VERTICAL DISTRIBUTION AND OTHER ASPECTS OF THE ECOLOGY OF CERTAIN MESOPELAGIC FISHES TAKEN NEAR HAWAII

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ABSTRACT

Data on abundance, size, depth and time of capture, and sexual development are presented for 37 species of 15 families of rare to moderately abundant mesopelagic fishes taken in the central Pacific. These exhibit a wide variety of patterns of vertical distribution and diel migration. Several undertake migrations similar in extent to those of most myctophids and migrating stomiatoids, while others remain at depth both day and night. In between are species where occurrence or extent of migration are related to size. A trend for juveniles to occur shallower than adults, already noted in myctophids and stomiatoids, is present in most species covered here regardless of migration pattern. Sexual differences in adult size and uneven sex ratios are indicated for several species. The interplay between sexual dimorphism, size difference, and sex ratio and the consequences to reproductive strategy are briefly discussed.

Most ecological studies of mesoplagic fishes have dealt primarily or exclusively with the two groups which dominate the fauna in most parts of the ocean—the family Myctophidae and the stomiatoid fishes. Because other forms are generally collected in small numbers, our knowledge of their ecology is limited to minor parts of general reports (e.g., Badcock 1970) or short notes on a few new specimens. Systematic or zoogeographic studies have assembled data from earlier collections, but in most cases the ecological value of such data is limited because sampling programs were not designed with ecological objectives in mind. Also the gear used was in many cases undoubtedly ineffective at sampling many forms and was fished without really good knowledge of depth of tow.

Recent, ecologically designed collections in the central Pacific Ocean near Hawaii by our program and that of R. E. Young have yielded a large amount of material involving some 225-250 species of mesopelagic fishes. Data on the myctophids and certain stomiatoids have already been reported (Clarke 1973, 1974), and material including many of the remaining species, which has been passed to other investigators, will eventually be covered in broader reports, e.g., family revisions, etc.

In this paper we report on a rather heterogeneous group of rare to moderately abundant fishes taken in these collections. Included are representatives of several families which are present and often moderately abundant in most parts of the world ocean, but of which knowledge of even the depth distribution is rather poor. Even though we are able to consider only a few other ecological parameters in detail for most of these, we feel that presentation of this data contributes to a broader understanding of the patterns of life history exhibited by the diverse mesopelagic fauna.

MATERIALS AND METHODS

Most of the specimens considered herein were taken near Oahu, Hawaii in a series of collections described in detail in Clarke (1973). These included six approximately quarterly series of extended horizontal tows with 2-m (one series) and 3-m Isaacs-Kidd midwater trawls (IK) and a series of samples in the upper 250 m with the larger Cobb Pelagic Trawl (CT). Because the program was designed primarily for study of vertically migrating species, the upper 250 m at night and the 400-1,200 m zone by day were covered most thoroughly; effort in the deeper zone at night was roughly one-fourth that by day. Thus for some of the nonmigrating species considered here, we have examined deep night collections made by R. E. Young with an opening-closing Tucker Trawl (TT). We have also examined collections from

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Manuscript accepted March 1976.
FISHERY BULLETIN: VOL. 74, NO. 3, 1976.

seven TT collections taken between 1,200 and 2,300 m. Finally, to present as much data as possible on rare species, we have included more recent collections with 3- and 5-m IK, deep-day and shallow-night TT collections, and a variety of CT and IK tows made by the National Marine Fisheries Service (NMFS).

The lower depth limits given are subject to question because most of the specimens considered were taken by the IK or CT, neither of which were equipped with opening-closing devices. As discussed in Clarke (1973, 1974), this problem is not great in dealing with abundant species, but for rare species–as were many considered here–there is no basis upon which to discriminate captures made at the principal towing depth from those made in transit to and from towing depth. Consequently, some of our conclusions about depth ranges and vertical migration must be regarded as tentative.

Lengths of all specimens were measured to the nearest millimeter. For each species discussed individually, the total number examined and the length range in millimeters are given in parentheses after the species name. (Unless noted as TL-total length, SL or standard length is used.) Gonads were examined under a dissecting microscope to estimate size at maturity (defined here as the smallest female with well-developed ova), seasonal trends in gonad development, and sex ratios. For rarely taken species, we examined all specimens and have reported results for undamaged specimens large enough to be reliably sexed by our routine technique. In species where we examined only a fraction of the total available material, we selected tows taken from throughout the day and night depth range and from all seasons and examined all individuals of the size range of interest from these selected tows. Hopefully this procedure minimized any potential bias due to sexual differences in depth distribution, etc. In all cases where we discuss population sex ratio, at least 50% (usually 70-80%) of the total individuals of the appropriate size range were sexed.

Numbers of specimens captured per tow were, for all species considered here, too low to treat in a rigorous quantitative fashion. Consequently, we have pooled data from all seasons to estimate depth ranges, pooled fish from all depths to consider seasonal changes in abundance, etc. Since both depth coverage and effort were roughly equal for each of the seasonal series of collections, it is unlikely that any serious bias resulted from our procedures.

