VERTICAL DISTRIBUTION, DIEL VERTICAL MIGRATION, AND ABUNDANCE OF SOME MESOPELAGIC FISHES IN THE EASTERN SUBARCTIC PACIFIC OCEAN IN SUMMER[1]

BRUCE W. FROST AND LAWRENCE E. MCCRONE[2]

ABSTRACT

Vertical distributions of myctophid fishes and other components of the mesopelagic micronekton were determined during the summers of 1973-75 at two stations in the eastern subarctic Pacific Ocean. Stratified samples were collected with a multiple net Tucker trawl so that the entire water column extending to between 385 and 460 m could be sampled during a daytime or nighttime period; two to four day and night vertical series of samples were obtained each summer. Four species of myctophids made up 87% of the total fish catch: *Stenobrachius leucopsarus* and *Diaphus theta*, which performed diel vertical migrations of 300 m vertical extent; and *Protomyctophum thompsoni* and *S. nannochir*, which exhibited only slight diel variation in vertical distribution. Populations of each myctophid species tended to be vertically stratified by age or size with larger individuals occurring in samples taken progressively deeper. Two other major components of the micronekton were euphausiids and decapod shrimps, chiefly *Euphausia pacifica* and *Sergestes similis*; both species were conspicuous diel vertical migrators. Samples collected in horizontal hauls immediately following sunset showed that three migratory species, the two migratory myctophids and *E. pacifica*, were closely associated with the single migratory sound-scattering layer (12 kHz); *S. similis* lagged the ascent of the migratory scattering layer. A single, deep, nonmigratory sound-scattering layer corresponded closely to the distribution of *P. thompsoni* during both day and night. As in other subpolar oceanic waters, abundance and standing stock of myctophids were high—0.9 fish/m^2 and 0.37 g dry weight/m^2.

In 1973 we began a field study of some small mesopelagic fishes of the family Myctophidae, commonly known as lanternfishes or myctophids, in the eastern subarctic Pacific Ocean. The objectives of the study were to determine the vertical distribution and migration characteristics of the numerically dominant species, to document their feeding behavior, and to ascertain if the distributions of fish were in any way influenced by the distribution of their preferred prey. Myctophids are major components of the mesopelagic fauna throughout the world ocean, and in most areas they are sufficiently abundant and stratified in the water column to cause deep sound-scattering layers (Baird et al. 1974; McCartney 1976). Indeed, study of these fishes has been heavily oriented toward aspects of their distribution in relation to sound-scattering layers (e.g., Tucker 1951; Barham 1966; Taylor 1968; Holton 1969; Farquhar 1971; Baird et al. 1974), although some investigations emphasized aspects of biological and ecological significance, such as individual growth rates, seasonal changes in abundance, and association among species (e.g., Pearcy and Laurs 1966; Harrisson 1967; Lavenberg and Ebeling 1967; Smoker and Pearcy 1970; Badcock 1970; Clarke 1973; Pearcy et al. 1977). Much of the research on myctophids has, in addition, stressed description of the prominent diel vertical migrations which are apparently undertaken by almost all species.

In the few species studied in detail, both the occurrence and pattern of vertical migration vary with age or ontogeny. Larval myctophids are nonmigratory, spending day and night in near-surface waters (Ahlstrom 1959). Diel vertical migration is first evident at or shortly after metamorphosis and usually persists throughout the remaining life of the fish, although in very old fish, migrations may differ substantially in character from those of younger fish and may even be supressed (Nafpaktitis 1968). Apart from this variation with age, diel vertical migrations of myctophids seem to be relatively regular, on a day-to-day basis, and exhibit little or no seasonal variation (Pearcy and Laurs 1966; Halliday 1970; Pearcy et al. 1977). Among some species, however,

[1]Contribution No. 1039 from the Department of Oceanography, University of Washington, Seattle, WA 98195.

[2]Department of Oceanography, University of Washington, Seattle, WA 98195.

Manuscript accepted May 1978.
FISHERY BULLETIN: VOL. 76, NO. 4, 1979.

there may be a portion of the population which does not migrate, while other members of similar size and age do migrate (Clarke 1973; Badcock and Merrett 1976; Pearcy et al. 1977).

Virtually nothing is known about the biological causes or consequences of these diel vertical migrations, either with respect to the myctophids or their environment. Marshall (1954) suggested that myctophids migrate into the surface layer each night in order to feed on zooplankton, which is usually most abundant in surface waters (Vinogradov 1968). As pointed out above, larval myctophids spend both day and night in the zooplankton-rich surface layer, but as the larvae grow they perhaps become more conspicuous to visual predators and, after metamorphosis, they descend to greater depths,returning to the surface layer only at night, if at all. Vertical migrations may indeed have evolved as a means of avoiding or minimizing predation, but it is unlikely that this hypothesis can be tested in the ocean.

On the other hand, it is practicable to investigate the feeding ecology of myctophid fish in relation to their migrations; for example, what types of prey the fish utilize, when and where in the water column the fish feed, and whether the vertical distributions of the fish are affected by the vertical distribution and abundance of their preferred prey. As necessary background for such a study, in this paper we present details of the vertical distributions of the numerically dominant species of myctophids in the eastern subarctic Pacific Ocean.

METHODS

Study Area

We conducted the investigation during three summer cruises in areas centered at lat. 50°N, long. 145°W (July-August 1973 and July-August 1975; Station P in Figure 1) and at lat. 51°N, long. 137°W (July 1974; Station Q in Figure 1). These stations lie within the hydrographic province designated the Central Subarctic Domain by Dodimead et al. (1963). We chose the subarctic region for ease of sampling and identifying the fish and zooplankton. For example, in an earlier meridional cruise from Kodiak, Alaska, to Honolulu, Hawaii (August-September 1972), we found that deep sound-scattering layers are fewer in number, shallower, and more intense in the subarctic region than in transition and subtropical waters (Frost unpubl. data). Apparently related to this, the subarctic myctophid fauna is a simple one; only a few species are abundant, and they are relatively shallowly distributed in the daytime (Taylor 1968). Further, the study area is an open ocean environment, outside the potentially complicating influences of coastal and transitional waters (cf. McGowan 1971) and is roughly in the middle of the latitudinal range of several species of myctophids. Finally, the zooplankton assemblage in subarctic waters is also less diverse than in lower latitudes, it is well known taxonomically, and relatively few species are abundant.

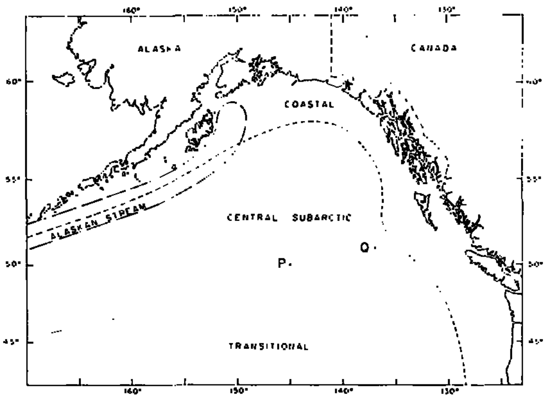


FIGURE 1.—Sampling stations in the eastern subarctic Pacific Ocean. Representative hydrographic domains for summer conditions after Dodimead et al. (1963).

Sampling Gear

Nekton samples were collected with a modified Tucker trawl (Tucker 1951) described by Frost and McCrone (1974). Briefly, the trawl had a rigid rectangular mouth with a 4-m² area when inclined forward at a 45° angle from vertical, and carried five separate nets (6.35-mm stretch mesh, knotless nylon ace netting) stacked one on top of another (much like fig. 4 in Harding et al. 1971). The net shape followed the design of Clarke (1969). The trawl carried an electronics package containing a strain gage pressure transducer (range 0-1,500 lb/in²) for determination of depth and a precision pendulum-type tilt transducer (range 0°-90° from vertical) for determination of angle of inclination of the trawl mouth. A TSK (Tsurumi-Seiki Kosakusho)[3] flowmeter fitted with a magnetic

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

reed switch was mounted on the top beam of the trawl.

