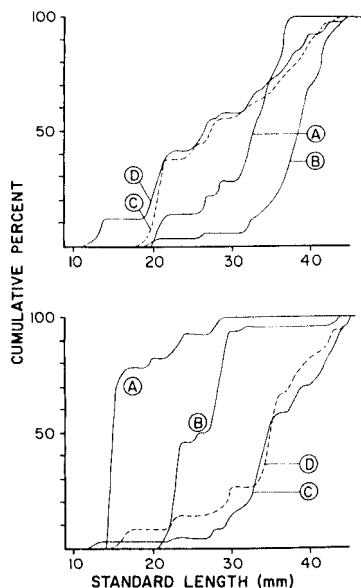


FIGURE 4.—Cumulative size-frequency curves for *Hygophum proximum* collected at different depths in the upper layers at night. Top: Cobb trawl samples taken at new moon during March 1971; depths of tows and number of individuals were: 25 m, 14 (A); 50 m, 150 (B); 75 m, 276 (C); and 100 m, 83 (D). Bottom: Isaacs-Kidd samples taken at full moon in September 1971 at 20 m, 23 (A); 50 m, 30 (B); 75 m, 48 (C); and 100 m, 43 (D).

from the curves at 75 and 100 m. The catch was almost all <15 mm at 25 m, 20-30 mm at 50 m, and over 30 mm for the deeper tows. In full moon tows during September 1970 at 80 and 100 m, the size-frequency curves differed significantly and indicated that most fish at 80 m were <30 mm and most at 100 m were >30 mm.

In the daytime during September 1970, size-frequency curves for *H. proximum* differed significantly, with a greater proportion of juveniles in shallower water. In March 1971 and June 1971, similar nonsignificant trends were present. All data indicated that individuals over 40 mm rarely occurred above 600 m.

At new moon during September 1971, high catches were made at 125 and 150 m with a few at 80 m (Figure 2). At full moon, catches were high between 20 and 100 m with practically none deeper. The calculated total for full moon was 3× that for new moon, and the calculated size-frequency curves indicated that new moon tows had missed most of the larger fish. These data, combined with the changes in size composition with depth, indicate that the smaller fish occur about 75-100 m deeper at new moon and the adults about 25-50 m shallower at new moon. The latter, however, appear to avoid the IK much more at new moon. Consequently, *H. proximum* was not sampled well by most IK night series.

The CT data also indicate that avoidance of the IK by larger fish was substantial. The calculated total for the CT series was 14.5× that for the March 1971 IK night series, and calculated size-frequency curves indicated much lower proportions of larger fish in the IK catches. The greatest difference was at 75 m where the IK caught only 5 as opposed to the CT's 276. Comparison of individual size-frequency curves indicated that some fish under 20 mm probably passed through the CT's meshes. Thus avoidance of the IK by larger fish is even greater than indicated by comparison of the calculated totals.

The calculated totals were much larger for the day series in March 1971 and June 1971, but day and night totals were close for September 1970 when the night tows in *H. proximum*'s depth range were taken during full moon. (Few were caught in December 1970 during day or

night.) Both of the September 1970 estimates were close to that for full moon in September 1971. Thus there appears to be less avoidance of the IK during the day than at night during new moon.

For March 1971, the calculated total from the CT series was only about $3.7\times$ that of the day IK series, and the calculated size-frequency curves for the two series agreed closely. Thus the IK appears to sample *H. proximum* by day better than the CT at night. Since day tows and full moon night tows with the IK appear to sample this species about equally well, the IK may give better estimates of abundance and size composition than the CT at full moon. Kuba (1970) found that the IK sampled *H. proximum* better than the CT in night tows in equatorial waters. Most of his tows where this species was caught were taken near full moon.

The calculated day totals indicated that *H. proximum* was distinctly more abundant in September and March than in December or June. The calculated size-frequency curves for March 1971 and September of both years were similar and indicated that most fish were mature or nearly so. None less than 15 mm were caught in September or December, but a few 10-15 mm were caught in March 1971. Fish 12-14 mm long were present in fair numbers during the June 1971 series and abundant in July 1970. This suggests that *H. proximum* spawns principally in spring or early summer. The percentages of mature females with developed ova were highest in March and June but did not differ significantly from the other values.

Hygophum reinhardti

H. reinhardti was less abundant and occurred slightly deeper than its congener, *H. proximum*, but the data indicated that similar sampling problems existed. So few *H. reinhardti* were caught in the March 1971 IK series that it was impossible to make quantitative comparisons with the CT data, but it appeared the IK missed substantial numbers at 75-100 m and sampled about as well as the CT in deeper water. Though catches were low during both September 1971 series, the full moon series caught overall higher numbers and indicated a

shallower night depth than the new moon series. In all four regular series, catches of day tows were generally higher than those of night tows.

Size-frequency curves from the CT series indicated no trends in size composition with depth. The curves for IK tows in September 1970 at 150 and 195 m differed significantly with few fish >20 mm at 195 m and few <20 mm at 150 m. Three-day tows in September 1970 showed no individuals over 20 mm at 520 m and most over 20 mm at 775 and 900 m. There were no obvious seasonal changes in abundance. Juveniles (<15 mm) and females with developed ova were present at all seasons.

Myctophum spp.

Three species of *Myctophum*—*M. nitidulum*, *M. obtusirostrum*,⁵ and *M. spinosum*—apparently occur at or near the surface at night. They were regularly dipnetted at the surface at night, but few were caught in the trawls, even in preliminary tows at 10-m depth. Individuals considerably larger than the trawl-caught specimens were frequently taken by dip net. These species are relatively solid-bodied and are probably strong swimmers. They probably avoid the trawl easily in the process of avoiding the ship itself.

The few day catches of these species were mostly from 500 to 800 m but may well have been due to contamination. These species are distinctly countershaded, and in life the upper color is quite blue, suggesting that they occur at shallow, well-lighted depths during the day where they can avoid the trawl. Nevertheless, the rarity of even small individuals in the trawl catches indicates that none of the three were abundant.

Myctophum selenoides

At night, small (<30 mm) *M. selenoides* were taken mostly between 50 and 100 m. The larger fish were below 100 m and mostly around 150 m. Only three were taken during the day, one by

⁵ *Myctophum obtusirostrum* is the correct name for the species called *M. brachygnathum* by Nafpaktitis and Nafpaktitis (1969) and others (B. G. Nafpaktitis, pers. comm.).

CT at 300 m and two by IK at 500 m. The low numbers of juveniles as well as adults in the trawl catches suggest that rarity of *M. selenoides* was not due to avoidance. Small fish (8-13 mm) were caught only in March and June 1971, indicating that this species spawns locally—probably in the spring.

Symbolophorus evermanni

The larger individuals of *S. evermanni* are undersampled by the IK. Kuba (1970) showed this in Equatorial Pacific waters. During March 1971 CT catches were 28-35/tow as compared with 1-2/tow for the IK at similar depths. The CT tows indicated that *S. evermanni* was most abundant at 50-100 m at night and showed no differences in size frequency with depth. On one occasion, November 1969, several large individuals were dipnetted at the surface.

Day tows with the IK caught no individuals above 500 m and most between 600 and 800 m. A few substantial catches, 6-8/tow, came from 800 to 900 m. There was some indication that fish <20 mm do not regularly migrate; particularly in September 1970, most of the shallow catches were larger fish, and most small individuals were taken in night tows around 800 m.

Centrobranchus choerocephalus

Most catches of *C. choerocephalus* were at 550-650 m during the day. The night depth appeared to be between 100 and 200 m for both IK and CT samples, but on one occasion, September 1969, seven individuals were dipnetted at the surface.

Lobianchia gemellari

L. gemellari was never taken in large numbers. At night, all individuals caught above 100 m were <25 mm, and those over 40 mm were caught only below 150 m. The CT series, which caught fair numbers, also showed this trend with significant differences in size-frequency curves. Substantial catches of larger fish were made as deep as 300 m at night, but there were no differences in sex ratio or

percentage of ripe females between deep and shallow catches of adults.

There was no evidence that this species avoided the IK better than the CT nor that there was a day and night difference in avoidance of the IK. Also the depth distributions and abundances in full and new moon were not grossly different.

The pooled IK data indicated that juveniles, <25 mm, were most abundant in the summer (July 1970, June 1971) and least so in December 1970. Curiously, there were few juveniles present in September 1970 but many in September 1971. Adults were most abundant in March 1971 when few juveniles were present.

Lobianchia urolampa

Only two juvenile *L. urolampa* were taken in this study. This species is apparently nearshore or epibenthic. Adults (48-99 mm) have been taken in bottom trawls at depths between 124 and 190 m at night (P. J. Struhsaker, pers. comm.).

Diaphus bertelseni

The identity of this form with the Atlantic *D. bertelseni* is not certain since only one large individual was taken. The species was caught on only two occasions. Many were taken in the March 1971 series including 70 in one CT tow at 125 m at night. One each was taken at 300 and 400 m with the CT during the day suggesting that this species has a shallow day depth. All March 1971 specimens were between 17 and 31 mm—most between 17 and 25 mm. The only other individual taken was a 38-mm specimen from 100 m at night during the July 1970 series.

Diaphus "glandulifer"

The form designated here as *D.* "glandulifer" appears to be an undescribed species (R. L. Wisner, pers. comm.). Gill raker counts were mostly 8+1+15-16, lower than those for *D. glandulifer* from the Western Pacific (Wisner, see footnote 3). Accessory luminescent tissue occurred regularly in specimens over 30 mm

at POL, VLO, SAO-3, Pol, and Prc-4. In 8 out of 20 specimens over 50 mm, there was accessory tissue at PO-4, VO3, or both.

Only small (<20 mm) *D. "glandulifer"* were caught above 150 m, the larger individuals being around 200 m and deeper at night. This species was rare at all seasons, and most specimens were either in a 27-39 mm group or over 45 mm. Catches of a few less than 20 mm suggest that this species may occasionally spawn in the area.

Diapbus schmidti

There was no indication that any sizes of *D. schmidti* sampled by the trawl did not regularly migrate to the upper layers at night. There were significant differences in size-frequency curves from different depths at night. The number and percentage of juveniles (<25 mm) were greatest around 25 m. The number of larger fish was greatest at 50 m, but the percentages of small and large fish were roughly equal. At 75-80 m most or all the individuals were larger. Only the day samples from March 1971 were spaced closely enough to suggest that there were similar size-frequency changes within the day depth range.

Because *D. schmidti* occurred over a relatively narrow depth range during the day and was frequently caught in only one tow per series, it was impossible for some series to assign realistic weighting factors for calculation of total numbers. However, the calculated night size-frequency curves agreed closely with those of the day samples.