Specimens of all species considered here will be deposited in the National Museum of Natural History, Washington, D.C.

TABLE 1.–Lengths and capture data for 11 species taken near Hawaii (lat. 22°20-30'N; long. 158°20-30'W) and two specimens (*) taken in the central equatorial Pacific (lat. 3°30'N; long. 145°W). Total length is given for *Isistius* and *Snyderidia*; standard length for the others. For horizontal tows, the most frequently fished depth is given; oblique tows are noted by 0-maximum depth. Catches by opening-closing trawl are noted by (OC).

	Length (mm); depth (m)	
Family, species	Night (2000-0500)	Day (0700-1800)
Squalidae:		
Isistius brasiliensis	355; 70 398; 0-500 492; 170	
Argentinidae:		
Microstoma microstoma		89; 490
Nansenia sp.	85; 525 (OC)	46; 560 73; 0-1,100 86; 725 107; 620
**Xenophthalmichthys danae*	ca. 75; 300	
Opisthoproctidae:		
Rhynchohyalus natalensis	61; 600 156; 0-400	80. 0-1,100 85; 0-800 107; 530 (OC)
**Winteria telescopa*	41; 450	
Rondeletiidae:		
Rondeletia loricata	15; 190 21; 200 28; 175 38; 450 85; 100	30; 800 33; 1,150 47, 69 (2); 775 86; 0-1,900 52; 925
Barbourisiidae:		
Barbourisia rufa	125; 800 276; 750 314; 0-1,200	67; 750
Zoarcidae:		
Synderidia canina	176; 0-350 188; 150 227; 500 ca. 240 (3); 0-500	79; 0-1,160 188, 247 (2); 800
Gempylidae:		
Lepidocybium flavobrunneum	15; 200 29; 0-350	
Nesiarchus nasutus	22; 370 67; 170	
Scombrolabrax heterolepis	10; 190 26; 25 26 (2); 250	18, 26 (2); 800 27; 1,000 27, 29 (2); 750
Trichiuridae:		
Aphanopus carbo	19; 170 40; 150 59; 190	197; 1,100 252; 660

RESULTS

Table 1 gives length and capture data for 11 rare and sporadically taken species from our collections near Hawaii. We also have included in Table 1 capture data for two rather infrequently collected species of argentinoid fishes which were taken by a series of IK trawls in the central equatorial Pacific (cruise 47 of the NMFS RV *Townsend Cromwell*). Other species are considered under individual headings below.

Opisthoproctidae

Opisthoproctus soleatus Vaillant (150; 28-84 mm)

Almost all *O. soleatus* were taken at 450-600 m during the day; highest catch rates were at 500-550 m. Large (> 50 mm) fish were caught throughout the day depth range, but smaller fish were taken mostly above 550 m. Only six specimens were taken at night—also in the same depth range. The day:night ratio of total trawling time in this depth range was about 4:1; thus the difference in catch is only partially explained by differences in effort. Since the night catches did not indicate that *O. soleatus* is spread more thinly over a broader depth range, the difference in catch per effort indicates that this species avoids the net better at night.

Female *O. soleatus* mature at about 60 mm. Data for each season were few, but there was no indication of seasonality in gonad ripeness, size composition, or abundance.

Opisthoproctus sp. (3; 11-17 mm)

A 17-mm specimen, tentatively identified as *O. grimaldii* Zugmayer, was taken in a day tow at 500 m in September. Two smaller specimens (11 and 15 mm) taken in June are apparently *O. soleatus*. One was taken at night in an oblique tow from 0 to 350 m; the other was caught, possibly in transit, by a day tow which fished at 725 m.

Alepocephalidae

Photostylus pycnopterus Beebe (12; 62-113 mm)

Photostylus pycnopterus was taken within the same depth range day and night. Five day catches were at 750-975 m, and the two night catches at 750 and 875 m. Five other day catches were from oblique tows which fished to 800-1,000 m.

Photostylus pyncopterus appears to mature at about 100 mm and to spawn relatively few but large eggs. Goodyear (1969) recorded a 93-mm female with eggs 1.4 mm in diameter and two specimens (84 and 96 mm) with much smaller eggs. Our three largest females (101-113 mm) carried eggs about 1.75 mm in diameter. One undamaged specimen had only 80 eggs in the ovaries. Another apparently had spawned some already; there were 26 eggs—mostly in the anterior sections of the ovaries. The gonads of two large males (106 and 110 mm) filled most of the body cavity. The remaining specimens (62-89 mm) were clearly immature.

The eggs of *P. pycnopterus*, both absolutely and relative to body size, were larger than those of any other species examined from our collections. Mead et al. (1964) have pointed out that other species of Alepocephalidae also have large eggs.