The trawl was towed on a two-conductor coaxial cable and its depth, angle of inclination of the mouth, and revolutions of the flowmeter were monitored continuously during trawling by means of a shipboard display unit. The nets were opened and closed at the mouth by means of a net-tripping assembly which was controlled electronically from the ship. The bottom net (without cod end) was left open during deployment to eliminate kiting of the trawl when a net was first opened (Clarke 1969; Badcock and Merrett 1976); thus, four sequential samples could be collected in one haul. The volume of water filtered by each net (assuming 100% filtration efficiency) was calculated from flowmeter revolutions and average angle of inclination of the net mouth.

To determine vertical distributions of fish and other components of the nekton, we towed the trawl obliquely and collected samples on the upward leg of a haul. We monitored the speed of the ship during trawling by reference to a Doppler ship's speed indicator.

Recordings of deep sound-scattering layers were obtained using an Edo-Western transducer operating at 12 kHz (pulse length 3-10 ms, beam width about 33°) and a Precision Depth Recorder (PDR) operating on the 0-400 fm (0-732 m) depth range scale. At the beginning of each cruise, echosounder characteristics (pulse length, power output) and recorder gain were set to give optimal resolution of the sound-scattering layer and were not varied thereafter.

Sampling Program

Taylor (1968) found a close correlation between distribution of abundant species of myctophid fishes and distribution of deep sound-scattering layers in the eastern subarctic Pacific near the Queen Charlotte Islands. Relying on this correlation, at each station we designed our sampling program after observing the depth and migrations of deep sound-scattering layers. The number, depth, and migration of scattering layers were virtually identical at Stations P and Q. We observed no differences between years at Station P, and our observations do not differ substantially from those of Bary (1967) who also used a 12-kHz echosounder in summer at Station P. In the daytime, a single, diffuse, sound-scattering layer extended from about 275 to 375 m depth (Figure 2A). In the late afternoon and early evening, this scattering layer became broader, chiefly by upward movement of the top of the layer, and it persisted with relatively little further change throughout the night. At about 2130 h (local time), a single, upwardly migrating layer became evident, and within half an hour it merged completely with the surface reverberation (Figure 2B). This migratory scattering layer began descent at about 0530 h and merged with the deep nonmigratory layer shortly after 0600 h. Slight variations in times of ascent

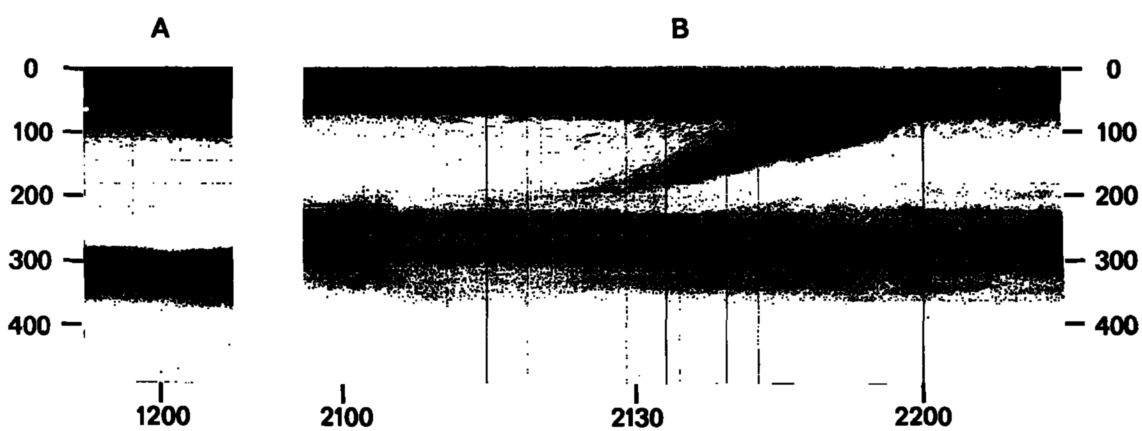


FIGURE 2.—12-kHz echograms typical of the summer period (July-August) in the sampling areas in the northeastern Pacific Ocean. A. Daytime record about noon, local time. B. Evening record taken on the same day showing the upward movement of the migratory sound-scattering layer and the persistence of the nonmigratory layer at depth. Local time, depth in meters. The dark areas above 100 m are due to surface reverberation.

and descent of the migratory sound-scattering layer depended on weather conditions; also, year-to-year differences are attributed to slight variations in time of cruises. We usually set the lower limit of nekton sampling at least 50 m below the depth of the deep nonmigratory scattering layer. With the exceptions noted below, nighttime sampling was confined to the time period between ascent and descent of the migratory scattering layer.

Somewhat different sampling programs were carried out in different years (Table 1). At Station P in 1973 the objective was to obtain information on vertical distributions of fish and zooplankton to aid in developing an optimal sampling strategy for studying diet and feeding behavior of myctophids. The 0-440 m water column was sampled in 55-m depth strata, and seven successive vertical series of samples, 4 night and 3 day series, were obtained. A shallow haul (0-220 m) and a deep haul (220-440 m) were required for each complete vertical series. The first nighttime series was not completed before the descent of the migratory sound-scattering layer. In order to obtain both the shallow and deep hauls during one night, the hauls were of relatively short duration, and consequently the nekton samples were relatively small.

At Station Q in 1974, the objectives were to confirm the vertical distributions found in 1973 at Station P and to document the feeding chronology of the common myctophids. The sampling for vertical distributions (Table 1) extended from the surface to between 400 and 460 m, depending on the depth of the deep sound-scattering layer, and usually included one sample collected below the scattering layer. Complete daytime vertical series (both shallow and deep hauls) of samples were collected on 2 days; as no fish were collected in the upper 200 m, two additional daytime vertical series were made with only one haul extending from below the depth of the sound-scattering layer to about 200 m. In order to achieve adequate sample size, the duration of each haul was long, but because there were so few hours of darkness, only one nekton haul could be made each night. Data from a shallow haul and a deep haul on successive nights were therefore combined to give a single, complete, night vertical series; two such night series were obtained, and all sampling was performed between ascent and descent of the migratory sound-scattering layer.

In addition to vertical series of nekton samples taken at Station Q, we utilized two types of horizontal hauls. To identify components closely associated with the migratory sound-scattering layer, on two evenings the trawl was launched near sunset and towed horizontally at 125 m. The 12-kHz echosounder was operated continuously during the hauls. Approximately 30 min before the scattering layer began to ascend from its daytime depth, a trawl net was opened and sampling began. The second net was opened just as the scattering layer reached 125 m, and the net was closed after the layer had passed that depth. The trawl was towed at 125 m for an additional 30 min, taking a third sample, then closed and retrieved. As part of the study of diel variations in feeding intensity of myctophids, a series of three horizontal hauls, each yielding four samples of 30 min duration, was made in the upper layer (40-m depth) throughout one night.

The sampling program at Station P in 1975 was similar to that at Station Q, although the nekton sampling for vertical distributions (Table 1) was much less extensive than in the previous two cruises. We obtained only one complete nighttime vertical series (400-0 m) and two deep daytime vertical series (385-220 m) to check on vertical distributions of myctophids. We collected one shallow vertical series in the 0-60 m layer in 15-m depth strata to examine the vertical distribution of myctophids within the surface layer at night, and we took one very deep daytime vertical series (782-440 m) to determine the distribution of myctophids below our usual sampling depths.

All samples obtained with the nekton trawl were preserved in a 4% formaldehyde seawater solution buffered with sodium borate.

TABLE 1.—Sampling data for vertical series of nekton samples in the northeastern Pacific. The three lower entries for Station P (1975) represent data for: first, the routine day-night vertical series (0-400 m); second, a single shallow (0-60 m) night vertical series; and, third, a single deep (440-782 m) daytime vertical series.

Stn.	Dates	Ship speed (km/h)	Mean (range) duration of samples (min)	Mean (range) volume filtered per sample (m^3)	
P	5-9 Aug. 1973	7.2±0.5	29 (16-45)	8,412	(4,863-13,357)
Q	18-22 July 1974	6.2±0.5	45 (24-66)	14,229	(6,833-20,361)
P	26-28 July 1975	6.9±0.5	32 (19-43)	10,984	(7,664-14,731)
	27 July 1975	6.9±0.5	21 (16-29)	7,638	(6,184-10,052)
	31 July 1975	6.9±0.5	68 (58-79)	23,232	(20,012-28,614)

Analysis of Samples

All organisms in the nekton samples were counted. Fish were identified from descriptions in Hart (1973) and Wisner (1976). The standard length (SL) (distance from the tip of the snout to the end of the vertebral column) of each fish was measured to the nearest millimeter. Among the invertebrates collected in nekton samples, only euphausiids and decapod shrimps were consistently captured in substantial numbers. The numbers of fish and shrimp were standardized to number per 10,000 m^3 of water.