The calculated size-frequency curves for CT and IK in March 1971 agreed quite closely, but the calculated total for the CT was $15 \times$ that of the IK. The difference in totals was due to relatively much greater catches by the CT at 75 and 100 m. The CT caught only 1.7 and $6.3 \times$ the IK at 25 and 50 m, but caught 65 and $45 \times$ more at 75 and 100 m, respectively. The pairs of individual size-frequency curves at 25 and 50 m differed significantly and indicated that the IK caught more larger fish, while the curves at 75 and 100 m from the CT did not differ from those of the IK at 80 m. Since both large fish and juveniles occurred shallower and only

large fish deeper, it appears that the CT under-sampled larger fish in shallow zones and the IK undersampled them in deeper zones.

The full moon samples indicated that peak depth was around 75 m and caught none at 20-50 m where new moon tows indicated maximum abundance. The calculated total for full moon was about three-fourths that of new moon, and the calculated size-frequency curves indicated a somewhat larger proportion of juveniles during full moon. Thus *D. schmidti* occurs deeper at full moon, and larger individuals may avoid the net more frequently.

D. schmidti apparently spawns in late spring and summer and matures in about 1 year. In June 1971, the population consisted mostly of either juveniles or adults with few individuals between 20 and 30 mm. Both juveniles and 20- to 30-mm individuals were present in September 1970 and 1971. In December 1970, almost all were 20-30 mm, and in March 1971, almost all were over 30 mm. Percentages of ripe females were significantly higher in the March and June 1971 series than in the September 1971 series. Practically none were mature in December 1970.

Diapbus fragilis

D. fragilis was caught most frequently at night at 25-50 m (new moon) and 100-125 m (full moon). The CT catches were low and did not indicate that this species was avoiding the IK in appreciable numbers. *D. fragilis* was distinctly more abundant in September 1970 and 1971 and least so in December 1970 and March 1971. It is one of the dominant species of myctophids in Pacific equatorial waters (Hartmann, 1971) but its presence in low numbers near Hawaii cannot be ascribed entirely to immigration. Fair numbers of small (<20 mm) individuals were caught in September, suggesting that some spawning occurs in the summer.

Diapbus rolfbolini

Pooled size-depth data indicated that *D. rolfbolini* <20 mm occurred principally above 100 m, those 20-45 mm around 100 m, and

those over 45 mm below 125 m. *D. rolfbolini* was caught in roughly similar numbers at all seasons; however, trends in size composition were evident from the pooled data. In July 1970, September 1970 and 1971, and June 1971, 50% or more of the catches were <20 mm. In December 1970, almost all were between 20 and 40 mm, and in March 1971, both CT and IK catches were mostly between 45 and 55 mm. Individuals over 55 mm were present in low but consistent numbers all year round and may be more than 1 year old.

Diaphus elucens

D. elucens showed definite changes in size composition with depth at night. Size-frequency curves from the CT series in March 1971 differed significantly. There were two size groups present at that time, 32-47 mm and 49-63 mm. The smaller size group made up 80%, 73%, and 20% of the catches in tows at 50, 75, and 100 m, respectively. The number of smaller fish was roughly equal in the two shallower tows and those of larger fish comparable in the two deeper ones. In September 1971, full moon, 98 individuals 7-11 mm long were caught at 20 m, and 12 of 13-17 mm at 50 m. Few of these sizes were taken in deeper water where some larger individuals were caught. No trends could be recognized in the daytime samples.

The pooled IK data indicated that *D. elucens* spawns in late summer and reaches maturity in about 1 year. In June 1971 and July 1970, most individuals were over 40 mm. In September 1970 there were two distinct size classes, 10-13 mm and over 46 mm with practically none in between. In September 1971, new moon, there was a broad group 10-29 mm and a few over 50 mm. In the full moon series, there was a distinct group at 7-11 mm, a smaller group at 12-18 mm, and practically none larger. In December 1970, 70% were 23-41 mm, and in March 1971, the two size groups mentioned above were present in both IK and CT data.

Diaphus sp. A and B

D. sp. A and B are superficially similar to

each other and resemble most closely *D. mollis* from the Atlantic, but both appear to be distinct species. All but the smallest specimens can be readily distinguished. Species A has a rounded opercular margin, and the eyes of Formalin-preserved specimens are distinctly green. In species B, the upper opercular margin is distinctly angular or hooked, and the eyes are yellow-white. The counts for fully developed gill rakers were usually 4+1+10 for species A and 5+1+10-12 for species B. Species B matures at and reaches a much larger size than species A.

Species A was taken in abundance (>10/tow) only 13 times, and size-frequency curves could be compared only for samples from the July 1970 and March 1971 CT series. These both indicated significant differences with the smaller fish occurring in shallower water. The one daytime comparison possible, in September 1970, showed no difference between tows at 500 and 575 m. There was no evidence that any sizes did not migrate regularly.

There were no obvious differences in abundance and size frequency between day and night tows. Two CT tows in March 1971 caught species A similar in size composition to the two positive IK tows, but the CT catches were highest at 50 m and substantial at 75 m whereas the IK indicated a peak at 25 m and only a few at 50 m. At new moon, the depth of highest catch was at 45 m and at full moon was at 75 m. The catch at new moon was about 5× that at full moon, indicating greater avoidance as well as depression during full moon.

Abundance was distinctly higher during July 1970 and September 1970 and 1971 with the largest proportion of small fish at these times. Abundance was distinctly lowest in June 1971 and almost all were adults. These data suggest that species A spawns in the summer and reaches maturity in about 1 year. However, the condition of the ovaries did not indicate a restricted spawning season; 89-100% of the mature females were ripe at all seasons (Table 2).

Only the juveniles (<15 mm) of species B occurred above 100 m. Abundance was highest in June 1971 and most of the catch was juveniles

at that time. Juveniles were also present in July 1970 and September 1971.

Diaphus anderseni

At night, adults of *D. anderseni* occurred mostly around 200 m whereas the juveniles (<13 mm) were found only around 100 m. *D. anderseni* had one of the shallowest day depths (Table 1) and most limited migrations of all the species considered, the adults covering only about 100-200 m each night. In all series but March 1971, catches were mostly small juveniles and adults, but in March 1971 both CT and IK tows indicated the population was composed entirely of intermediate-sized fish. Apparently this species spawns over the greater part of the year.

Diaphus brachycephalus

Numbers of *D. brachycephalus* were quite low except in September 1970 when large numbers of juveniles (<20 mm and most <15 mm) were collected around 50 m at night. The larger individuals caught at 150-200 m were mostly females. Five of the 10 larger males (over 40 mm) taken at night were caught below 300 m, suggesting that the larger males migrate little or not at all. Presence of 9- to 12-mm fish in June, July, and September and their absence in December and March indicated that *D. brachycephalus* spawns in the summer. The June and September samples included both very small and adult fish; the March samples were mostly intermediate sizes (15-30 mm) suggesting that this species reaches adult size within 1 year.

Diaphus adenomus and *D. chryisorhynchus*

D. adenomus and *D. chryisorhynchus* are both apparently epibenthic and associated with shallow water. *D. chryisorhynchus* (54-98 mm) is frequently taken in bottom trawls at 75-190 m at night and *D. adenomus* (41-153 mm) at 180-185 m at night. Both are taken down to 500-600 m during the day (P. J. Struhsaker, pers. comm.). Individuals of the sizes taken near the bottom were rarely caught in mid-

water. The *D. adenomus* were all taken during the day by IK. Thirteen of the *D. chryisorhynchus* collected were larger fish (56-84 mm). These were taken sporadically at all seasons, eight of them in the upper layers at night. The remaining 21 specimens were all 11-17 mm and all taken in the upper layers at night during the September 1971 series, 11 of them in one tow at 80 m. This suggests that this species spawns in late summer and that the young are pelagic. Unless substantial numbers of adults of these species are able to avoid both CT and IK, it appears that the larger fish caught pelagically were wanderers.

Notolychnus valdiviae

Significant differences in size-frequency curves from several series indicated that smaller *N. valdiviae* occurred higher in the water column. In both September 1970 and 1971 series, the catch at night at 80-100 m was almost totally <15 mm and at 115-145 m mostly over 20 mm. In other series, single pairs differed significantly, but trends were not as obvious because most of the fish were of one size class. Two day tows in September 1970 at 525 and 725 m also differed significantly with 60% of the fish <20 mm in the shallow tow and over 90% >20 mm in the deep tow.

In September and December 1970, night catches of *N. valdiviae* near the day depth were larger than that expected from contamination. Substantial catches were also made in the upper layers during these series. In September 1970, roughly 70% of the population remained at depth. There were relatively more larger fish in the nonmigrating fraction (Figure 5). In December 1970, roughly 50% did not migrate, but there was little difference in size composition between shallow and deep catches. There were no significant differences in either sex ratio of mature fish or ripeness of mature females between the shallow and deep night catches. There was no indication that any sizeable fraction of the population did not migrate in either March or June 1971.

The calculated totals for day and night agreed fairly closely and indicated no differential avoidance. Likewise, the calculated size-

frequency curves were quite similar. The agreement of numbers and curves was closest for June 1971. This indicates that since the night data were all from shallow tows, most, if not all, of the population migrated at that time. There was little point in comparing CT-IK data since most fish were apparently small enough to pass through the coarser CT meshes.

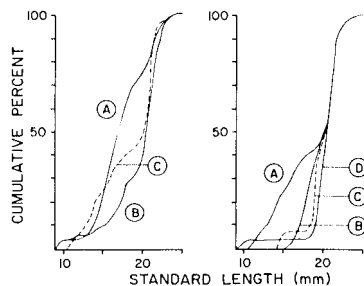


FIGURE 5.—Cumulative size-frequency curves calculated for *Notolychnus valdiviae* (left) from samples taken during September 1970 in the upper layers at night (A), near the day depth at night (B), and during the day (C); and (right) from samples taken throughout the water column in September 1970 (A), December 1970 (B), March 1971 (C), and June 1971 (D).

The new moon series in September 1971 indicated the population was mostly between 75 and 145 m while at full moon it was between 130 and 190 m. The calculated size-frequency curves agreed closely, but the new moon series calculated total was about 3× that of full moon. This suggests that *N. valdiviae* occurs about 50 m deeper and avoids the net better during full moon. The latter seems questionable since even adults are quite small and unlikely to avoid the trawl. Although full moon tows below 200 m in other series made no substantial catches, it is possible that some of the population was below the deepest depth sampled during the September 1971 full moon series.