Giganturidae

Bathyleptus lisae Walters (89; 49-195 mm)

Although a few *B. lisae* were caught as shallow as 500 m, the majority were taken at 750-1,000 m both day and night. Of the 70 specimens taken in horizontal tows, only 7 were taken above this range and 3 deeper. There was no apparent trend in size with depth.

Female *B. lisae* appear to reach much greater size than males. Of 26 fish sexed, there were 14 females of all sizes (67-195 mm) and 12 males—all between 63-81 mm. All nine specimens over 81 mm were females. Of these, only one (171 mm) appeared mature.

Eurypharyngidae

Eurypharynx pelecanoides Vaillant (34; 89-575 mm TL)

Except for two day captures of small individuals (126 and 155 mm at 425 and 550 m, respectively) *E. pelecanoides* was taken between 650 and 1,300 m. Twenty-five specimens were taken during the day within this range. Of the 14 less than 300 mm, only 2 were taken below 1,000 m, and all over 300 mm were taken below 1,000 m. Thus, the small fish appear to occur shallower than the large ones. There were only seven night catches in horizontal tows, but these agreed with the size-depth pattern apparent in the day data.

Among 19 specimens that could be sexed, there were 8 males and 11 females. The seven largest fish included two males (440 and 507 mm), three apparently mature females (ca. 490-575 mm), and two nearly mature females (464 and 494 mm).

Bregmacerotidae

Two species of the genus *Bregmaceros* were taken in our collections. One fits published data (D'Ancona and Cavinato 1965) on *B. japonicus* Tanaka reasonably well, while the other is closest to but not identical with *B. macclellandi* Thompson. The latter is apparently distinct from another form similar to *B. macclellandi* which has been taken in the southern Pacific (E. H. Ahlstrom and J. E. Fitch, pers. commun.). The exact identity of all of these must await a thorough review of this badly confused genus.

The two Hawaiian forms were, however, quite distinct from each other. Dorsal and pectoral ray counts were 56-62 and 19-21 for *B. macclellandi* vs. 50-54 and 17-19 (rarely 20 or 21), respectively, for *B. japonicus*. The latter was the more slender species with SL/greatest body depth of 7.3-10.0 vs. 6.5-7.3 in *B. macclellandi*. *Bregmaceros japonicus* adults were distinctly darker dorsally, while *B. macclellandi* were not countershaded. The isthmus and pelvic fins of all larger *B. macclellandi* were grey, while in juveniles (<25-30 mm), the isthmus was covered with small melanophores. In most *B. japonicus* the isthmus and pelvics were totally unpigmented. A few small (ca. 20-25 mm) specimens whose counts fit *B. japonicus* had a few large melanophores on the isthmus.

Bregmaceros japonicus Tanaka (284; 18-52 mm)

The great majority of *B. japonicus* were taken at 25-125 m at night; however, 40 specimens, possibly contaminants, were taken at 125-200 m. Those under 30 mm were taken mostly above 100 m, while larger individuals were taken with roughly equal frequency throughout the 25- to 125-m range. Only 32 specimens were taken during the day; most (25) were large individuals (>35 mm) and taken at 600-800 m. This suggests that during the day the juveniles may occur shallower than the upper limit of our day samples (ca. 300 m).

Female *B. japonicus* appear to mature at about 40 mm, and almost all specimens over this size carried well-developed ova at all seasons. Small fish (<30 mm) were most abundant in March; they made up about 50% of the catch then as opposed to less than 10% at other seasons.

Bregmaceros cf. *macclellandi* Thompson (274; 14-94 mm)

Bregmaceros macclellandi occurred between 100 and 250 m at night. Most individuals less than 30 mm were caught about 150 m, and most 30-50 mm above 175 m, but larger fish were taken with roughly equal frequency throughout the night depth range. Day catches were mostly between 600 and 1,000 m with those less than 30 mm occurring above 800 m. Seven specimens (65-80 mm) were taken in tows that fished between 1,200 and 1,400 m; three of these were from an opening-closing trawl.

Bregmaceros macclellandi over about 35 mm appear to avoid the IK. Of the total specimens, 152 were taken by the CT in March 1971. Of these only about 12% were less than 35 mm, whereas, about half of the IK specimens were less than 35 mm for either the March data alone (12/23) or the total IK collection (56/122).

Females mature at about 60 mm. There were so few mature females in most series that no trends in gonad ripeness could be ascertained. The size composition of the catch showed no obvious seasonal changes.

Melamphaidae

Scopelogadus mizolepis mizolepis (Günther) (201; 7-74 mm)

Ebeling and Weed (1963, 1973) concluded from their data that *S. mizolepis* does not undertake diel vertical migrations and gave the upper depth limit of "adults" (66-94 mm) as 500 m. Our data, in contrast, clearly indicate that *S. mizolepis* of all sizes undertake a definite vertical migration. During the day, *S. mizolepis* occurred between 600 and 1,000 m and possibly deeper (the few tows below 1,000 m do not allow us to guess whether IK catches there were made in transit). Most of the fish less than 25 mm were taken between 600 and 800 m, and most larger ones at 700-1,000 m. At night the smallest fish occurred at 100-180 m, those 25-50 mm mostly at 150-250 m, and the larger ones at 200-400 m. There were no night catches between 400 and 600 m, but several specimens of all sizes

were taken at night within the daytime depth range, suggesting that a small fraction of the population does not migrate.