Myctophid fish, preserved for about 3 yr, were sorted from samples for determination of body length and dry body weight. Intact, undamaged specimens were dried to constant weight at 65°C on glass slides in a drying oven. Drying usually took 3-4 days, but up to 10 days for some of the largest fish. Dried fish were weighed to the nearest milligram. The relationship between standard body length and dry body weight for each species of myctophid was determined by linear regression analysis of logarithmically transformed measurements.

RESULTS

The vertical series of nekton samples collected at Stations P and Q yielded nine species of myctophids, one abundant species of chauliodontid, and one relatively rare melanostomiatid. All other families combined made up only 2-6% of the total catch by number (Table 2). In addition to fish, the samples contained considerable numbers of euphausiids and decapod shrimps. Other invertebrate groups, such as siphonophores and squids, were only sporadically captured. The more common fishes had similar relative abundances at the two stations. More than 80% of the myctophids consisted of three species (*Stenobrachius leucopsarus*, *Protomyctophum thompsoni*, and *Diaphus theta*) whose vertical distributions were generally well bracketed by the sampling. The other species of myctophids were either rare or appeared to be distributed below the usual range of sampling; therefore, emphasis in this study was placed on the above three, abundant, relatively shallowly distributed species.

Vertical Distribution of Fish

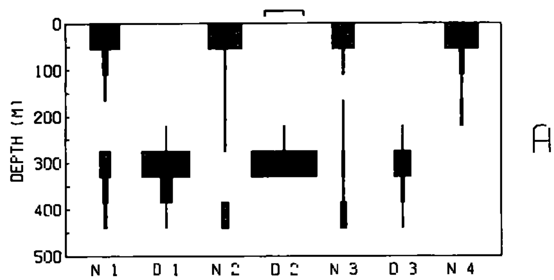
The most abundant fish in our samples was *S. leucopsarus*. Its only congener, *S. nannochir*, was rarer (Table 2). As discussed later, with the exception of the very deep vertical series (782-440 m) in 1975, only small specimens (<35 mm) of *S. nannochir* occurred in the vertical series. The fish caught at Station P in 1973 were in such poor condition that it was not possible to discriminate the smaller specimens of the two species of *Stenobrachius*. However, there is evidence (presented below) that *S. nannochir* was extremely rare at Station P in 1973, much rarer than at Station Q or Station P in 1975 (Table 2). Redesign of the cod ends, after the 1973 cruise, provided us with good specimens which permitted discrimination of the two congeners.

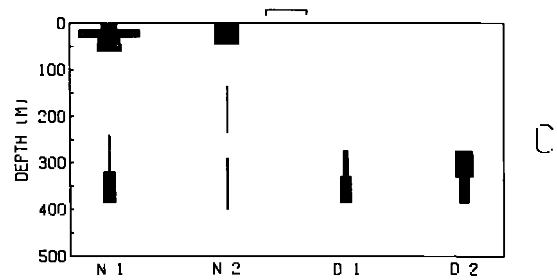
TABLE 2.—Composition of the total fish catch in vertical series of nekton samples in the northeastern Pacific. Data for each station combine all vertical series.

Family and species	Station P, 1973 No.	Station P, 1973 %	Station Q, 1974 No.	Station Q, 1974 %	Station P, 1975 No.	Station P, 1975 %
Myctophidae:						
Stenobrachius leucopsarus	720	63.8	1,038	45.4	461	49.3
S. nannochir	([1])	([1])	268	11.7	92	9.8
Protomyctophum thompsoni	125	11.1	413	18.1	210	22.5
Diaphus theta	111	9.8	304	13.3	61	6.5
Tarletonbeania crenularis	16	1.4	26	1.1	3	0.3
Lampanyctus regalis	9	0.8	11	0.5	0	0
L. ritteri	3	0.3	11	0.5	0	0
Notoscopelus japonicus	1	0.1	0	0	0	0
Symbolophorus californiense	1	0.1	0	0	0	0
Chauliodontidae:						
Chauliodus macouni	57	5.0	147	6.4	84	9.0
Melanostomiatidae:						
Tactostoma macropus	21	1.9	15	0.7	3	0.3
Others	64	5.7	55	2.4	21	2.2
Totals	1,129		2,288		935	

[1]Due to the poor condition of the fish caught at Station P in 1973, it was impossible to discriminate the smaller specimens of the two species of *Stenobrachius*. It is possible that some of the fish listed here as *S. leucopsarus* were in fact *S. nannochir*, but for reasons described in the text, we do not believe this to be the case.

At Station P in 1973, *S. leucopsarus* occurred in largest numbers in the surface layer (0-55 m) at night and at 275-330 m during the day (Figure 3A). This pattern could occur if most specimens undertook a diel vertical migration over a depth range of 250-300 m. To be certain that the data reflect a vertical migration and not simply light-aided avoidance of the net by fish in the daytime, it was necessary to compare day and night total catches of fish integrated over the water column sampled (Table 3). Assuming that the entire vertical range of *S. leucopsarus* was sampled (this assumption is qualified below), then it is clear that, since the total catches for day and night series were statistically indistinguishable (Table 3), there was no evidence of daytime avoidance of the trawl by fish. Further, judging from the results of replicate sampling of zooplankton with nets (Wiebe and Holland 1968), the day and night totals in Table 3 are well within the range of variability expected for repeated samples from a pelagic population. Thus, the observed diel differ-





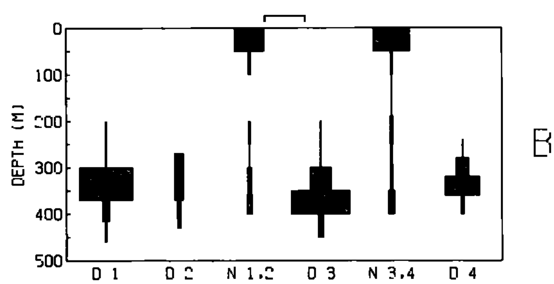


FIGURE 3.—Vertical distribution of *Stenobrachius leucopsarus* at Stations P and Q in the northeastern Pacific Ocean. A. 1973, Station P: four night (N) and three day (D) vertical series. B. 1974, Station Q: four day and two composite night vertical series. C. 1975, Station P: two composite night and two day vertical series. The profiles for each year are presented in the chronological order in which they were taken. Scales represent 100 individuals/10^4 m^3.

TABLE 3.—Day and night total catches for the water column sampled, of selected fish and crustacean species at Stations P and Q in the northeastern Pacific; means and ranges (parentheses) as number/100 m^2. Ratios given of largest to smallest estimate of abundance for a station.

Species	Station	Day		Night		Ratio
Stenobrachius leucopsarus	P, 1973	67.7	(28.6-82.0)	59.8	(47.3-73.7)	2.9
	Q, 1974	101.1	(48.4-153.6)	62.1	(56.5-67.7)	3.2
	P, 1975	28.0	(20.3-35.8)	37.6	(29.2-46.1)	2.3
Diaphus theta	P, 1973	6.8	(1.1-13.8)	12.4	(3.9-18.2)	16.5
	Q, 1974	22.6	(15.2-34.4)	[1]11.5	(11.0-12.0)	3.1
	P, 1975	3.6	(3.1-4.0)	5.4	(3.6-10.4)	3.4
Protomyctophum thompsoni	P, 1973	15.6	(12.7-20.9)	7.9	(0.0-13.8)	[2]4.8
	Q, 1974	26.7	(21.6-39.1)	23.6	(20.0-27.3)	2.0
	P, 1975	17.3	(17.2-17.3)	47.0	(28.9-65.2)	3.8
Chauliodus macouni	Q, 1974	10.1	(3.2-15.7)	8.2	(7.5-9.0)	4.9
Euphausia pacifica	P, 1973	169.7	(24.2-323.9)	[1]1,075.3	(214.5-5,825.0)	240.7
	Q, 1974	417.4	(272.0-531.5)	154.0	(17.5-290.5)	30.4
	P, 1975	322.5	(223.8-421.3)	423.7	(294.5-532.9)	2.5
Sergestes similis	P, 1973	19.8	(0.5-31.3)	[1]50.3	(28.0-80.8)	161.6
	Q, 1974	33.0	(14.0-47.6)	[1]72.9	(57.5-88.3)	6.3
	P, 1975	10.2	(9.3-11.0)	11.1	(9.6-12.6)	1.4

[1]Day and night abundance significantly different ($P<0.1$) by rank test (Tate and Clelland 1957).
[2]Estimate based on smallest nonzero catch.

ences in the vertical distribution of *S. leucopsarus* (Figure 3A) indicate that the majority of individuals do perform a diel vertical migration.