Both day and night calculated totals indicated that *N. valdiviae* was distinctly most abundant in September and least so in March; the values for December were slightly higher than those for June. Both September series indicated large proportions and numbers of smaller (<15 mm) fish. A few small fish were present in March and June, but in December none were <17 mm (Figure 5). The percentages of mature females

with developed ova for March and June were significantly higher than those for September and December.

Lampadena luminosa

No individuals of *L. luminosa* over 32 mm were caught above 100 m at night, but a few, 16-24 mm, were taken shallower. The rest of the catches, of both large and small fish, were mostly between 150 and 250 m. Five fish, 16-18 mm, were taken during the day at 525-550 m, but most day catches of all sizes were between 650 and 750 m. In June 1971 and July 1970, the catch was almost exclusively <25 mm fish; in September these small fish still predominated but there were also several 25- to 40-mm individuals caught. Only one specimen was caught in December 1970, and in March 1971, 80% of the catch was over 35 mm. None of the individuals captured were mature, suggesting that the adults are larger than the maximum size collected and likely take more than 1 year to mature.

Lampadena urophaos

L. urophaos was caught rather sporadically; only one each was caught at night in September and December 1970, and none during the day in December 1970 or June 1971. All sizes appeared to be present throughout the ranges given. One fish 18 mm long was caught in December and several <30 mm were taken in March, June, and July. Otherwise, most of the fish were 35-65 mm with a few individuals over 90 mm. One ripe female, 98 mm, was collected in March.

Taaningichthys bathyphilus

T. bathyphilus was taken regularly between 600 and 1,000 m and occasionally deeper both day and night. Highest catches were between 700 and 800 m. It was the only myctophid which definitely did not migrate. Size composition of the catches was roughly similar at all seasons with most individuals 30-60 mm long.

Taaningichthys minimus

Other reports, e.g., Davy (1972), have stated that *T. minimus* does not migrate, but all night catches in this study were well above the day depth range. Individuals 20-30 mm long were caught between 150 and 250 m at night and larger fish between 200 and 400 m. None were taken in night tows below 475 m. Of 32 fish caught in March 1971, 27 were 20-24 mm and only 1 was over 50 mm. In other seasons, all were over 30 mm, and most over 50 mm, suggesting that *T. minimus* spawns principally in late winter or early spring. Too few mature females were taken to correlate gonad ripeness with the changes in size composition.

Lampanyctus niger

Most *L. niger* less than 25 mm long were taken at depth both day and night, indicating that the majority of the smaller fish do not regularly migrate. In December 1970, no individuals under 50 mm were caught in the upper layers, and large catches with about 50% larger than 50 mm were taken near the day depth at night (Figures 6 and 7). The mature individuals taken in deep night samples did not differ from those of shallower samples in sex ratio or percentage of ripe females. Smaller peaks at depth during the night were present during other series, but catches of fish over 25 mm could not be discriminated from contamination.

In the upper layers at night, the size-frequency curves from catches above 150-165 m were usually significantly different from those in deeper tows (Figure 7). Few individuals over 50 mm were caught above 165 m, and below 200 m, 50-100% of the catches were over 50 mm. Similar stratification by size was evident in some day series and suggested, nonsignificantly, that individuals less than 50 mm rarely occurred deeper than 750 m.

The calculated totals for day and night agreed well for all but the June 1971 series (day was 1.6× night). The calculated size-frequency curves differed greatly for the September 1970 and June 1971 series. The difference for September 1970 may well have been due to missing

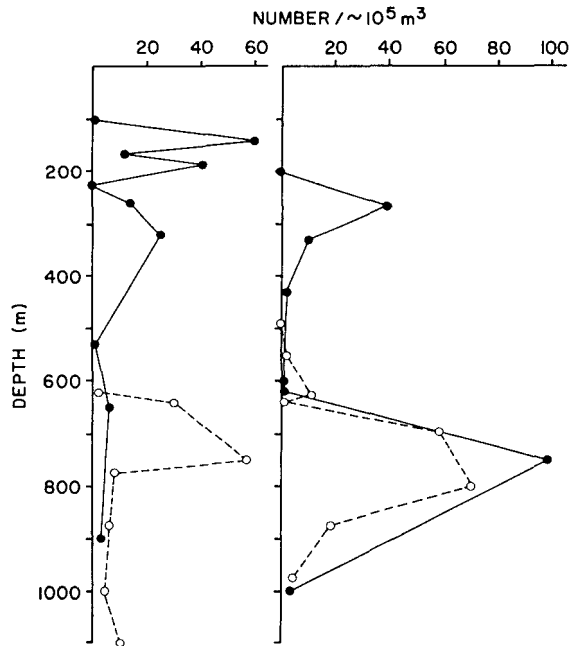


FIGURE 6.—Depth-abundance profiles for *Lampanyctus niger* from samples taken by Isaacs-Kidd trawl during June 1971 (left) and December 1970 (right). Night samples are designated by solid circles connected by solid lines; day samples by open circles and dashed lines. Numbers collected were adjusted to a 2-hr towing time with volume filtered of ca. 10^5 m³.

juveniles at depth at night. The discrepancies for June 1971 were principally due to an exceptionally large catch of 30- to 36-mm fish at 140 m at night.

L. niger, especially the larger individuals, apparently avoided the CT more than the IK. The ratio of CT to IK catches was low (1.2-5.8) for all depth pairs except at 100 m where the CT caught 18 to only 1 in the IK. The calculated total for the CT was only 2.3× that for the IK tows above 200 m. The individual size-frequency curves were significantly different in three of four pairs but not consistent in direction. The calculated size-frequency curves indicated that the CT caught lower percentages of 50- to 70-mm individuals.

During the new moon series, *L. niger* was caught at 145 and 165 m—the deepest samples, but at full moon none were caught. It is not known whether all of the population occurred below 190 m, the deepest depth sampled at full moon, or whether there was increased avoidance.

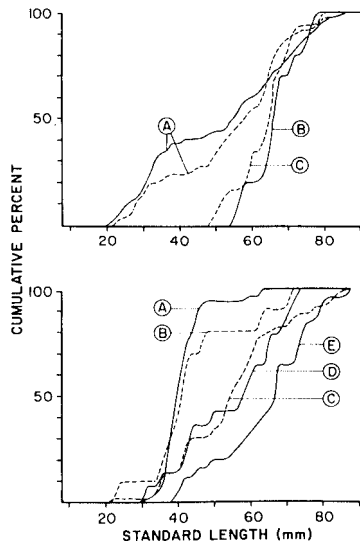


FIGURE 7.—Cumulative size-frequency curves for samples of *Lampanyctus niger* collected at different depths at night. Top: December 1970—two samples from 750 m of 119 and 174 individuals (A); 320 m, 10 (B); and 250 m, 39 (C). Bottom: June 1971—140 m, 60 individuals (A); 165 m, 12 (B); 185 m, 41 (C); 260 m, 14 (D); and 300 m, 25 (E).

The calculated totals indicated for both day and night series that *L. niger* was most abundant during December 1970; the figures for other series were all similar and about one-half of those from December 1970. Except for slightly higher percentages of smaller (<40 mm) fish in December and September 1970, there were no distinct differences in the calculated size frequencies. The percentages of mature females with developed ova for both December 1970 and March 1971 were significantly higher than those for June 1971 and September 1970. Together these data indicate that *L. niger* spawns principally in the early part of the year and that most of the juveniles are recruited to the trawlable population by December.

NOTE (Added in press)

The name *Lampanyctus niger*, used above, included both individuals with weakly developed pectoral fins and those without pectoral fins. Recently, M. A. Barnett informed me that, in specimens collected north of Hawaii, there are differences in other features which correlate

with the presence or absence of pectoral fins. All of our specimens have been reexamined and, regrettably, there appear to be at least two forms present. The taxonomic status of these forms cannot be evaluated. A world-wide revision of species of the *Lampanyctus niger-ater-achirus* complex will be necessary to fully elucidate the problem (cf. Nafpaktitis and Nafpaktitis, 1969). Consequently, the text above was left unaltered, and the following supplementary data is offered here. The latter must be regarded as tentative since it was impossible to identify all specimens with certainty due to damage during collection.

Roughly one-half the specimens have no pectorals. These, designated as Form A, also differ from the others in that the PVO₂ photophore is well separated from PVO₁ and above the level of PO₄. The SAO₃ is usually posterior to AOa₁, and AOa + AOp is 5-6 (rarely 4) + 6-7 (rarely 8) = 12-13 (rarely 11). Form A appears to reach maturity at about 57-58 mm and reaches a maximum size of 74 mm.

In the remaining specimens, the pectoral fin was variously developed but always present. The PVO₂ was closer to PVO₁ and at or below the level of PO₄. SAO₃ was usually anterior to or above AOa₁. The majority of these had AO counts of 5(4) + 6(7) = 11. These, Form B, reached maturity at about 70 mm, and the maximum size was 84 mm. Among the specimens with pectorals, the eleven largest individuals (85-125 mm) and about two percent of the smaller ones had higher AO counts—5-6 + 6-7 (rarely 8) = 12-13 (14). None of these larger fish were mature, suggesting the presence of a third form, Form C.

Thus there appear to be two very similar forms that were common and roughly equal in abundance and a larger, much rarer form. The depth distributions, migrations, size-depth patterns, and seasonal changes of Forms A and B are quite similar and essentially as described above under *Lampanyctus niger*. The co-occurrence in abundance of two such similar forms contrasts with the patterns of most other closely related species. Further investigation of not only the taxonomic status, but also the geographic distribution of these forms will be necessary to determine if, as with the *Hygophum*

spp., Hawaii is near the edge of their ranges. Little can be said about Form C; it appears to have a depth distribution and migration pattern similar to those of the other two.

Lampanyctus nobilis

L. nobilis apparently does not begin migrating until about 25-30 mm long. A few small fish were taken in shallow tows at night, but most were taken at 625 and 750 m at night during September and December 1970. The absence of small individuals in deep night tows during March and June 1971 was probably due to widely spaced sampling since substantial numbers of small ones were caught in day tows then. There was no evidence that other sizes did not migrate regularly.

There were few instances where enough *L. nobilis* were taken to make comparisons of size composition and depth, but several pairs of size-frequency curves showed significant differences. Individuals <30 mm were mostly above 75-80 m at night, and most fish below 100 m were >40 mm. All night catches of exceptionally large individuals (16 of >95 mm) were below 100 m. During the day, catches above 750-800 m were almost all <25-30 mm, and the only substantial catches of fish >40 mm were at 1,150 and 1,200 m in September 1970. The only mature individual caught during the day, 100 mm long, came from a tow at 1,250 m. It is possible that the lower end of the day depth range was not adequately sampled.