We examined the gonads of 127 specimens. Of 39 females (19-74 mm), those less than 50 mm were clearly immature, 2 56-mm fish were nearly mature, and 8 of the 10 largest (57-74 mm) carried well-developed ova. The 88 males were 18-60 mm.

There were too few mature females to consider any seasonal trends in ripeness. Juveniles (7-12 mm) were taken in March, June, and September, and made up the largest fraction of the catch (59%) in March. There were other peaks in size-frequency distributions at all seasons, but none could be clearly traced from season to season.

Poromitra crassiceps (Günther) (57; 16-130 mm)

All sizes of *P. crassiceps* occurred shallower at night than during the day. Day catches were between 750 and 1,000-1,200 m. No specimens over 60 mm were caught above 900 m. At night, two small fish were caught near the day depth, the remaining small fish (19-51 mm) at 150-400 m, and the larger fish (84-128 mm) between 340 and 825 m.

The seven smallest fish (16-25 mm) were taken in March, June, or July, and 16 intermediate-sized individuals (27-35 mm) were all taken in September. The others (39-130 mm) were scattered seasonally. Twenty-four specimens were 80 mm or larger. Nineteen of these (80-101 mm) were males; several of those over 90 mm appeared, subjectively, to be mature or nearly so. The five females were 97-130 mm, and none were mature.

Poromitra megalops (Lütken) (56; 13-41 mm)

All but one *P. megalops* were either 13-21 mm or 28-41 mm. Four of the small fish were caught at 625-1,000 m during the day. At night, five were taken at 250-380 m, and five at 690-775 m. Of the large fish, 27 were taken at 725-1,000 m during the day and 13 at 640-850 m at night. Thus some of the small fish undertake a fairly substantial upward migration at night, but the large fish appear to shift upwards only slightly, if at all. There were no obvious seasonal trends in size composition of the catches; specimens of both size groups were present at all seasons.

Of the 34 specimens sexed, there were 18 females (26-41 mm) and 16 males (28-39 mm). The 5 smallest females (26-35 mm) were immature, while the 13 large ones (37-41 mm) appeared mature. Ebeling and Weed (1973) reported the size range of mature *P. megalops* as 45-62 mm. Possibly, *P. megalops* matures at a smaller size in certain parts of its range. (Ebeling and Weed did not give specific geographic data for their mature specimens.)

Poromitra oscitans Ebeling (19; 44-71 mm)

Poromitra oscitans is a deep-living, nonmigrating species (Ebeling 1975). It occurred only at the lower edge of the depth range sampled in detail. One specimen each was taken at 750 and 850 m; the others were caught in nine tows all of which fished below 1,000 m. Four of these were taken in opening-closing TT' tows which fished only below 1,350 m. Three were males (44-53 mm), and the others, immature females (45-71 mm).

Scopeloberyx opisthopterus (Parr) (93; 14-38 mm)

Scopeloberyx opisthopterus was taken between 540 and 1,200 m during the day. Night catches by the IK were at 650-1,175 m, and one specimen was taken by the TT fished open between 1,300 and 1,450 m. There was thus no evidence of any diel change in depth range. Most small specimens (<25 mm) were taken above 800 m and most large ones below 750 m.

Out of 55 specimens (25-38 mm) sexed, there were 10 immature females (26-30 mm), 24 mature females (31-38 mm), 7 males (27-33 mm), and 4 (25-29 mm) that were too small to sex with certainty but which were probably males. Mature females were taken at all seasons except December (when only four *S. opisthopterus* were taken). There were two rough size groups in the catch; all but seven specimens were either 14-20 mm or over 26 mm. Representatives of the smaller group were absent from samples taken in July and nearly absent in June, suggesting possible seasonality in recruitment.

Scopeloberyx robustus (Günther) (120; 12-31 mm)

Scopeloberyx robustus was taken at 550-1,200 m during the day. With the exception of three small (14-20 mm) specimens taken at 340-425 m, the night depth range was similar—600-1,175 m. Thus there is no indication that any but the small *S. robustus* vertically migrate. There was a distinct increase in size with depth. With few exceptions, fish less than 20 mm were caught above 800 m,

those 20-25 mm at 750-1,000 m, and those over 25 mm below 900 m.

Of 41 specimens (21-31 mm) sexed, 24 were females of which 6 (29-31 mm) were mature. The 17 males were 22-30 mm. Fish less than 16 mm were taken only in July and September. There were no seasonal trends in abundance of the larger fish.