The occurrence of some *S. leucopsarus* in the deepest samples at night (Figure 3A) indicates that the entire population was not participating in the vertical migration described above. Differences in migratory pattern appear to be largely a function of size or age of individual fish. The length-frequency histogram for our entire catch of *S. leucopsarus* at Station P in 1973 (Figure 4A) indicates that several size classes of fish were sampled. Since *S. leucopsarus* metamorphoses to the juvenile stage at 18 mm (Smoker and Pearcy 1970), the abundant 19-35 mm size class (Figure 4A) probably represented the youngest juvenile fish. The largest specimens caught at Station P attain the maximum size expected for *S. leucopsarus*, 85-111 mm (Kulikova 1957; Smoker and Pearcy 1970).

To determine the effect of size on vertical migration, we examined the three obvious size classes of *S. leucopsarus*: 19-35 mm, 38-82 mm, and 90-112 mm. The smallest size class (19-35 mm) performed a clear diel vertical migration from 275-330 m in the daytime to 0-55 m at night (Figure 5A). The anomalously low density of fish on the third day must be attributed to horizontal patchiness of fish. Note especially that only on one night (N3, Figure 5A) was one small-sized *Stenobrachius* captured below 275 m. The medium size class (38-82 mm) shows a similar migration (Figure 5B), though these fish seemed to be more dispersed vertically, both at night and in the daytime, than the smallest size class. The high density of medium-sized fish at 275-330 m on the first night, not apparent on the other three nights, probably reflected the fact that this sample was collected between 0554 and 0613 h, a time period when the migratory sonic scatterers, and presumably myctophids, were descending. Some of the medium-sized fish probably had already descended into the 275-330 m layer at the time this sample was collected. The largest size class of *S. leucopsarus* (90-112 mm) had a pattern of vertical distribution totally different from those of the two smaller size classes. Individuals of the largest size class were not captured at all in the first two daytime series and were caught only in the two deepest samples in the third daytime series (Figure 5C). They were captured in all four night series, but never in the surface layer (0-55 m), and in three of the four night series, the greatest density of large-sized fish occurred between 330 and 440 m. It is tempting to conclude from these data that the individuals of the largest size class also perform a diel vertical migration, moving from daytime depths below our lower limit of sampling (440 m) into our sampling range at night. Of course, a similar vertical distribution pattern could be obtained if the largest fish avoid the trawl in the daytime, although it seems unlikely that all fish of this size class could effectively do so. Nevertheless, with the data from Station P (1973), it is impossible to discriminate between these two possibilities for the largest fish.

Stenobrachius leucopsarus had a very similar pattern of distribution and diel vertical migration at Station Q (Figure 3B). The length-frequency distribution of the species was strongly skewed to juvenile fish (19-31 mm), which made up 88.7% of the total catch of the species. There was only one relatively distinct secondary mode, consisting of very large fish (81-108 mm), which composed 3.9% of the total catch (Figure 4B). Fish in the smallest mode and also the rarer intermediate sizes of fish (32-79 mm) were clear vertical migrants, closely following the pattern described above for Station P, and there was no difference in vertical distribution between the small- and medium-sized fish. Also, as at Station P, representatives of the largest size class of fish were captured, with the exception of 1 fish (out of 45 caught) in the deepest sample on day 4, only in the night hauls and almost always (43 out of 44 fish) below 50 m.

At Station P in 1975, the same patterns of diel vertical migration (Figure 3C) and size-dependent variation in vertical distribution of *S. leucopsarus* were evident, though far fewer fish were collected, both because of the fewer vertical series taken and an apparent decrease in abundance of the species compared with the previous 2 yr (Table 3). This decrease appears due partly to reduced abundance of the smallest size class (17-32 mm) which made up only 47.2% of the total catch in 1975 (Figure 4C), compared with 62.6% at Station P in 1973 and 88.7% at Station Q. In the one deep daytime vertical series (782-440 mm) at Station P, large *S. leucopsarus* were captured between 440 and 740 m (Table 4), thus supporting our earlier hypothesis that the largest fish caught at night above 440 m migrated in the daytime below our usual range of sampling. However, extensive day and night sampling over the entire vertical range of the large fish is required to completely rule out daytime avoidance of the trawl.

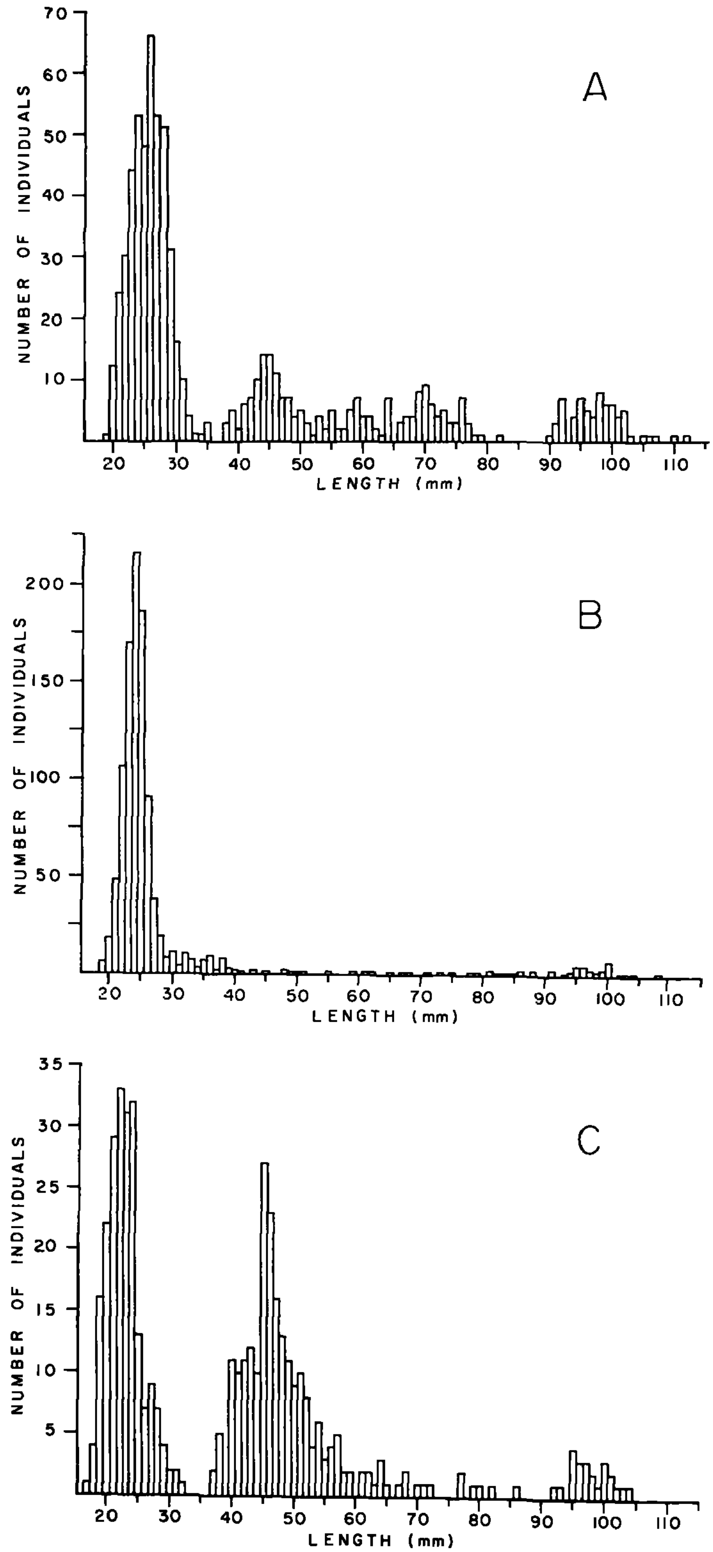


FIGURE 4.—Length-frequency distributions of *Stenobrachius leucopsarus* from all vertical series. A. 1973, Station P, N = 720. B. 1974, Station Q, N = 1,038. C. 1975, Station P, N = 461.