L. nobilis avoids the IK in substantial numbers. In March 1971, the CT tows indicated a depth range similar to that of the IK series (Figure 8), except that a large catch was made at 175 m, below a catch of almost none at 150 m. The size-frequency curve from the 175 m CT tow looked like a composite of the shallower tows. This catch was likely due to excessive contamination and was disregarded. The calculated total for CT was $18\times$ that for the IK principally due to catches at 100 and 125 m which were $21.4\times$ and $24.8\times$ the IK catches at these depths. The size-frequency curves for individual pairs differed significantly and like the calculated total curve indicated that the IK missed individuals over 40-45 mm. Thus

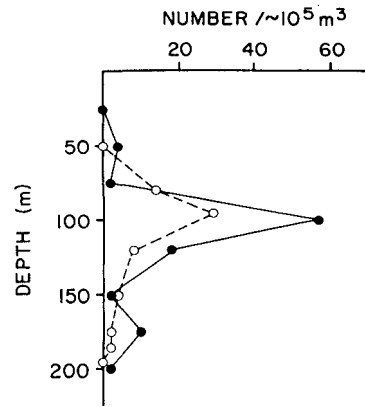


FIGURE 8.—Estimates of abundance of *Lampanyctus nobilis* at different depths at night during March 1971 from samples with the Cobb trawl (CT) (solid circles and lines) and Isaacs-Kidd trawl (IK) (open circles, dashed lines). CT catches were adjusted to the same volume filtered by 2-hr tows with the IK, ca. 10^5 m³.

L. nobilis was probably about twice as abundant as the IK tows indicated.

At new moon in September 1971, *L. nobilis* occurred between 60 and 125 m with peak abundances at 75 and 100 m. At full moon, the only individual caught was from 190 m. Tows below 200 m taken during full moon in other series made no substantial catches. Thus the difference between the new and full moon series was probably due to greatly increased avoidance at full moon.

There were no gross seasonal differences in abundance or size composition apparent from the IK data except that *L. nobilis* may have been slightly less abundant in June 1971. Small (<25 mm) fish were present in comparable numbers in September 1970, December 1970, and June 1971 (the proper depth zone was not adequately sampled in March 1971 day or night).

With the exception of a 78-mm individual, all ripe females were over 97 mm and were rarely caught—once in September, once in March, and twice in June. The presence of juveniles indicated that spawning regularly occurs in the area, and the presence of immature sizes in fair abundance suggests that adults should be more abundant than catches of either IK or CT indicated. It seems likely that these larger fish avoided both trawls in substantial numbers.

Lampanyctus steinbecki

All postlarval *L. steinbecki* appeared to migrate regularly. Within the night and day depth ranges, the size-frequency curves were usually displaced to the right with increasing depth (Figure 9). The differences were significant only in September and December when several size classes were present in abundance. In these cases the differences were due to changes in absolute numbers of both small and large individuals, the shallower samples being composed almost entirely of juveniles and the deeper ones of adults only. Consistent, significant differences in size-frequency curves of day samples indicated that adults (>40 mm) occurred mostly below 850-900 m and few smaller fishes occurred at these depths.

The percentages of females among mature fish tended to decrease with depth in the March 1971 night samples. The values for samples from 95, 120, 135, 175, and 265 m were 82, 63, 64, 55, and 44%, respectively. The only significant differences were between the highest

value and the two lowest ones. There were some significant differences among the June 1971 night samples, but no trend with depth was evident.

The calculated totals were higher for the day series in all cases. The day totals were relatively highest for the September and December 1970 series ($2\times$ and $1.6\times$ night totals, respectively) and were probably in part a result of poor timing of the night samples with respect to moon phase. For March and June 1971 the day totals were about $1.5\times$ higher than night. Except for December 1970 the calculated size-frequency curves for day and night series were quite similar. Thus all sizes appear to avoid the IK better at night.

The individual CT tows caught from 0.7 to $4.5\times$ their paired IK tows, and there was no obvious trend in differences of the size-frequency curves. The calculated curve for the CT was displaced slightly to the right of both night and day IK curves for March 1971, but the calculated CT total was only $3.4\times$ the night IK total. Apparently *L. steinbecki* avoids the CT more than the IK.

During new moon in September 1971 the peak depths were at 80 and 100 m, and at full moon none were caught above 120 m. The catches at 170 and 190 m at full moon both exceeded the peak catches at new moon. The water column totals were nearly equal, but the full moon calculated curve and the individual curves were displaced far to the left of new moon curves indicating substantially greater numbers of 20- to 40-mm individuals. The new moon tows seemed to miss substantial numbers of juveniles; and if large numbers of larger fish occur below 190 m at full moon (there was some evidence for this from full moon tows in other series), it is possible that full moon tows may also sample the larger fish better. The increase in night depth with full moon, about 100 m for the juveniles, was about twice that observed for other species.

Both day and night calculated totals indicated that *L. steinbecki* was least abundant in March 1971 and present in comparable numbers during the rest of the seasons. The calculated size-frequency curves (Figure 9) indicated that 80% of the individuals were immature in September

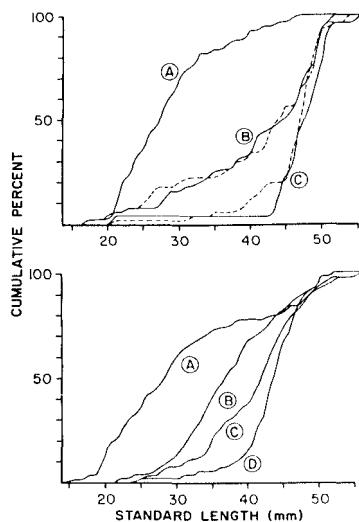


FIGURE 9.—Top: Cumulative size-frequency curves for samples of *Lampanyctus steinbecki* collected at night during new moon, September 1971, at depths of 80 m, 58 individuals (A); 100 m, 59 (B, solid line); 125 m, 46 (B, dashed line); 145 m, 49 (C, dashed line); and 165 m, 28 (C, solid line). Bottom: Cumulative size-frequency curves for *L. steinbecki* calculated from samples taken throughout the water column in September 1970 (A); December 1970 (B); March 1971 (C); and June 1971 (D).

1970, with 50% under 30 mm. In December 1970, most fish were still immature, but the peak size group was 30-40 mm. In March and June 1971, about 65 and 90% of the fish, respectively, were mature. The percentages of ripe females among mature females were highest in March and June 1971 and were significantly lower than all others in December 1970. Thus *L. steinbecki* appears to spawn principally in the spring and summer and to reach trawlable size by September. Most fish appear to live about 1 year.

Lampanyctus tenuiformis

L. tenuiformis differs from *L. steinbecki* principally in size at maturity and relative positions of a few photophores. Counts of fin rays, etc., for the two species were either identical or overlapping. Individuals over about 40 mm could be distinguished by the relative development of the gonads, but it is possible that some smaller, damaged *L. tenuiformis* were erroneously identified as *L. steinbecki*. Owing to the former's rarity, as evidenced by the few larger individuals, any error is almost certainly negligible.

Only four *L. tenuiformis* were taken at night, and the larger two of these (120 and 138 mm) were taken in tows near the day depths. Thus the night depth range given in Table 2 is quite uncertain. *L. tenuiformis* appears to spawn near Hawaii; four females (123-138 mm) with ripened ova and two small juveniles (28 and 32 mm) were collected.

Tripnoturus nigrescens

T. nigrescens <15 mm were caught only in a night tow at 650 m in June 1971, suggesting that small juveniles do not migrate. In December 1970, high catches of larger fish were made during the night both in the upper layers and at the day depths. Calculated totals indicated roughly 60% of the population did not migrate. Calculated size-frequency curves for shallow night, deep night, and day samples all were quite similar and also agreed closely with the curve from fish taken in three short night

oblique tows from 0 to 300 m. Differences in sex ratio and percentage of mature females with developed ova between the deep and shallow samples were small and nonsignificant.

Large numbers of more than one size class were caught only in July and September 1970. There were significant differences between size-frequency curves indicating that fish <20 mm occurred mostly above 50 m at night and above 650 m during the day. Adults occurred mostly below 50 m at night and below 650-700 m during the day.

Owing to low numbers in June 1971 and poor timing of shallow night tows in September 1970, day and night comparisons could be made only for December 1970 and March 1971. The day calculated totals were larger in both series, 1.3× for December 1970 and 3.8× for March 1971. The larger discrepancy in March 1971 may have been due to missing nonmigrating fish at night. The calculated size-frequency curves for day and night agreed closely.

The CT tows in March 1971 caught only 2.5-4× the IK tows; the calculated total for the CT was 2.6× that for the IK night series. The calculated size-frequency curve for the CT was nearly identical to both the day and night IK curves, and most fish were over 30 mm. Apparently *T. nigrescens* is better able to avoid the CT, but it is possible that some fish of even the larger sizes could have escaped through the coarser CT meshes.

T. nigrescens appears to have a 1-year generation cycle with spawning principally in spring and summer. Abundance was distinctly highest in December and extremely low in June and September 1971 with substantial and roughly equal numbers present in September 1970 and March 1971. *T. nigrescens* was also abundant in July 1970 with most of the population either adults or <20 mm. In September 1970, 65% of the population was 20-28 mm with few adults, and in December, 85% were over 25 mm. In March 1971, 85% were over 30 mm and none <24 mm. In June 1971, the catches were made up almost entirely of adults or fish <15 mm. The conditions of the ovaries were correlated with the changes in size frequency. The percentages of mature females with developed ova (Table 2) were low

in September and December 1970 and were significantly higher in March and June 1971.

The decline in abundance observed for *T. nigrescens* in June and September 1971 was the most dramatic change observed among all the species during the study period. The difference between the series in July and September 1970 and those of June and September 1971 suggest that either spawning success or larval survival was markedly lower in 1971. The only obvious factor correlated with this change was a significant increase in the percentage of females among mature fish in June 1971. Whether there was a causal relationship between the two changes cannot be determined from the data.

Bolinichthys longipes

Apparently almost all *B. longipes* of the sizes sampled regularly migrate. The only indication of nonmigration was a catch of seven small (12-14 mm) individuals at 650 m during the night in June 1971; individuals of these sizes were caught frequently during the day tows but rarely at night in the upper layers suggesting that some small individuals do not migrate. Within each series there were relatively few significant differences between size-frequency curves of the separate tows. These indicated that the smaller fish tended to be found shallower at night. Differences between day tows clearly indicated (Figure 10) that few fish less than 20 mm occurred deeper than 625 m and few larger than 30 mm occurred above this depth.