Melamphaes danae Ebeling (627; 11-22 mm)

During the day, *M. danae* occurred principally at 750-1,200 m; a few were taken as shallow as 650 m. Fish less than 15 mm were almost all taken above 1,000 m, while larger ones occurred throughout the day depth range. Most night captures were between 75 and 200 m; the small fish were mostly taken at 75-100 m, while the larger ones occurred throughout the depth range. There were no night captures between 400 and 650 m, but 27 specimens of all sizes were taken at night in tows that fished within the day depth range. Although this catch was numerically small, and possibly due to in transit captures, it was large enough relative to effort to suggest that a small, but not insignificant fraction of the population did not regularly migrate.

Female *M. danae* matured at about 17-18 mm. Mature females were present in comparable numbers and percentages at all seasons, but the size composition of the catches indicated that juveniles were recruited primarily in the spring and early summer. For the series where the proper depth ranges were adequately and roughly equivalently sampled, the small (11-14 mm) fish made up 27% of the total catch in March, 15% in June, and 42% in July as opposed to 1% in September and 2.5% in December.

Melamphaes simus Ebeling (4; 14-24 mm)

Data on *M. simus* indicate little more than that it is present in low abundance in the area. The two night captures were at 300 and 800 m, while the two day captures were at ca. 700-800 m (the latter depths are estimates from wire out; depth records for both day tows were invalid).

Melamphaes indicus Ebeling (20; 16-55 mm)

Eleven *M. indicus* were taken at night at 125-150 m—nine of these in one tow. Nine specimens were taken during the day at 640-900 m. Two large females (51 and 55 mm) were mature, and four males (47-53 mm) appeared mature or nearly so.

Melamphaes sp. (*janae?* Ebeling) (10; 17-54 mm)

Seven *M. "janae"* were taken at night at 190-250 m and three during the day between 650 and 900 m. All were taken in September or November. The two largest specimens (43 and 54 mm) were both males and larger than the maximum size of this species given by Ebeling (1962). Ebeling, however, did note geographic differences in size at maturity. Our specimens fit the description of *M. janae* in other respects and could be reliably distinguished from similar-sized individuals of *M. indicus*. Study of more specimens will be necessary to determine whether *M. janae* is more variable in size than Ebeling noted or more than one species is involved.

Melamphaes sp. (*longivelis?* Parr) (2; 18, 20 mm)

Two small specimens of the *"typhlops"* group are tentatively identified as *M. longivelis*. The smaller was taken at 625 m at night, the larger at 640 by day.

Melamphaes polylepis Ebeling (10; 17-57 mm)

One *M. polylepis* was taken at night at 930 m; the remainder were taken during the day at 640-1,150 m. They included two mature females (56 and 57 mm), six males (46-56 mm), and two juveniles (17 and 19 mm).

Anoplogasteridae

Anoplogaster cornuta (Valenciennes) (93; 3-126 mm)

Juvenile *A. cornuta* undertake a substantial upward migration at night. At least some of the large fish also move upwards, but occur deeper than the juveniles both day and night. Seventy-two specimens were small (3-24 mm) and were taken in February-March. Fifty-eight were taken at night between 135 and 185 m; the remaining 14 were taken during the day—12 at 650 m and 2 at ca. 800 m. Larger specimens (all >70 mm) were taken throughout the year. At night six (77-87 mm) were taken between 275 and 475 m, one each at ca. 600 m (108 mm), 900 m (109 mm), and in an oblique tow to

980 m (94 mm). The 12 large (77-126 mm) individuals taken during the day were from 750-1,150 m.

Among the 18 fish sexed, there were 12 males (80-109 mm) and 6 females (78-126 mm). None appeared mature. The collection of so many small individuals in one of the seasonal series indicates that *A. cornuta* has a rather short spawning season.

Stylephoridae

Stylephorus chordatus Shaw (19; ca. 60-315 mm)

Seven *S. chordatus* (ca. 60-315 mm) were taken at night between 300 and 600 m. Eleven (63-282 mm) were taken between 625 and 800 m during the day, and one at dusk at 500 m. Thus *S. chordatus* appear to migrate about 200-300 m upward at night.

Two females (282 and 315 mm) appeared mature; the next largest female was 147 mm. The four largest males were 235-243 mm.

Gempylidae

Gempylus serpens Cuvier (29; 7-148 mm)

All but two *G. serpens* were taken at night in the upper 250 m; 19 were from 30-100 m. During the day, a 60-mm specimen was taken at 450 m and a 30-mm one at 800 m. It seems likely that the latter or both of the day catches were made in transit and that *G. serpens* migrates downward only a short distance, if at all, during the day. None were near maturity.

Nealotus tripes Johnson (95; 7-173 mm)

Most *N. tripes* were small (9-41 mm) taken at 50-200 m at night. Seventy-three were taken in December—58 in three tows at 170-200 m and 12 in a tow at 250 m. The CT collected four large specimens at night, three (75, 168, 173 mm) at 100 m and one (68 mm) at 250 m, while only one (49 mm at 150 m) was taken by the IK. No small fish and only three large ones were taken during the day. The CT captured a 49-mm individual at ca. 350 m, and the IK took two (63, 105 mm) in separate tows at ca. 750 m. The small *N. tripes* apparently stay in the upper layers both day and night. Since the larger fish were obviously inadequately sampled by the IK and there were no deep day tows made with the CT, it is not clear whether adults descend or not. The two deep day catches by the IK may well have been coincidentally taken in transit by tows which fished the same depth.