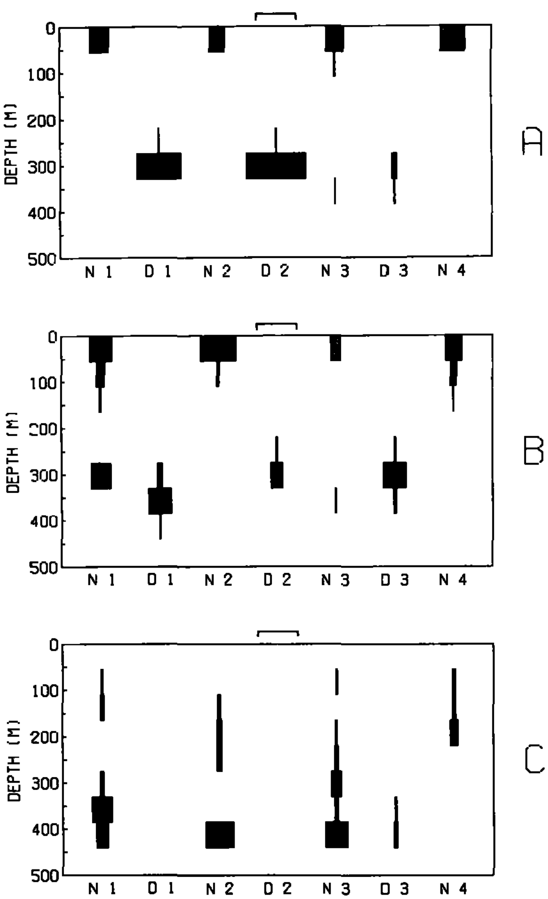


FIGURE 5.—Vertical distribution of three sizes of *Stenobrachius leucopsarus* at Station P, 1973. A. 19-35 mm, scale represents 100 individuals/10⁴m³. B. 38-82 mm, scale represents 50 individuals/10⁴ m³. C. 90-112 mm, scale represents 25 individuals/10⁴ m³. Sequence of vertical series as in Figure 3A.

The one shallow night vertical series (60-0 m) at Station P indicated that *S. leucopsarus* were distributed throughout the surface layer but were concentrated between 15 and 30 m (Figure 3C). Examination of sizes of fish caught in this series suggested very fine-scale vertical stratification by age or size (Table 5). Recall that in all other vertical series taken at night very large fish (>80 mm) were always captured (except for one fish) below 50 m. Because we took only one such shallow vertical series, we cannot evaluate the frequency of occurrence or temporal persistence of this apparent stratification of fish by age in the surface layer at night.

The third most abundant myctophid in our samples, *Diaphus theta*, also performed a diel vertical migration (Figure 6); there was no consistent difference between day and night catches (Table 3). At night, *D. theta* ranged over the upper 165 m but was concentrated near the surface (0-55 m), while during the day most of these fish were collected below 275 m. As stated above for *S. leucopsarus*, the occurrence of *D. theta* at 275-330 m the first night at Station P (1973) is misleading because the sample was probably collected after the downward vertical migration of myctophids had begun.

The size range for the total catch of *D. theta* was 36-88 mm in 1973 and 46-84 mm in 1975 at Station P, and 33-76 mm at Station Q. The size-frequency distributions were similar in all 3 yr. Considering only Station Q, for which we have the largest collection, the size-frequency distribution (Figure 7A) was quite different from *S. leucopsarus* (Figure 4B). Small and large fish were rare and the samples contained primarily intermediate sizes (45-58 mm). Distinguishing, somewhat arbitrarily, three classes in the size-frequency distribution, there is indication of size-dependent

TABLE 5.—Vertical distribution of size classes of *Stenobrachius leucopsarus* in the shallow night vertical series at Station P (1975) in the northeastern Pacific, as number/10,000 m³. Data based on a single haul with a single sample at each depth.

Depth (m)	17-32 mm	37-82 mm	>85 mm
0-15	37.2	1.6	0
15-30	140.5	13 6	0
30-45	7.8	46.8	0
45-60	15.9	42.8	1.0
Total no. captured	138	89	1

TABLE 4.—Deep daytime vertical distribution of selected species of micronekton at Station P (1975) in the northeastern Pacific, as number/10,000 m³. For *Stenobrachius leucopsarus*, the numbers in parentheses are abundances of large fish (91-112 mm SL). Data based on a single haul with a single sample at each depth.

Depth (m)	*Stenobrachius leucopsarus*	*Stenobrachius nannochir*	*Protomyctophum thompsoni*	*Lampanyctus ritteri*	*Chauliodus macouni*	*Sergestes similis*
440-540	4.5 (3.5)	49.6	0.7	0	2.4	10.8
540-640	8.5 (7.5)	7.0	0	0	0	7.5
640-740	4.4 (1.3)	4.9	0	0.9	0.4	0
740-782	0	2.7	0.5	0.5	0	0
Total no. captured	40 (28)	173	3	3	8	45

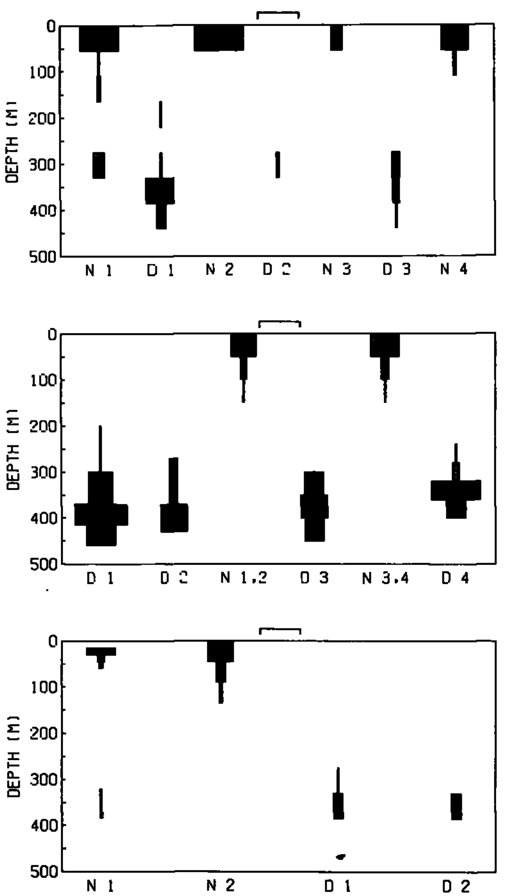


FIGURE 6.—Vertical distribution of *Diaphus theta*. A. 1973, Station P. B. 1974, Station Q. C. 1975, Station P. Scales represent 25 individuals/10^4 m^3. Sequence of vertical series as in Figure 3.

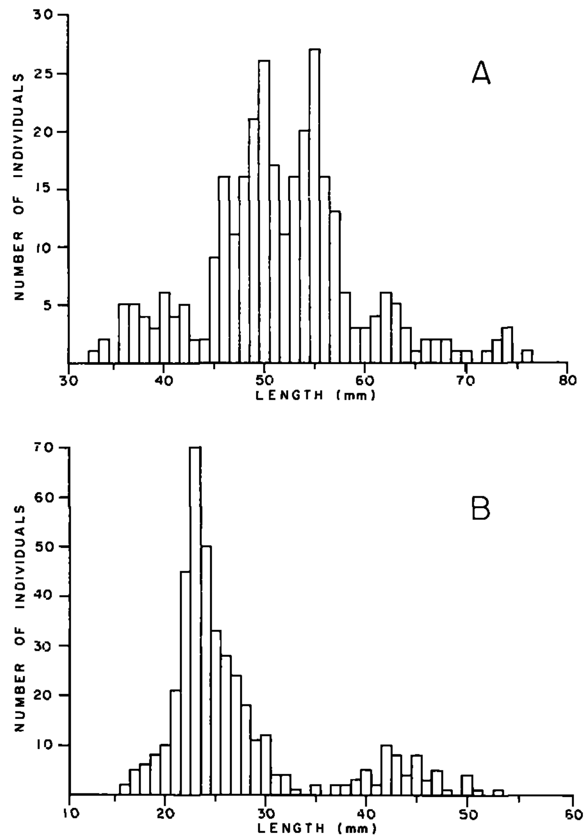


FIGURE 7.—Length-frequency distributions of *Diaphus theta* (A), N = 304, and *Protomyctophum thompsoni* (B), N = 413, from all vertical series at Station Q, 1974.

variation in vertical distribution and vertical migration. The smallest sizes (35-44 mm) of fish were consistently shallower than larger sizes both during the day and at night (Table 6); although the numbers of fish are small, they do indicate a possible trend. *Diaphus theta* was not captured in the very deep (782-440 m) daytime vertical series at Station P in 1975.