In the March 1971 night samples, the per-

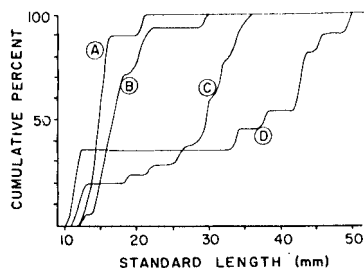


FIGURE 10.—Cumulative size-frequency curves for samples of *Bolinichthys longipes* collected during the day during June 1971 at depths of 560 m, 11 individuals (A); 600 m, 18 (B); 620 m, 21 (C); and 640 m, 11 (D).

centages of females among mature fish decreased with depth. The values were 73% at 80 m, 59% at 95 m, 32% at 120 m, and 46% at 135 m. The first two values were significantly different from the latter two. Insufficient mature fish were caught to compare values at different depths in other series.

The calculated totals agreed well for the day and night series, but calculated size-frequency curves differed for almost all pairs. Depth coverage was best for the March and June 1971 series, and the calculated curves were closest for the March 1971 series. The curves for the June 1971 series differed mostly because of a greater frequency and number of small individuals in the day. The numbers caught were quite low for all tows of this series, and inclusion of seven small individuals from a deep night tow (see above) in the calculations brought both the calculated totals and curves into very close agreement for the June 1971 series.

The CT tows indicated that peak depth was at 75-100 m and caught fair numbers of *B. longipes* at 25-50 m where the IK caught few or none. The IK peak depth was at 100 m and substantial numbers were caught at 125 and 135 m where CT catches were relatively low. The ratios of CT to IK numbers were 9.4 and 5.6 at 75 m and 100 m, respectively, but only 1.1 at 125 m. The calculated CT total was 5× that for the IK. The IK and CT size-frequency curves were similar at 75 m but differed significantly at 100 and 125 m due to larger percentages of fish over 35 mm in the CT catches. The calculated CT curve was displaced to the right also due to higher percentages of fish over 35 mm. Thus it appears that the CT sampled *B. longipes* as well or better than the IK above 100 m, but in the deeper zones the IK gave higher estimates of abundance in spite of missing some larger fish.

At new moon, *B. longipes* was abundant between 60 and 125 m and peaked at 80-100 m. At full moon, practically none were caught above 130 m and the peak was at 170-190 m. Full moon tows in other series indicated that few occurred deeper. The new moon catch at 60 m and the full moon catches at 130 and 170 m were similar in size composition; almost all fish were <20 mm. The 190-m curve at full

moon resembled those from 125 m and 145 m at new moon. The calculated total for full moon was $1.4\times$ that for new moon and the calculated size-frequency curves differed considerably. Both differences were due to larger catches of 17- to 23-mm fish at full moon. Both these data and the CT-IK comparisons indicate that the IK missed some smaller fish in the upper layers at new moon. If these differences are real, they could in part account for the apparent lower numbers and percents of juveniles estimated in night series (see above).

There were substantial numbers of juveniles (<20 mm) in the June, July, and September series with few in December 1970 and practically none in March 1971. The percentages of mature females with developed ova (Table 2) were highest in March and June 1971 and significantly lower in December 1970. These suggest that spawning occurs principally in spring and summer and that the juveniles have reached trawlable size within a few months.

Bolinichthys supralateralis

No *B. supralateralis* over 53 mm long were taken above the day depth range. Out of 15 such individuals, only 3 were caught during deep night tows. These could well have been contaminants and do not clearly confirm that the larger individuals do not migrate. However, out of 50 smaller fish caught at night, 10 were caught in tows within the day depth range suggesting that all sizes may not regularly migrate. In the upper layers at night, fish less than 20 mm occurred between 100 and 200 m, but only two between 20 and 30 mm and none over 30 mm were caught above 200 m. All sizes appeared to occur throughout the day depth range.

The pooled IK size-frequency data indicated that *B. supralateralis* spawns principally in late summer and fall and that it may take at least 2 years to reach maturity. There were distinct, well-separated size classes in all but the March 1971 series where only 11 fish were caught. Small fish, 12-20 mm long, were most abundant and made up the majority of the catch in September and December 1970. It appeared that this group was represented by

24- to 35-mm individuals in June 1971. A second year class was suggested by size classes present only in the December 1970 and June 1971 series (41-53 mm and 47-59 mm, respectively). A few fish larger than 60 mm were caught in all series and may represent a third year class. The only female with developed ova was 88 mm long, almost the largest specimen taken. It is likely that such large individuals avoid the trawl in addition to being rather rare.

Ceratoscopelus warmingi

The smallest *C. warmingi* regularly collected in the trawl do not appear to regularly migrate. At night, individuals 15-19 mm long were caught both between 20 and 100 m and at 600-700 m. In June 1971, when these sizes were most abundant, about two-thirds of the juveniles remained at depth. There was no indication that larger fish did not regularly migrate.

Within both day and night depth ranges the size-frequency curves differed significantly. Except during June 1971, at night few fish over 40 mm were caught above 50 m and few smaller individuals were caught below 75 m. In the June 1971 series, however, large numbers of 15- to 19-mm fish were caught down to 140 m, throughout most of the night range. During the day, few individuals over 20 mm occurred at 600-700 m, and larger individuals occurred principally below 750-800 m.

At night the percentage of females among mature *C. warmingi* tended to decrease with depth. In March 1971, when large numbers of mature fish were caught at several depths, 89% of the mature fish from 25 to 30 m were females. At 50 and 80 m the value was 64%, significantly lower. The value at 95 and 100 m was 33%, and at 120 m was 31%. Both were significantly lower than the values from shallower tows. Similar, but nonsignificant, trends were present in the September and December 1970 series. The only day series where sufficient numbers of mature fish were collected at several depths was in December 1970; there were no trends or significant differences in percentages of females.

Comparison of day and night series was possible only for the June 1971 series due to poor timing of the night samples with respect to moon phase in September and December 1970 and inadequate coverage in March 1971. Both the calculated totals and size-frequency curves for June 1971 agreed quite closely. Since about 85% of the fish in this series were <20 mm, any differences for larger fish would be difficult to detect, but the other series showed no obvious indications of differential day-night avoidance.

The CT caught only 4 × as many *C. warmingi* as the IK at 25 m, but outfished the IK by factors of 12-14 × between 50 and 100 m. The calculated CT total was 7.4 × the IK total; when only fish over 25 mm were included, the factor was 8.3. The size-frequency curves were similar at 25 m but differed significantly for the deeper tows, the CT catching larger proportions of larger individuals. The calculated curves differed similarly, even when only fish over 25 mm were included. Apparently, some of the smaller fish passed through the CT meshes, thus accounting for the differences at 25 m where these fish were more abundant, but the CT appeared to sample the larger fishes, particularly those over 35 mm, better than the IK.

At new moon in September 1971, the depth of peak abundance was at 45 m, and the majority of the population was between 15 and 100 m. During full moon, the peak depth was at 130 m, and the population was mostly between 100 and 170 m. The calculated total for new moon was about twice that for full moon, and the new moon tows caught slightly larger proportions of fish over 35 mm.

The calculated totals indicated that *C. warmingi* was present in comparable numbers in December 1970, March 1971, and June 1971 and much less abundant in September 1970, but the calculated size-frequency curves differed greatly (Figure 11). In June 1971, the population was about 90% juveniles (14-17 mm), and in December 1970, about 60% were over 40 mm with few under 20 mm. In March 1971, 70% of the juveniles were 20-40 mm, and in September 1970, most were either under 25 mm or over 45 mm. Changes in the numbers of juveniles accounted for most of the changes in abundance,

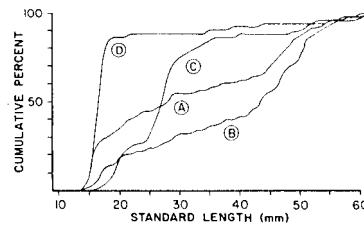


FIGURE 11.—Cumulative size-frequency curves of *Ceratoscopelus warmingi* calculated from samples taken throughout the water column in September 1970 (A); December 1970 (B); March 1971 (C); and June 1971 (D).

but adults were definitely most abundant in December 1970 and almost absent in June 1971.

The large numbers of immature fish in March 1971 (particularly, a peak at 25-30 mm) suggest that some recruitment had taken place between December and March. The size composition of the population in June 1971 indicated a spring-time spawning also. The percentage of ripe females was highest in June 1971, but none of the differences between series were significant. It appears that *C. warmingi* spawns over a long season, but principally during the first half of the year, and that there are either peaks within this season or marked fluctuations in larval and juvenile mortality.

Notoscopelus caudispinosus

N. caudispinosus was captured very rarely, but several fish, 20-25 mm, caught in March and June 1971 suggest that it may spawn in this area or nearby. It is possible that the larger individuals avoid both the CT and IK and are more abundant than the collections indicate.

DISCUSSION

Rare species

The majority of the species collected were rather rare. Only 19 species were present in moderate to high abundance and showed strong evidence of spawning in the area. A few of the rarer species appear to have primary centers of abundance elsewhere. The single *Diaphus theta* collected was certainly an expatriate from North Pacific transitional waters (Paxton, 1967), and four species are restricted to nearshore waters

(*Benthoosema fibulatum*, *Diaphus adenomus*, *D. chrysohyndus*, and *Lampadena urolampa*). *Diogenichthys atlanticus* and *Diaphus fragilis* are more abundant in Equatorial Pacific waters (Hartmann, 1971). The principal range of *Lampanyctus tenuiformis* is not clearly known.

Nineteen of the rarer species—*Protomyctophum beckeri*, *Myctophum* spp., *Loweina* spp., *Centrobranchus* spp., *Diaphus bertelseni*, *D. metopoclampus*, *D. "glandulifer,"* *Lampadena luminosa*, *L. anomala*, *Taaningichthys* spp., *Bolinichthys supralateralis*, and *Notoscopelus caudispinosus*—appear to be typical of central or equatorial-central waters but are nowhere commonly collected (Bekker, 1966; Nafpaktitis, 1968; Nafpaktitis and Nafpaktitis, 1969; Gibbs et al., 1971; Wisner, 1971; Davey, 1972). Five of these species—*Myctophum selenoides*, *Diaphus "glandulifer,"* *Lampadena luminosa*, *Taaningichthys minimus*, and *Bolinichthys supralateralis*—appear to spawn in the study area. *Lampadena urophaos*, although designated as a transitional water mass species by Paxton (1967), would appear to belong with the above group. It appears to spawn in this area, and a rough comparison of the present study's and Paxton's catch per effort indicates that it is more abundant near Hawaii.