Diplospinus multistriatus Maul (224; 8-239 mm)

Most of the *D. multistriatus* were small individuals caught at night at two depth zones and at two separate seasons. Of the 100 specimens taken in December, 78 (8-30 mm) were taken in three tows at 170-200 m. In July, 62 specimens were taken; 31 (7-18 mm) were from four tows at 100-110 m. Other small fish taken at night were mostly from the upper 200 m with a few, probably captured in transit, taken in deeper tows. Of the 18 larger (35-239 mm) specimens taken at night, 13 were taken in the upper 130 m, 4 at 200-300 m, and 1 probably captured in transit, at 500 m.

Only 37 were taken in day tows, all but 2 between 500 and 1,000 m. Only one of these (11 mm) was in the size range which dominated the night catches. Three specimens were slightly larger (36-42 mm) and the remainder 68-221 mm. Most less than 140 mm were taken above 800 m, and most over 140 mm were taken below 700 m.

The near absence of small *D. multistriatus* in the day samples suggests that they either remain in the upper layers during the day (and were not sampled by our tows) or occur deeper and avoid the net during the day. The latter seems improbable for such small fish. Assuming the former is true and considering the data on larger fish, it appears that *D. multistriatus* occurs in the upper 100-200 m at night and that the larger sizes migrate to progressively greater depths by day.

Of the 46 specimens sexed, 12 were males (93-207 mm) and 34 females (75-239 mm). Eight females (163-239 mm) were mature.

DISCUSSION

Vertical Distribution and Migration

The diverse group of fishes considered here, as might be expected, exhibit a greater array of vertical distribution patterns than the myctophids and stomiatoids which occur in the study area. Most species of the latter two groups undertake substantial diel vertical migrations. The remaining species do not vertically migrate at all. Among the species considered here, migrators and nonmigrators are about equally represented, and

almost every conceivable intermediate pattern is represented as well.

Four of the common species, *Bregmaceros japonicus*, *B. macclellandi*, *Scopelogadus mizolepis*, and *Melamphaes danae*, are typical migrators. Both juveniles and adults move from well below 500 m during the day into the upper 250 m at night. The data indicate that four rarer species, *Rondeletia loricata*, *Melamphaes indicus*, *M. "janae,"* and *Scombrolabrax heterolepis* probably perform similar migrations.

The first four species were the most abundant of all considered here and ranked with all but the 8-10 most abundant myctophids and migrating stomiatoids (see Clarke 1973, 1974). The night size-depth patterns of the four were similar to the general types observed in the latter groups. *Bregmaceros japonicus* cooccurred with similar-sized individuals of several abundant myctophid species and *Vinciguerria nimbaria*, while *B. macclellandi* and the melamphaids had patterns similar to those of deeper-living species, e.g., *Lampanyctus niger* and *Gonostoma* spp. In the case of the *Bregmaceros* spp. and *M. danae*, the adults occurred throughout the depth range instead of primarily at the lower end as was usually the case with the other fishes.

During the day, the four migrating species exhibited a trend for increased size with depth. The day depth range of *B. japonicus* was similar to those of many other migrating species, but the other three were the only migrating species besides the myctophid *Lampanyctus nobilis* whose day depth range extended well below 1,000 m. *Lampanyctus nobilis*, *B. macclellandi*, and *Scopelogadus mizolepis* are relatively large species, but *M. danae* is one of the smallest species of fishes encountered in our study area.

The species for which there was no indication of diel change in vertical distribution are a rather heterogeneous group. *Opisthoproctus soleatus* inhabited a relatively shallow depth range and cooccurred with several stomiatoid species with similar, and probably convergent, morphological features (see Clarke 1974). Other nonmigrating species (*Scopeloberyx* spp.; *Poromitra oscitans*, *Photostylus pycnopterus*, *Bathyleptus lisae*, *Eurypharynx pelecanoides*, and probably *Barbourisia rufa*) occurred mostly below 600 m. Many of these species are commonly referred to with the too casually used adjective "bathypelagic," which has the connotation (if not always the denotation) of extremely great depths well removed from direct influences of surface phenomena. Our data indicate that most of these should more properly be considered members of the mesopelagic community. Even taking into account the relatively few hours of sampling below 1,000-1,200 m, the only species which appear to occur in any abundance below this depth are *Poromitra oscitans* and *E. pelecanoides* (of course, other fishes not covered here do occur deeper and some, e.g., certain ceratioids and the eel *Cyema* appear to occur only below 1,000-1,200 m). In fact, *B. lisae*, the *Scopeloberyx* spp., and probably all the others except *P. oscitans* have their primary centers of abundance above 1,000-1,200 m. During the day, they cooccur and presumably interact with vertically migrating species. Thus at least some aspects of their ecology must be affected by diel light changes.