The second most abundant myctophid, *Protomyctophum thompsoni*, did not perform an extensive diel vertical migration similar to that of *S. leucopsarus* or *D. theta*; it remained below about 200 m both day and night (Figure 8). Nevertheless, the species tended to be somewhat more shallowly distributed at night than in the daytime. This is best demonstrated by the data from Station Q where the largest catches of this species were made. At Station Q, *P. thompsoni* ranged from 16 to 53 mm SL and the length-frequency distribution of the population was bimodal (Figure 7B). Calculations of mean depths of the two size classes showed that the smaller fish were always slightly more shallowly distributed that the larger fish (Table 6). Moreover, both size classes tended to be deeper in the daytime than at night, although the average change in depth (30-40 m for both size classes) was relatively small (Table 6). *Protomyctophum thompsoni* was rare below 440 m at Station P in 1975 (Table 4). The size range of the species at Station P was 18-51 mm (1973) and 16-50 mm (1975), and the size-frequency distribution was similar to that of Station Q.

The above three species of myctophids had vertical distributions which were, with the possible exception of the rare large specimens of *S. leucopsarus*, well bracketed by our vertical series of samples. Two other relatively abundant species of fish seemed to have vertical distributions which

TABLE 6.—Mean depth (meters) of size classes of *Diaphus theta* and *Protomyctophum thompsoni* in day (D1-D4) and night (N1, N2) vertical series at Station Q in the northeastern Pacific. Mean depth D was calculated from the equation $D = \Sigma n_i \bar{Z}_i / \Sigma n_i$, where n_i is the population density (number/10,000 m³) of a size class in sample i and $\bar{Z}_i$ is the midpoint of the depth range of sample i.

Size class (mm)	D1	D2	D3	D4	N1	N2	Total no. captured
Diaphus theta:							
35-44	342	357	325	336	25	25	40
45-58	394	382	377	351	32	30	224
>58	390	400	404	344	76	69	40
Protomyctophum thompsoni:							
16-35	332	316	330	301	294	257	354
36-53	381	338	340	340	307	309	59

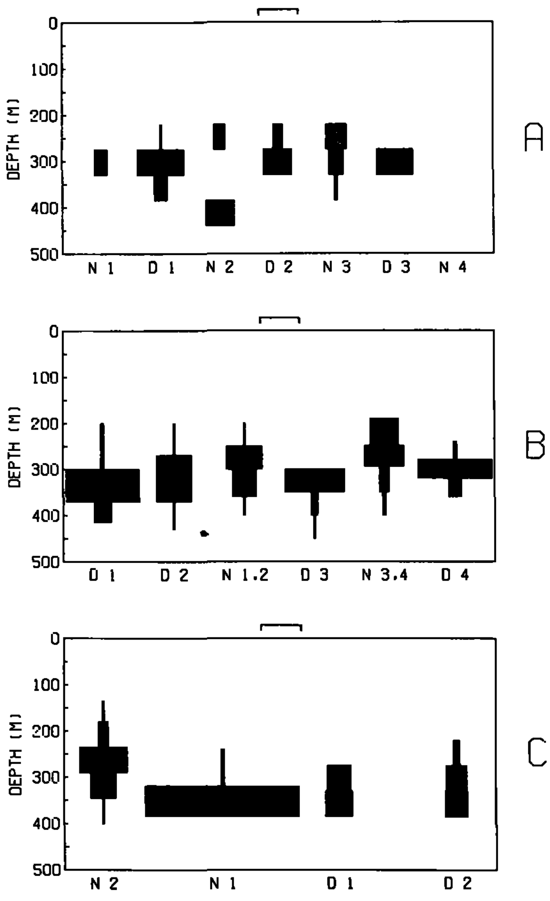


FIGURE 8.—Vertical distribution of *Protomyctophum thompsoni*. A. 1973, Station P. B. 1974, Station Q. C. 1975, Station P. Scales represent 25 individuals/10⁴ m³. Sequence of vertical series as in Figure 3.

extended deeper than our usual range of sampling. *Stenobrachius nannochir* was only captured below 275 m in the routine vertical series at Stations Q (1974) and P (1975). As noted earlier, due to the poor condition of the catch, small specimens of *S. nannochir* and *S. leucopsarus* were not distinguished in samples from Station P (1973). Half of the total catch of *S. nannochir* was from below 400 m, and all of the specimens caught above 440 m were <35 mm SL. It is for this reason that we think that the species must have been extremely rare in the 0-440 m layer at Station P in 1973, for we caught almost no small *Stenobrachius* in the deep samples at night (Figure 5A). The virtual restriction of catches of *S. nannochir* to our deepest samples, day and night, indicates that its distribution probably extended below our range of sampling. Indeed, it was the most abundant fish in the one very deep daytime vertical series at Station P (1975); it occurred down to 782 m and was concentrated in the 440-540 m layer (Table 4). Furthermore, an interesting vertical stratification by size was evident in this series, with the smallest fish dominating the shallowest sample and largest fish dominating the deepest two samples (Table 7). Note that we captured only small specimens (<35 mm) in all of the other, shallower vertical series. *Stenobrachius leucopsarus* and *S. nannochir* of similar body size tended to be vertically well separated in the water column at all times (Tables 4, 7; Figure 5).

TABLE 7.—Vertical distribution of size classes of *Stenobrachius nannochir* in the deep daytime vertical series at Station P (1975) in the northeastern Pacific, as number/10,000 m³.

Depth (m)	22-37 mm	38-70 mm	85-113 mm
440-540	37.0	12.2	0.3
540-640	0.5	6.5	0
640-740	0	2.2	2.7
740-782	0	0.9	1.8
Total no. captured	107	55	11

The only other moderately abundant fish was the chauliodontid *Chauliodus macouni*, and only at Station Q was it captured in sufficient numbers to warrant description. *Chauliodus macouni* always occurred below 150 m, and there was no conclusive evidence of change in its vertical distribution during the day-night cycle (Figure 9, Table 3). However, in contrast to *P. thompsoni*, whose range of vertical distribution apparently was well sampled day and night (Figure 8B, Table 4), it appears from the abrupt truncation of histograms in Figure 9 that the deepest portion of the population of *C. macouni* was not sampled either in the daytime or at night. Indeed, in the very deep vertical series at Station P (1975), a number of *C. macouni* were captured in the 440-540 m layer

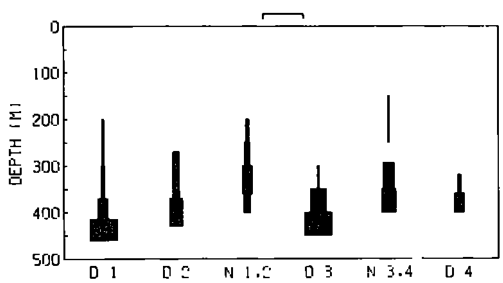


FIGURE 9.—Vertical distribution of *Chauliodus macouni* at Station Q, 1974. Scale represents 25 individuals/10^4 m^3. Sequence of vertical series as in Figure 3B.

TABLE 8.—Abundance (number/10,000 m^3) of *Stenobrachius leucopsarus* and *Diaphus theta* in three series of half-hour samples collected in horizontal tows at 40-m depth during one night at Station Q in the northeastern Pacific. Sampling commenced after the migratory scattering layer had merged with the surface reverberation and terminated after the scattering layer had descended below the surface reverberation (0425). Time is when net was opened.