Avoidance

Although it was not possible to set confidence limits for the calculated totals and size-frequency curves, in most species the differences between day and night totals were not large enough to suggest that there was substantially greater avoidance at either time. The exceptions, *Lampanyctus steinbecki* and the *Hygophum* spp., were sampled better during the day than at new moon at night. They also apparently avoid the IK better at new moon than at full and may be sampled equally well by night tows at full moon and day tows.

These results contrast with those of Percy and Laurs (1966) off Oregon. They noted substantial differences in day-night avoidance among mesopelagic fishes. The differences were in the opposite direction of the few noted in this study; most of their species avoided the net better during the day. Percy and Laurs used

a 6-ft IK, and perhaps the larger trawl used in the present study sampled fishes relatively better during the day.

The IK-CT comparisons show that, as Harrison (1967) and others have suggested, no single net will adequately sample all species. The IK gave higher estimates of overall abundance than the CT for many species analyzed, but greatly underestimated the abundance of two species, *Symbolophorus evermanni* and *Lampanyctus nobilis*. The CT sampled the *Hygophum* species better at night during new moon, but the IK probably samples them as well or better during the day or during full moon at night. Even allowing for escapement of small fishes through the CT meshes, the CT caught higher proportions of larger fishes of some species, e.g., *Ceratoscopelus warmingi* and *Lampanyctus steinbecki*. Neither net effectively sampled the mature sizes of *Lampanyctus nobilis*, *Lampadena luminosa*, and *Bolinichthys supralateralis*.

There was evidence for some species that one trawl sampled better at some depths only. The IK appeared to sample *Hygophum reinhardti* and *Bolinichthys longipes* as well or better than the CT at the deeper end of their night depth ranges, but the CT sampled as well or better at the shallower end. For *Diaphus schmidti* and *Diaphus* species A, the CT appeared to underestimate abundance at the shallower end of the depth range and caught relatively more fish at the deeper end. Obviously, more data are needed since one or two very high or low catches could have produced these results.

Harrison (1967) using only roughly comparable pairs of samples, suggested that a larger otter-type trawl towed at 1 m/sec caught more larger fish than an IK towed at 1.5 m/sec. Aron and Collard (1969), however, have shown that towing speed had an important effect on an IK's estimates of abundance and size composition for one of the more abundant species collected in their study. Kuba (1970) found that in the Equatorial Pacific, the IK at 2 m/sec sampled most species' abundance and size composition as well or better than the CT at 1.5 m/sec. It would appear that the higher speed used for the IK tows in this study gave

a greater overall advantage than the increased "stealth" of the larger CT.

The full-new moon series indicated that most species occurred deeper at full moon and that several avoided the trawl better at full moon. The *Hygophum* species appeared to do just the opposite. The changes suggest that it is best overall to sample the upper 200 m at new moon only. A mixed sampling program can result in some populations being sampled twice and the depth range and abundance overestimated, or most of the population being missed and abundance underestimated.

Most species appeared to occur 50-75 m deeper at full moon. Data presented by Clarke (1970), however, indicate that in clearest ocean water, the depths of isolumens at full moon are about 200 m greater than at new moon. This suggests that the fishes occurred at higher light levels at full moon and may explain the increased avoidance noted then. The data of Blaxter and Currie (1967) indicate that this is possible. They observed that the depth of a sonic scattering layer was depressed by artificial light but to a light level about 10 times brighter than that at which the layer normally occurred.

Intraspecific Variations in Migration

Most myctophid larvae appear to occur in the upper layers (Ahlstrom, 1959). Whether they descend just prior to or just after metamorphosis is not known, but at least some species do not begin to undertake regular, extensive diurnal migrations immediately after metamorphosis. The data indicate that the recently metamorphosed juveniles of *Benthoosema suborbitale*, *Lampanyctus niger*, *L. nobilis*, and *Ceratoscopelus warmingi*, and possibly *Hygophum proximum*, *Symbolophorus evermanni*, and *Bolinichthys longipes*, do not regularly migrate. More thorough sampling of the deeper layers at night with opening-closing devices may show this to be a general feature of myctophids.

Nafpaktitis (1968) has suggested that gravid females of some myctophids do not migrate. No evidence of this was found. The larger males of *Diaphus brachycephalus* and the larger individuals of *Bolinichthys supralateralis* ap-

peared to remain at depth both day and night, but in both cases data were too few to be certain. In the latter species, there was no clear relation to maturity or reproductive condition. Most of the "nonmigrating" *B. supralateralis* were immature.

Large fractions of the populations of three species, *Notolychnus valdiviae*, *Lampanyctus niger*, and *Triphoturus nigrescens*, appeared to remain at the day depth during the night on some occasions. It is unlikely that the deep night catches were due to contamination, i.e., encountering aggregations in the upper layers on the way up or down. The numbers caught at depth during the December 1970 series were in all cases considerably larger than those caught in short oblique tows made during the same series. Also it seems unlikely that patches would be encountered only by tows made to the same depths where the species were found during the day. Finally, the day and night calculated totals and size frequencies agreed well for all three species in December. If the deep night catches had been contaminants, the night totals would have been much larger than those for the day.

There were no obvious differences between the migrating and nonmigrating fractions of the populations. The nonmigrating fraction of *Lampanyctus niger* tended to be smaller and that of *Notolychnus valdiviae*, larger in September 1970, but there was considerable overlap between both fractions of the populations in both cases. For *Triphoturus nigrescens* and *N. valdiviae* in December 1970, both fractions of the populations were nearly identical in size composition. Thus the difference in behavior was not entirely a function of size. There was no case where shallow and deep night samples differed in sex ratio or percentage of ripe females. The number of specimens involved was rather large in all cases, so it is doubtful that more data would produce clearer trends or any explanation related to the parameters measured here.

Most species showed significant differences in size composition with depth. *Symbolophorus evermanni* was the only species present in abundance for which all sizes appeared to occur throughout the depth range. In the great

majority of species, the juveniles tended to occur shallower than adults. The trend was more obvious in the night samples due to closer sample spacing, but probably holds for the daytime depth distribution in most cases. *Hygophum proximum* and *H. reinhardti* were anomalous in that at night during new moon the adults tended to occur shallower than the juveniles.

The changes in size composition with depth may be an artifact caused by larger fish avoiding the trawl better at lesser better-lighted depths. However, many small species such as *Benthoosema suborbitale*, *Diaphus schmidti*, *Triphoturus nigrescens*, and *Notolychnus valdiviae* are unlikely to avoid the trawl even as adults, and the trends with depth were as evident with these species as with the larger species. Also the same trends were evident from CT data for species which the CT appeared to sample larger individuals relatively better. Furthermore, avoidance by larger fish would only partly explain the changes noted for many species, i.e., the smaller fish were absolutely less abundant with depth.

The ecological significance of the trends in size with depth is not clear. The juveniles are removed to some extent from predation by adults, but this is of doubtful significance since other predators are probably more important. Possibly the smaller fish are less visible to predators than are the adults in the better-lighted shallow layers. In those species where adults occur farther below the juveniles in the day than at night, it may be related simply to the juveniles being unable to make longer migrations. This pattern could be related to distribution of food. It is quite likely that juveniles require greater concentrations and smaller average particle size of food than adults, and optimal conditions for juveniles may occur shallower than for adults.

Sex Ratios

Sex ratios of mature and juvenile fish of several species are compared in Table 3. The difference is significant for only one species, *Diaphus schmidti*, and in that case, the ratios did not differ significantly when data for mature

TABLE 3.—Proportions of females among juveniles and mature fish for nine species of myctophids. Number of specimens examined is given in parentheses.

Species	Juveniles	Adults
<i>Benthoosema suborbitale</i>	0.48 (54)	0.51 (230)
<i>Hygophum proximum</i>	.58 (67)	.46 (192)
<i>Diaphus schmidti</i>	.43 (56)	.62 (127)
<i>Notolychnus valdiviae</i>	.50 (70)	.45 (402)
<i>Lampanyctus niger</i>	.65 (55)	.57 (456)
<i>Lampanyctus steinbecki</i>	.65 (48)	.51 (535)
<i>Triphoturus nigrescens</i>	.59 (49)	.48 (452)
<i>Bolinichthys longipes</i>	.58 (66)	.48 (239)
<i>Ceratoscopelus warmingi</i>	.59 (96)	.58 (456)

fish from a single sample with a very large proportion of females was not included. For most species there was a tendency for higher proportions of females among immatures, but the figures are suspect in the sense that the data were not properly weighted to account for possible trends with depth or season. Legand and Rivaton (1970) have noted opposite trends in sex ratio with size for three species of myctophids. (However, their criteria for separating "larger" from "smaller" fish is not entirely unbiased and the proportions given for one species, *Benthoosema simile*, do not differ significantly.)

Given that there may be trends in sex ratio with size, recognition of trends with depth or season was made difficult because there were only a few series where sufficient numbers of similar-sized fish were captured at several depths or several seasons. Thus, significant trends in sex ratio with depth were observed for mature fish of only a few species. Quite possibly, more data would show that these trends are the rule rather than the exception. When data were pooled for all mature fish examined from each series (Table 4), some significant differences in sex ratio were observed. In most cases one series showed significantly higher or lower percentage of females than the rest with no suggestion of seasonal trends. Again, however, differences in depth composition of the samples or size composition of the fishes pooled for a series may have either obscured trends or have been responsible for the few significant differences observed.

Seasonal Trends

In considering seasonal trends, it was assumed

TABLE 4.—Proportion of females among total mature fish at different seasons for 10 species of myctophids. Total number examined is given in parentheses.

Species	September	December	March	June
<i>Benthosema suborbitale</i>	0.51 (35)	0.59 (105)	0.42 (90)	—
<i>Hygophum proximum</i>	.56 (66)	.32 (22)	.34 (64)	0.55 (40)
<i>Diaphus schmidti</i>	.36 (22)	—	.71 (100)	.52 (21)
<i>Diaphus</i> sp. A	.57 (81)	—	.32 (28)	.52 (27)
<i>Notolychnus valdiviae</i>	.48 (133)	.49 (141)	.23 (48)	.48 (80)
<i>Lampanyctus niger</i>	.58 (86)	.52 (183)	.58 (119)	.69 (68)
<i>Lampanyctus steinbecki</i>	.42 (99)	.55 (40)	.63 (163)	.52 (233)
<i>Triphourus nigrescens</i>	.52 (25)	.45 (314)	.48 (85)	.80 (45)
<i>Bolinichthys longipes</i>	.41 (29)	.43 (40)	.50 (139)	.55 (31)
<i>Ceratoscopelus warmingi</i>	.73 (15)	.59 (29)	.32 (41)	.46 (26)

that the same or equivalent populations were sampled on each cruise. Possible changes due to horizontal advective transport were ignored. Advection rates, especially for organisms which spend one-half of their time below the surface layers, and horizontal gradients in the parameters measured—abundance, size composition, etc.—are probably low. It seems unlikely that populations which had been subjected to greatly different environmental conditions were advected into the study during the periods between cruises.