Four species showed limited diel changes in depth distribution. *Stylephorus chordatus* moved somewhat shallower at night, but did not occur in the upper 250 m. Juveniles of *P. crassiceps* and *Anoplogaster cornuta* undertook fairly substantial upward migrations at night, but the adults shifted only slightly shallower. Juvenile *P. megalops* occurred somewhat shallower at night, but there was no conclusive evidence that the adults moved at all. Juvenile *Scopeloberyx robustus*, considered a "nonmigrator" above, may also move up at night. Since only *P. crassiceps* and *P. megalops* were taken in even moderate numbers, the patterns for the other species must be regarded as tentative. Size-related differences in migration have been noted for some myctophids and stomiatoids (Clarke 1973, 1974). As examples, the adults of *Bolinichthys distofax* (identified as *B. superlateralis* in Clarke 1973) appear not to migrate while the juveniles do, and the larger individuals of *Gonostoma elongatum* appear to occasionally remain at depth during the night.

Interpretation of data on the gempylid-trichiurid species is limited because, with the exception of *Diplospinus*, only the small juveniles were collected, and even these either avoided the net during the day or occurred so shallow that they were not sampled by our program during the day. The data indicate that all sizes of *Gempylus serpens* (to 148 mm) and *Nealotus tripes* (to 173 mm) collected probably remain in the upper layers during the day. Although the deep day catches of small *Scombrolabrax heterolepis* may have been made in transit, the absence of this species from day tows above 750 m suggests that it may mi-

grate. *Diplospinus multistriatus* exhibited a pattern opposite to that of *P. crassiceps*; the small fish either remain in the upper layers or descend only slightly during the day while the larger juveniles (>ca. 60 mm) and adults undertake a substantial migration.

Avoidance

With the exception of the gempylid-trichiurid species, there were few obvious indications of sampling error due to avoidance, but in most cases data were too few to even discuss the subject. The failure to capture mature specimens of the two large *Poromitra* spp. indicates avoidance by these and probably a fraction of the populations of other large melamphaids. *Bregmaceros japonicus* was apparently undersampled during the day, and the large *B. macclellandi* were sampled better by the CT than by the IK. It is not unexpected that avoidance was indicated for the larger, more "solidly built" species rather than for small species such as *M. danae* and the *Scopeloberyx* spp. or species such as *Bathyleptus lisae* and *Eurypharynx pelecanoides* which do not appear "designed" for swimming ability. The most puzzling indication of avoidance was that suggested for *Opisthoproctus soleatus*. This species not only has few characteristics indicating swimming prowess, but was undersampled at night rather than during the day as one might expect if vision were involved.

Sexual Dimorphism and Sex Ratio

In several species, the males appeared to be smaller than females (Table 2). The extreme case was *Bathyleptus lisae* where the largest female was about 2.5 times longer than the largest male. In *Scopelogadus mizolepis*, the females mature at about the size of the largest males observed and reach somewhat larger maximum size. A similar trend is suggested by the data for *Anoplogaster cornuta* and two other large melamphaids, *Poromitra crassiceps* and *P. oscitans*, but the numbers involved are too small to confirm it here. In two smaller species of the same family, *P.*

TABLE 2.–Summary of data on sex ratio and sexual differences in size for 10 species of fishes. Under Population sex ratio and left hand column gives the number and size ranges of all males in the population with 95% confidence limits (read to the nearest 0.01 from Chart 3 in Tate and Clelland 1957). Sex ratio was considered significantly different from 1:1 if these limits did not cross 0.50. Under Size Difference similar figures are given for only those specimens larger than the smallest mature female (since all *Melamphaes danae* were as large or larger than the smallest mature female, the data are the same for both pairs of columns). For *Bathyleptus lisae*, where the smallest mature female was much larger than the largest male, and for three melamphaids, where no mature females were taken, we have given only the number and size range of females larger than the largest male.