Time	*S. leucopsarus*	*D. theta*	Time	*S. leucopsarus*	*D. theta*
2200	157	31	0130	262	42
2230	89	15	0200	329	36
2300	102	10	0300	188	72
2330	109	8	0330	178	66
0030	80	21	0400	146	28
0100	197	54	0430	8	0

(Table 4), indicating that the distribution of this fish probably extended below the normal limit of sampling in the routine vertical series. At Station Q, specimens of *C. macouni* ranged from 29 to 189 mm SL. Very large fish (>100 mm) were usually captured at night in the deepest samples, but for fish <100 mm there was no clear trend of size-dependent variation in vertical distribution.

Other fish species (Table 2) occurred sporadically in the samples and were caught primarily at night: the only daytime catches were below 300 m (e.g., *Lampanyctus ritteri* in Table 4). Included in the category "Others" in Table 2 were members of the families Bathylagidae, Gonostomatidae, Melamphaeidae, Opisthoproctidae, Paralepididae, and Scopelarchidae.

Variability in Abundance of Myctophids in Replicated Samples

With a few exceptions, the estimates of abundance of myctophids integrated over the water column sampled did not vary by more than a factor of 4 between vertical series within cruises (Table 3). At Station Q, three series of half-hour horizontal hauls were made at 40 m throughout one night (Table 8). Excluding the sample (0430) collected after the scattering layer had descended, concentrations of *S. leucopsarus* varied by a factor of about 4, those for *D. theta* by a factor of about 9. For both species, there was a significant trend (P = 0.05, run test, Tate and Clelland 1957) toward increased abundance during the night, and their abundances were strongly correlated (rank difference correlation coefficient 0.74, $P \sim 0.01$, Tate and Clelland 1957). Myctophids were abundant in the surface layer until the migratory scattering layer descended.

Estimated Abundance and Standing Stock of Fishes

Our data for mean abundance of all fishes captured for the 3 yr ranged from 0.78 to 1.61/m^2 for the water column extending to between 385 and 460 m (Table 9). The three most abundant species of myctophids combined accounted for 77-85% by number of all fish collected. There was no consistent difference between day and night estimates of concentrations of fish.

Equations for the regression of dry body weight on body length (Table 10) were used in conjunction with the lengths and abundance of fish from each sample to calculate the population standing stocks of *S. leucopsarus*, *D. theta*, and *P. thompsoni* for

TABLE 9.—Estimated mean abundance and standing stock of mesopelagic fishes at Stations P and Q in the eastern subarctic Pacific Ocean. Myctophids includes only the three most abundant species, *Stenobrachius leucopsarus*, *Diaphus theta*, and *Protomyctophum thompsoni*. Estimated mean abundance and standing stock are based on average of all day and night vertical series; values in parentheses are means for night vertical series only.

Station	Abundance (no /m^2)		Standing stock (g dry wt/m^2)
	Myctophids	All fishes	Myctophids
P, 1973	0.85	1.00	0.53 (0.77)
Q, 1974	1.24	1.61	0.27 (0.39)
P, 1975	0.61	0.78	0.34 (0.55)

TABLE 10.—Equations for the regression of dry body weight, W (grams), on body length, L (centimeters), for three species of myctophids.

Species	Regression equation	Range of SL (cm)	N
Stenobrachius leucopsarus	$W = 0.00125\,L^{3.546}$	2.0-11.8	92
Diaphus theta	$W = 0.00537\,L^{2.943}$	3.0-7.4	79
Protomyctophum thompsoni	$W = 0.00212\,L^{3.391}$	1.7-4.9	54

each vertical series of nekton samples at each station. A slight (<1%) bias toward underestimation of weight was corrected using the approximation for minimum variance unbiased estimator of the mean given by Beauchamp and Olson (1973). Mean standing stock, averaged over day and night series, ranged from 0.27 to 0.53 g dry weight/m² of sea surface (Table 9). Variations in standing stock did not closely follow variations in abundance because of large year-to-year variations in the size-frequency distribution of the most abundant species, *S. leucopsarus* (cf. Figure 4). For example, the low standing stock at Station Q is due to the relative scarcity of medium-sized (40-80 mm) *S. leucopsarus* in the catch at that station (Figure 4B). This also accounts for differences between years in the composition by species of the standing stock of the three myctophids. At Station P in both years, *S. leucopsarus* represented, on the average, 63.4-75.7% of the standing stock of myctophids, but at Station Q it contributed only an average of 32.4%. At Station Q, the rarer, but relatively larger, *D. theta* made up 59.3% of the standing stock; however, at Station P it made up only 21.2-24.3%. *Protomyctophum thompsoni*, because of its small body size (Figure 7B), averaged <13% of the standing stock at all stations (range of means for the three stations, 4.2-12.3%). Estimates of mean standing stock based only on night vertical series tended to average more than those based only on day series (Table 9) because of the contribution from the relatively rare (Figure 5), but very large (>90 mm), specimens of *S. leucopsarus* which were caught chiefly at night.

Vertical Distribution of Crustaceans

The most abundant organisms in the vertical series of nekton samples were euphausiids, predominantly large individuals (>12 mm total length). At Station P in both 1973 and 1975, *Euphausia pacifica* made up more than 80% of the euphausiid catch by number. At Station Q, 51% of the total euphausiid catch was *E. pacifica*; other species were *Thysanoessa spinifera* (30%), *Tessarabrachion occulatum* (9%), *Thysanoessa longipes* (8%), and *Stylocheiron maximum* (2%). All of these species also occurred at Station P, but were rare. Consequently, only the data for *E. pacifica* are presented here.

During the day, large *E. pacifica* occurred in greatest concentration between 275 and 400 m, while at night they were usually concentrated in the upper 55 or 60 m (Figure 10). No consistent difference between day and night total catches was evident, but sporadic, extraordinarily large or small catches of *E. pacifica* were obtained in both 1973 and 1974. Variations such as these are common in euphausiid catches (Brinton 1962b) and are usually attributed to horizontal patchiness. Our ranges of estimated abundances were consequently very large (Table 3). The other four species of euphausiids were too rare to draw definite conclusions about their distributions.

The penaeid decapod shrimp, *Sergestes similis*, was the only other abundant invertebrate in our nekton samples. At Station P (1973) and Station

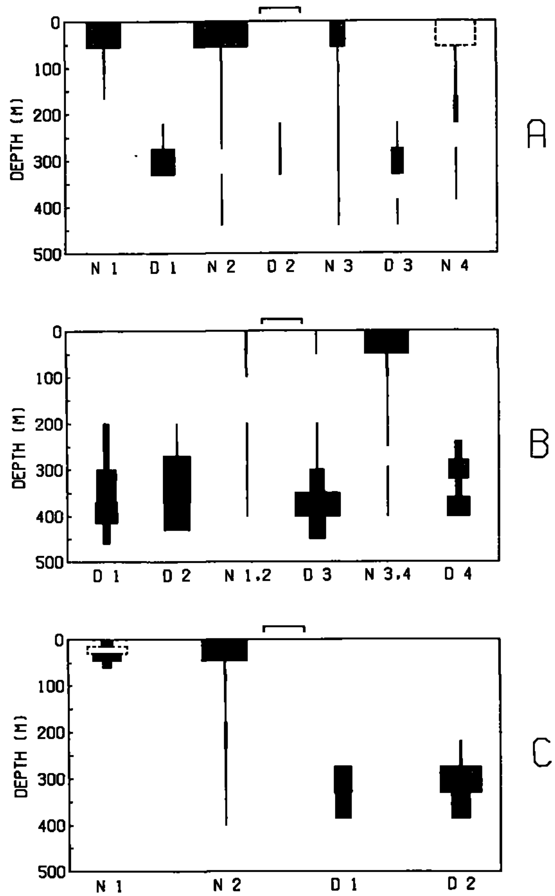


FIGURE 10.—Vertical distribution of *Euphausia pacifica*. A. 1973, Station P. Scale represents 1,000 individuals/10⁴ m³. (The 0-55 m sample on the fourth night represents 10,447 individuals/10⁴ m³.) B. 1974, Station Q. Scale represents 500 individuals/10⁴ m³. C. 1975, Station P. Scale represents 500 individuals/10⁴ m³. (The 15-30 m sample on the first night represents 3,086 individuals/10⁴ m³.) Sequence of vertical series as in Figure 3.