The most likely possibility of change due to advection would be related to seasonal north-south shifts of water masses. Near Hawaii in the upper layers, water transitional between North Pacific Central and North Pacific Equatorial displaces North Pacific Central water during the summer. This shift is known to affect the abundance of skipjack tuna (Seckel, 1969).

The absence of marked changes in species composition and relative abundance of the myctophid fauna suggest that north-south shifts of water masses did not, during the study period, markedly affect populations. Two examples illustrate this particularly well. *Diaphus schmidti*, a species of myctophid which apparently does not occur much further south than Hawaii, was consistently taken here in abundance, while a very similar congener, *D. garmanni*, which is very abundant from at least lat. 12°30'N and further south (Hartmann, 1971), was never taken. Two species, *Dio-genichthys atlanticus* and *Diaphus fragilis*, which are very abundant in equatorial waters (Hartmann, 1971), were taken consistently but never in great numbers near Hawaii.

Most species that showed seasonal changes in

size composition appeared to reach maturity in about 1 year. The larger species—*Lampadena* spp., *Lampanyctus nobilis*, *Bolinichthys supralateralis*, and *Notoscopelus caudispinosus*—probably take longer. In many species the adults nearly or completely disappeared at about the same time that juveniles became most abundant suggesting that few individuals live longer than 1 year.

The ages at maturity and life spans of colder water species of myctophids, e.g., *Benthosema glaciale* (Halliday, 1970), *Stenobranchnus leucopsaurus* (Smoker and Percy, 1970), are considerably greater than those suggested here for tropical species. Murphy (1968) has presented data on epipelagic clupeoid fishes which show a marked decrease in age at maturity, the number of reproductions, and life span related to year-to-year variability in spawning success. He suggests that the latter is directly related to year-to-year variability in the physical environment. It is not unreasonable that the same trend exists for a mesopelagic family that occurs in both variable high-latitude waters and in the more stable tropical open ocean.

Most species appear to spawn predominately in the spring or summer. Primary production measurements taken by S. A. Cattell near Hawaii during 1969-70 indicate that primary production and productivity index are much higher during March-June than the period from October to January. Zooplankton production probably lags behind the peaks in primary production only slightly. Assuming that this seasonal pattern recurred during the present study, the period of principal spawning for most myctophid species appears to be timed

with respect to the seasonal peak in production of food.

In many of the abundant species, the seasonal changes in abundance and size composition were quite pronounced. When these were combined with size-dependent differences in migration habits, the depth-abundance profile also changed with season. Consequently, samples from only one period may give a misleading picture of vertical distribution and abundance. This would be particularly true in the tropics where, as opposed to longer-lived species at higher latitudes, several different size classes are not often present in abundance at all seasons.

Interspecific Relations

Many species of myctophids, including some congeners that are very similar morphologically, occur together in the water column yet must be ecologically segregated. From this study it is possible to examine several relevant factors: depth distribution, size range, and size changes with depth and season. Owing to better data for some of these aspects for the nighttime, only night distributions will be considered. There are, however, some data (Backus et al., 1968; Barham, 1970) that suggest that myctophids are rather inactive during the day and that interspecific patterns at night are probably more meaningful ecologically.

In Figure 12, depth-size patterns are diagrammed for 16 of the 19 most abundant

species. For each species, a straight line is drawn connecting the size-depth coordinate for smallest size-shallowest depth with that for largest size-deepest depth. *Symbolophorus evermanni*, which showed no trend, and the *Hygophus* species, which will be discussed separately, have been omitted. Extremes of depth of capture and size range have been ignored; consequently, the ranges shown in Figure 12 are, in some cases, narrower than those given in Table 1. The straight lines are of course only a rough approximation to the actual patterns of size and depth; it is realized that more data would probably result in polygons for each species.

The species can roughly be separated into three groups. The first group includes eight species whose young occur principally at about 25 m and the adults between 75 and 125 m, depending on size. In the second group of three species, the pattern is similar except that the young occur principally at 80-100 m and the adults down to 150-250 m, again depending on size. The third group includes four species with sharper gradients in size with depth where juveniles occur around 50 m and larger fish are mostly between 150 and 200 m. Two of the rarer species, *Myctophum selenoides* and *Lampadena luminosa*, appear to have patterns like those of the third group. *Diaphus anderseni* has a depth-size pattern different from any of those illustrated, but two rarer species, *Taaningichthys minimus* and *Bolinichthys supralateralis*, appear to have similar patterns.

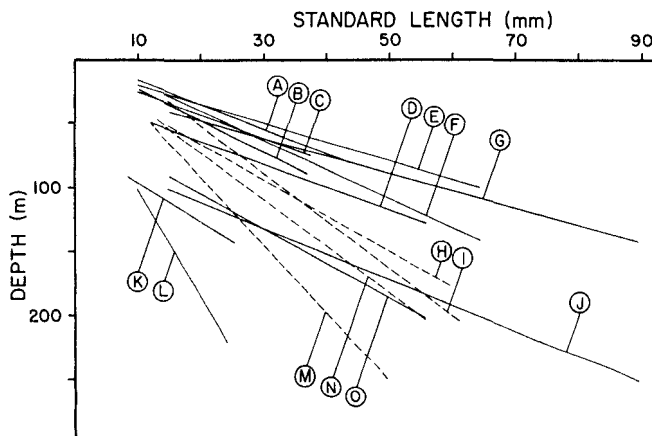


FIGURE 12.—Depth-size profiles (see text) in the upper 250 m at night for 16 species of myctophids: *Diaphus schmidti* (A), *Diaphus* sp. A (B), *Benthosema suborbitale* and *Triphoturus nigrescens* (C), *Bolinichthys longipes* (D), *Diaphus elucens* (E), *Ceratoscopelus warmingi* (F), *Lampanyctus nobilis* (G), *Diaphus rolfbolini* (H), *Diaphus* sp. B (I), *Lampanyctus niger* (J), *Noto-lychnus valdiviae* (K), *Diaphus anderseni* (L), *Lobianchia gemellari* (M), *Diaphus brachycephalus* (N), and *Lampanyctus steinbecki* (O).

Within the first two groups, similar sizes of the species tend to occur at similar depths. The depth-size patterns of four species in the first group—*Benthosema suborbitale*, *Diaphus schmidti*, *D. sp. A*, and *Triphoturus nigrescens*—are nearly identical. Within the third group, the juveniles co-occur with similar-sized individuals of the first group and the adults with larger fish of the second group.

Judging from the seasons of peak juvenile abundance (Table 1) most species in group one have similar reproductive cycles; large numbers of juveniles were present in the June or July samples. Juveniles were present in substantial numbers also in September for *Diaphus schmidti*, *D. sp. A*, and *Bolinichthys longipes*. *D. elucens* showed a peak in September only. *Benthosema suborbitale* and *Ceratoscopelus warmingi* showed large numbers of juveniles also in March. In group two, *Notolychnus valdiviae* and the smallest *Lampanyctus steinbecki* co-occur in summer and fall. *L. niger*, in spite of its apparent later season of maximum recruitment, is recruited at a larger size and co-occurs with similar sized *L. steinbecki* over much of the year. Thus there is a good deal of overlap in time as well as depth and size range for these species.

In general, congeners and closely related species, except *Hygophum* spp., have different size-depth patterns at night. Within each of the above groups, there are few congeners, and the co-occurring congeners are rather dissimilar. The four species of group one whose patterns are closest are of three genera, and the two congeners, *Diaphus schmidti* and *D. sp. A*, are quite different morphologically. Similarly, in group two, the *Lampanyctus* spp. belong to different groups within the genus.

Taaningichthys minimus and *T. bathyphilus* differ in that only *T. minimus* migrates. *Bolinichthys longipes* and *B. supralateralis* differ not only in morphology, size, and depth distribution but also in overall abundance. The two most similar *Lampanyctus* species, *L. steinbecki* and *L. nobilis*, which were present in abundance, have different night depth ranges and different sizes at maturity. Among the *Diaphus* species, closely related or similar species-pairs are distinctly separated even

though most species appear to have similar reproductive cycles with peak juvenile abundance in June or September and nearly the same day depths. *D. rolfbolini* and *D. elucens* have different depth distributions at night. *D. sp. A* and *D. sp. B* differ in depth distribution and also in size at maturity. The species-pair of *D. anderseni* and *D. brachycephalus* differs similarly.

The depth-size patterns of the different species suggest that closely related species differ in their responses to physical factors and that genera or groups within genera have different biological requirements. Strong gradients in temperature, salinity, and light exist in the upper 250 m, particularly for temperature and salinity between 100 and 250 m. These are the most obvious factors to explain the differences in patterns of closely related species. Within each group, however, similar-sized individuals of dissimilar species co-occur under identical physical conditions. For them to co-exist, it would seem that they must be specialized with respect to biological factors.

A likely hypothesis is that the species within a group have different food preferences. Morphological differences between species within the groups include many features probably related to finding or capturing food; relative size of the eye and gape and the number, spacing, and structure of gill rakers. Closely related species of different groups are often rather similar in these respects.

The behavior of the *Hygophum* species appeared to be different from that of the other myctophids. The change in size-depth pattern between new and full moon was unique. The juveniles of *H. proximum* co-occurred with those of species of the second group at new moon and occurred shallower than those of the first group at full moon. The changes in avoidance with moon phase were also unique and suggest that the *Hygophum* species responded to something besides the visual stimulus of the trawl.

The *Hygophum* species were the only two congeners that occurred together in even roughly comparable numbers [see Note (Added in press) under *Lampanyctus niger*]. The two species are quite similar morphologically. *H.*

reinhardti is more slender and has higher numbers of AO photophores, gill rakers, and fin rays. There was, however, a great deal of overlap in these features, and except for adult males separation of the two species was the most difficult of all species collected. (Indeed, comparison of Hawaiian specimens with *H. proximum* from equatorial waters, where *H. reinhardti* does not occur, indicated that the specimens from Hawaii were more like *H. reinhardti* in body proportions than those from the equator.)

The seeming overlap between these two species may be anomalous in that the study area is at the edge of the principal ranges of both. According to Bekker (1965), *H. proximum* occurs principally below lat. 20°N and *H. reinhardti* above lat. 20°N in the central part of the Pacific. Over most of their ranges these two species do not appear to occur together in abundance, and Hawaii appears to lie in the transition zone between one species and the other.