Species	Population sex ratio		Size difference	
	No. examined (Size range, mm)	Proportion of males (95% limits)	No. examined (Size range, mm)	Proportion of males (95% limits)
Bathyleptus lisae	12♂ (63-81)	0.46	9♀ (90-195)	—
	14♀ (67-195)	(0.26-0.67)		
Scopelogadus mizolepis	88♂ (18-60)	0.69	2♂ (60)	0.17
	39♀ (19-74)	(0.60-0.77)	10♀ (57-74)	(0.02-0.47)
Poromitra crassiceps	19♂ (80-101)	0.79	4♀ (121-130)	—
	5♀ (97-130)	(0.57-0.96)		
Poromitra megalops	16♂ (26-39)	0.47	3♂ (37-39)	0.19
	18♀ (28-41)	(0.29-0.66)	13♀ (37-41)	(0.04-0.47)
Poromitra oscitans	3♂ (44-53)	0.16	10♀ (53-71)	—
	16♀ (45-71)	(0.03-0.41)		
Scopeloberyx opisthopterus	21♂ (25-33)	0.38	8♂ (31-33)	0.25
	34♀ (26-38)	(0.25-0.53)	24♀ (31-38)	(0.11-0.45)
Scopeloberyx robustus	17♂ (22-30)	0.41	4♂ (29-30)	0.40
	24♀ (21-31)	(0.24-0.58)	6♀ (29-31)	(0.12-0.70)
Melamphaes danae	282♂ (17-22)	0.65	—	—
	144♀ (17-22)	(0.60-0.70)		
Anoplogaster cornuta	12♂ (80-109)	0.67	3♀ (110-126)	—
	6♀ (78-126)	(0.41-0.87)		
Diplospinus multistriatus	12♂ (93-207)	0.26	3♂ (184-207)	0.23
	34♀ (75-239)	(0.13-0.42)	10♀ (163-239)	(0.05-0.55)

megalops and *Scopeloberyx opisthopterus*, the maximum size of females was only slightly greater than that of males, but there were relatively few males larger than the smallest mature female. Thus there appears to be a slight but real difference in size of the two sexes. The two smallest melamphaids, *Melamphaes danae* and *S. robustus* showed no sexual differences in size. In all cases, except *P. crassiceps* and *P. oscitans*, there were sufficient small females to indicate that the size differences were not due to protandrous hermaphroditism.

Sexual differences in size have been reported for many species of dioecious mesopelagic fishes. Large differences comparable to that observed in *Bathyleptus* occur in the ceratioid anglerfishes (Bertelsen 1951) and the stomiatoid *Idiacanthus* (Gibbs 1964). Differences of the order observed for some of the melamphaids are known for several stomiatoids: *Stomias* (Gibbs 1969), *Echiostoma* (Krueger and Gibbs 1966), and *Cyclothone* (Kobayashi 1973). The usual explanation of the adaptive significance of smaller males (Marshall 1971) is that in a food limited environment–such as the deep-sea probably is–the energy required by the population is lowered without diminished fecundity.

Sexual dimorphism (as opposed to differences only in size) is quite common among meso- and bathypelagic fishes. Males of several groups exhibit better developed swimming muscles or sensory apparatus than the females (Marshall 1971). In many myctophids and stomiatoids, there are sexual differences in light organs. In most cases, sexual dimorphism seems related to increasing reproductive success by increasing the probability of heterosexual encounter.

No obvious external sexual dimorphism was observed in any of the species considered here (with the exception of *Isistius*), but at least two species appear to have uneven sex ratios (Table 2), an adaptation which, like the dimorphisms noted above, serves to increase the probability of a female meeting a conspecific male. Actually, the sex ratios of five species were significantly different from 1:1, and *Anoplogaster cornuta* showed a nearly significant trend. However, it seems wise to view the estimates for *Poromitra crassiceps*, *P. oscitans*, and *Diplospinus multistriatus* with suspicion since numbers were rather low and biases due to inadequate sampling and avoidance may be involved.

For both *Melamphaes danae* and *Scopelagadus mizolepis*, the numbers involved are relatively high and there is no indication that the populations were not adequately sampled. The estimated sex ratios for these two species indicate that the probability of an individual female encountering a male is about twice that expected for a population with the same density of females and 1:1 sex ratio. (The probability of an individual male encountering a female is lowered, but this has no consequences to population reproductive success.) In the case of *M. danae*, where the sexes are the same size, population fecundity would be less than that of a population of equal total biomass and 1:1 sex ratio because about two-thirds of the biomass are males. The males of *S. mizolepis* are, however, smaller than the females. Consequently, the effect of uneven sex ratio on population fecundity is to some extent balanced by the more nearly even division of population biomass between males and females. Better data on stages of maturity–particularly for males–and size distribution of mature fish of each sex would be needed to quantitatively describe the "trade off" between uneven sex ratio and sexual size difference.

The difference between *M. danae* and *S. mizolepis* may simply be due to the fact that *M. danae* is already a "dwarf" species–the smallest at maturity of all mesopelagic fishes in our collections. There may be other factors which select against the males being smaller than the already tiny females. On the other hand, *M. danae* may in some sense be less "food-limited" than *S. mizolepis* and thus able as a population to afford having two-thirds of the biomass as males. Further study of the interplay between sexual dimorphism, differences in size, and departure of sex ratio from 1:1 might prove to be a fruitful approach toward understanding the diverse life history features shown by mesopelagic fishes.

ACKNOWLEDGMENTS

We are indebted to the captain and crew of the RV *Teritu* and to the many people who assisted in collecting and rough-sorting the material. We also thank A. W. Ebeling for confirming our identifications of representatives of each of the melamphaid species considered here. This research was supported by NSF GB23931, NSF GA38423, and funds from the University of Hawaii, Hawaii Institute of Marine Biology.

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