Importance in the Ecosystem

The estimated total numbers of individuals per 10³ m² for nine abundant species is given in Table 5 for each of the quarterly series and the CT series in March 1971. These numbers are the calculated totals from the best series (day or night) from each quarter. Using the same weighting factors, the biomass per 10³ m²

TABLE 5.—Estimated number (individuals/10³ m²) for nine species of myctophids at different seasons. Numbers are totals calculated (see text) from samples taken throughout the water column by Isaacs-Kidd trawl (IK) during September 1970, December 1970, March 1971, and June 1971 and by Cobb trawl (CT) during March 1971.

Species	Number/10 ³ m ²				
	Sept.	Dec.	March		June
			IK	CT	
<i>Benthosema suborbitale</i>	23	40	26	20	14
<i>Hygophum proximum</i>	26	6	49	14	14
<i>Diaphus schmidti</i>	21	14	19	30	25
<i>Notolychnus valdiviae</i>	104	68	12	—	23
<i>Lampanyctus niger</i>	57	163	62	9	55
<i>Lampanyctus steinbecki</i>	82	75	43	16	81
<i>Triphoturus nigrescens</i>	45	248	96	7	23
<i>Bolinichthys longipes</i>	58	23	44	24	13
<i>Ceratoscopelus warmingi</i>	55	176	196	153	155
Total	471	813	547	273	403

TABLE 6.—Estimated biomass (wet weight in g/10³ m²) for nine species of myctophids at different seasons. Figures were calculated by the same method as those in Table 5.

Species	g/10 ³ m ²				
	Sept.	Dec.	March		June
			IK	CT	
<i>Benthosema suborbitale</i>	4	11	10	7	1
<i>Hygophum proximum</i>	19	2	29	11	2
<i>Diaphus schmidti</i>	4	3	10	17	4
<i>Notolychnus valdiviae</i>	6	5	1	—	2
<i>Lampanyctus niger</i>	59	244	102	18	37
<i>Lampanyctus steinbecki</i>	34	34	43	11	61
<i>Triphoturus nigrescens</i>	5	41	19	1	3
<i>Bolinichthys longipes</i>	13	5	30	20	8
<i>Ceratoscopelus warmingi</i>	56	221	103	130	40
Total	200	566	347	215	158

for each species was calculated and is given in Table 6.

The figures are probably low for several reasons. Neither IK nor CT filtered with 100% efficiency; Percy and Laurs (1966) estimated that filtering efficiency was 85% for a 6-ft IK with coarser mesh than used here. There is a negative bias due to avoidance. Substantial avoidance of either the IK or CT was demonstrated for many species, and some likely avoided both. This probably affected the biomass estimates more since the larger fish are more likely to avoid the net. (The CT figures for *Lampanyctus niger* are deceptively low since substantial numbers were caught by IK below the deepest depth sampled by the CT.) For March 1971, the estimated total number is about 7% higher and that for biomass about 20% higher if CT estimates for *Hygophum reinhardti* and *Lampanyctus nobilis* are included and the higher of the two estimates (IK or CT) is used for the other species. It was not possible to estimate reliably numbers and biomass for the less abundant species. They amounted to about 10% of the total numbers caught by the four quarterly series and would probably increase the estimates of total numbers and biomass by a similar factor.

The low totals in June reflect the fact that for most species few adults were present and the juveniles of the next generation were not fully recruited to the population. Other differences were largely due to changes in one or two important species. The peak in total numbers in December was due principally to

high values for *Triphoturus nigrescens* and *Lampanyctus niger*, and the peak in total biomass then was caused mainly by the larger numbers of *L. niger*, a large species, and the fact that *Ceratoscopelus warmingi* had the highest percentage of adults at this time. Overall, *C. warmingi* and *L. niger* were clearly the dominant species with respect to both numbers and biomass.

The average number of myctophids per m² was about 0.55 and the average biomass was about 0.32 g/m². These figures are lower than those given by Percy and Laurs (1966) for total mesopelagic fishes in the upper 1,000 m off Oregon—1.5 individuals and 3.6 g/m² for the night tows. The total number of the three dominant myctophids off Oregon was about 0.78/m². Analyses of other fishes collected off Hawaii is not yet complete, but inclusion of other groups, particularly the hatchetfishes, *Cyclothone*, and larger stomiatoids would likely raise the average number and possibly the average biomass to values comparable to those of Percy and Laurs.

Preliminary analyses of the biomass of other groups of micronekton indicate that most of the biomass in the upper 250 m at night is in the form of vertically migrating groups which are not present during the day and that the myctophids dominate the fauna as a whole. The only other important group of vertically migrating fishes were the gonostomatids whose biomass, principally from *Gonostoma* spp., was about one-fourth that of the myctophids. The myctophid biomass was one to two times that of the caridean shrimps and about one to four times that of the larger euphausiids, *Thysanopoda* spp.

The biomass of epipelagic fishes and larval fishes over 10 mm was about one-sixth that of the myctophids. The figure for epipelagic fishes may be low due to higher concentrations very near the surface, where the sampling was inadequate, and possibly greater avoidance. In general, however, the data agree with Ahlstrom's (1969) conclusions, based on abundances of larval fishes, that vertically migrating, mesopelagic groups—principally myctophids and gonostomatids—dominate the open ocean fish fauna.

Conservatively, the average biomass of micronekton is at least three times that of the myctophids or about 1.0 g/m². Most myctophids appear to have a 1-year life cycle, and in many species, the population is nearly totally replaced by each new generation. The difference between the highest and lowest estimates of myctophid biomass is greater than the average value. Yearly production is then probably higher than the average standing crop. It is not unreasonable to assume that the dynamics of other groups of micronekton are similar and that micronekton production is about twice the average standing crop.

If, following Ryther (1969), it is assumed that ecological efficiency in the open ocean is about 10% for each trophic level and the organisms are about 10% carbon, then a production of 0.2 g C/m² by the micronekton would require production of 2 g C/m²/yr by the trophic level below. The yearly primary production in this area is about 50 g C/m²/yr (S. A. Cattell, pers. comm.) with about 5 g C/m²/yr available to the third trophic level and 0.5 g C/m²/yr to the fourth. For the rather conservative estimate of micronekton production to result, ecological efficiencies must be higher than 10% or the food chain in the open ocean must be shorter than generally assumed by Ryther (1969) and others, i.e., the micronekton must be consuming a large fraction of production by herbivores.

A final point concerns the fate of micronekton production; about 2 g/m²/yr must be consumed by higher carnivores. Studies of the feeding habits of such predators as tuna; dolphin, *Coryphaena*; and lancet fish, *Alepisaurus* (Gibbs and Collette, 1959; King and Iversen, 1962; Haedrich and Nielsen, 1966; Fourmanoir, 1971) indicate that these predators consume few vertically migrating forms such as myctophids or gonostomatids. Tuna and dolphin appear to eat mostly epipelagic forms. Unless the standing crop of epipelagic micronekton has been greatly underestimated here or its turnover rate is greater than that of vertically migrating forms, the "typical" predators of the open ocean are consuming only a fraction of the production by micronekton. In order to identify the principal energy pathways in the open

ocean, more work is needed on the food habits of poorly studied pelagic predators such as sharks, porpoises, gempylids, and squids. Further attempts, such as those of Forster (1971), to collect potential mesopelagic predators are also needed.

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APPENDIX TABLE 1.—Catches of myctophids in two series of four night tows each taken at 50 m and 100 m during July 1970. Only species with an average catch of 10/tow or more are considered separately. All tows were 2 hr at depth. The first three tows of each series were taken successively on the same night; the fourth was taken on the night immediately preceding (50 m) or following (100 m) the other three.

Species	Catch/tow			
	1	2	3	4
50-m series:				
<i>Benthoosema suborbitale</i>	38	57	22	30
<i>Diaphus schmidti</i>	18	21	23	29
<i>Diaphus</i> sp. A	14	22	8	20
<i>Triphoturus nigrescens</i>	32	46	22	40
<i>Bolinichthys longipes</i>	24	49	40	38
<i>Ceratoscopelus warmingi</i>	237	226	120	214
Total myctophids in 50-m series	399	437	267	446
100-m series:				
<i>Hygophum proximum</i>	8	9	11	25
<i>Notolychnus valdiviae</i>	1	2	3	46
<i>Lampanyctus steinbecki</i>	7	30	47	73
<i>Lampanyctus nobilis</i>	0	12	20	64
<i>Bolinichthys longipes</i>	45	51	38	141
<i>Ceratoscopelus warmingi</i>	37	25	31	32
Total myctophids in 100-m series	127	164	184	447

APPENDIX TABLE 2.—Catches of several species of myctophids in short oblique tows and ranges of catches from horizontal tows. Given for each series are the range of catches considered positive in estimating lower limits of depth ranges (+ 's) and the range considered negative and due to contamination (-'s). For the December 1970 and June 1971 series, the catches of short oblique tows are also given. Each of the four December tows made two cycles simulating descent and ascent of the trawl during horizontal tows, each of the three June tows made one descent and ascent.

Species	September 1970		December 1970					March 1971		June 1971					
	+	-	+	-	1	2	3	+	-	+	-	1	2	3	4
<i>Benthoosema suborbitale</i>	14-68	0-9	10-114	0-4	1	3	1	12-84	0-5	6-24	0-4	0	0	0	0
<i>Hygophum proximum</i>	9-88	0-7	6-14	0-3	0	0	0	6-45	0-2	5-21	0-4	0	0	0	0
<i>Diaphus schmidti</i>	14-74	0-7	23-41	0-6	2	2	1	7-51	0-5	7-101	0-3	0	0	1	1
<i>Diaphus</i> sp. A	9-36	0-4	21	0-2	0	0	0	10-29	0-5	6-7	0-2	1	0	0	0
<i>Notolychnus valdiviae</i>	11-130	0-6	10-116	0-8	0	4	1	17-19	0-10	11-84	0-10	3	6	2	4
<i>Lampanyctus niger</i>	11-180	0-7	10-174	0-7	0	12	14	23-69	0-8	12-93	0-10	3	2	6	4
<i>Lampanyctus steinbecki</i>	18-311	2-13	15-77	0-12	7	9	6	12-58	0-5	9-90	0-6	6	0	0	0
<i>Triphoturus nigrescens</i>	11-108	0-7	27-288	0-13	11	32	17	15-116	0-8	5-34	0-4	1	0	0	0
<i>Bolinichthys longipes</i>	19-148	0-8	13-61	0-6	2	1	1	19-93	0-4	7-25	0-6	0	0	1	1
<i>Ceratoscopelus warmingi</i>	14-126	0-10	14-265	0-10	2	2	4	16-248	0-8	11-145	0-5	3	6	2	4