Q, the species appeared to be performing an extensive diel vertical migration (Figure 11A, B); however, the average daytime catches at both stations were a bit less than half the average nighttime catches, though only in 1973 and 1974 were there statistically significant differences (Table 3). Except for the largest size class of *Stenobrachius leucopsarus* (Figure 5C), *Sergestes similis* is the only species for which we found such a prominent, repeated, day-night difference in catches. Either *S. similis* is a diel vertical migrator and descends below our usual range of sampling in the daytime or it is capable of avoiding the nekton trawl in the daytime. Our very deep daytime vertical series taken at Station P (1975) bears on this question. Although the species seemed considerably less abundant in 1975 (Table 3), this was probably

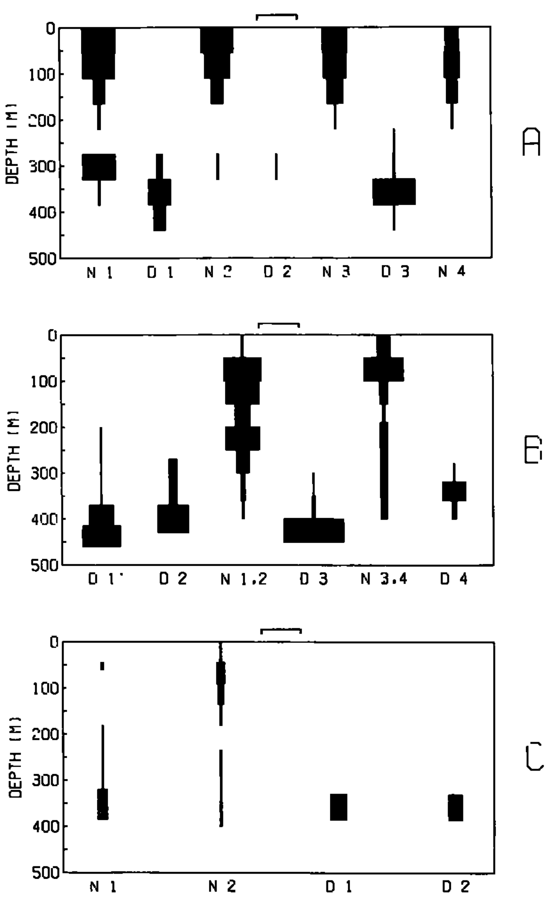


FIGURE 11.—Vertical distribution of *Sergestes similis*. A. 1973, Station P. B. 1974, Station Q. C. 1975, Station P. Scales represent 50 individuals/10^4 m^3. Sequence of vertical series as in Figure 3.

partly due to the shallower depth to which the routine vertical series extended in the daytime. In the very deep daytime vertical series, *S. similis* occurred in considerable numbers between 440 and 640 m (Table 4). Thus it probably was a migrator and in the daytime ranged well below the greatest depth of sampling on routine vertical series.

At both stations, *S. similis* tended to be rather broadly distributed over the 0-150 m layer at night and often was more abundant below 50 m than above (Figure 11). In this respect its diel migration differs from that of the two migratory myctophid fishes and *E. pacifica*, which tended to aggregate strongly above about 60 m at night.

In addition to *S. similis* several other types of malacostracans were collected in the samples: the caridean decapods *Hymenodora frontalis*, *Notostomus japonicus*, and *Pasiphaea* sp.; the penaeid decapod *Bentheogennema borealis*; and the mysids *Gnathophausia gigas*, *Boreomysis* sp., and *Eucopia* sp. All were rare, were collected only at night, and almost always occurred below 200 m.

Micronekton Associated With Sound-Scattering Layers

In the daytime, the position of the scattering layer corresponded closely with the daytime depth of occurrence of the smaller size classes of *Stenobrachius leucopsarus* and the populations of *D. theta* and *Protomyctophum thompsoni* (Figure 12A). For example, in the profiles shown in Figure 12A, the 300-400 m stratum contained an average concentration of 136 fish/10,000 m^3 of the three species combined. *Sergestes similis* is distributed too broadly and deeply in the daytime to contribute to the observed scattering layer (Figure 11B, Day 3). Excluding euphausiids, in our samples no other potential sound-scattering organism (e.g., physonect siphonophores) consistently had its center of abundance between 275 and 400 m in the daytime. The large *E. pacifica* collected with the nekton trawl had a pattern of vertical distribution (Figure 10B, Day 3) very similar to that of the migratory myctophid fishes.

Comparison of the vertical distribution and diel migration of *Stenobrachius leucopsarus* with the echosounder trace indicates a correlation between the fish and the migratory sound-scattering layer (Figures 2, 3). The correlation is best for individuals of the small and medium size classes (Figure 5). Similarly, the vertical distribution and diel mi-

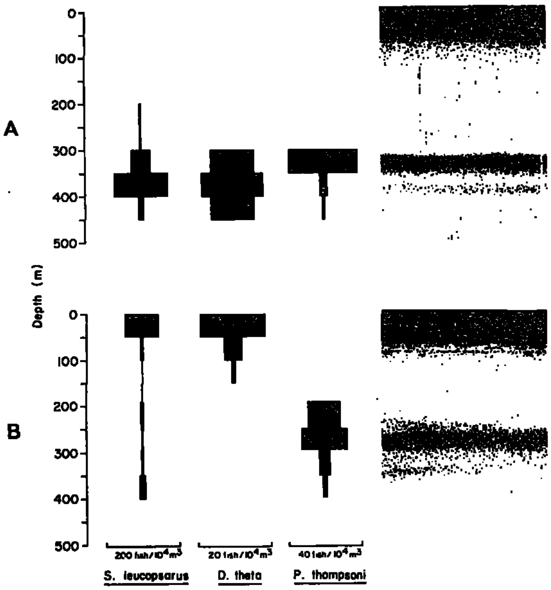


FIGURE 12.—Vertical distribution of three species of myctophids relative to a sound-scattering layer recorded with the 12-kHz echosounder. A. Midday distribution of fish and an echogram showing the position of the scattering layer at the time of sampling (Day 3 at Station Q). B. Nighttime distribution of fish and an echogram showing the position of the scattering layer at the time of sampling (Nights 3, 4 at Station Q).

gration of *D. theta* closely parallel the behavior of the migratory sound-scattering layer (Figures 2, 6). To examine this relationship more closely, at Station Q two series of three horizontal samples each were collected at 125 m in the periods preceding, during, and after ascent of the migratory sound-scattering layer past that depth. In the first series (Table 11, 17 July) both *S. leucopsarus* and *D. theta* were most abundant in the sample collected as the scattering layer was passing 125 m. Euphausiids (predominantly *E. pacifica*) and *Sergestes similis* were also abundant in the samples; however, maximum concentrations of each were obtained either in the sample collected before or after the scattering layer had passed 125 m (Table 11). Results from the second series (Table 11, 18 July) were similar except that euphausiids were not as abundant in the first sample of the series, and *Stenobrachius leucopsarus* was most abundant in the sample collected after the scattering layer had passed 125 m. The results, therefore, indicate that both migratory myctophids and euphausiids are associated with the migratory sound-scattering layer, whereas sergestid shrimps are not.

TABLE 11.—Occurrence of migratory myctophids and crustaceans (number/10,000 m³) in two series of three samples collected in horizontal hauls at 125 m depth before, during, and after ascent of the migratory sound-scattering layer past that depth.

	17 July			18 July		
Species	Before	During	After	Before	During	After
Stenobrachius leucopsarus	0	38	1	0	13	27
Diaphus theta	1	37	5	0	25	0
Euphausia pacifica	87	64	1	5	68	2
Sergestes similis	3	13	53	0	4	82

Position of the nonmigratory portion of the deep sound-scattering layer which was present at night was strongly correlated with the distribution of *P. thompsoni*, particularly the small size class. The scattering layer was broader and more diffuse at night, and so was the distribution of *P. thompsoni* (Figures 2, 8, 12B). Over the 200-300 m stratum, the average concentration of *P. thompsoni* was 16.3 fish/10,000 m³ for the profile shown in Figure 12B. The day-to-night persistence of the nonmigratory scattering layer (Figure 2) cannot be explained by reference to the distribution of either *S. leucopsarus* or *D. theta*. The two smaller size classes of *S. leucopsarus* and all *D. theta* have migrated into the surface layers at night, and the largest *S. leucopsarus* are not only rare but broadly distributed over 50-450 m. There are no other abundant potential sound-scattering organisms concentrated in the 200-300 m stratum at night.

DISCUSSION

Previous work on myctophids in open waters of the subarctic Pacific dealt chiefly with systematics and biogeography (Wisner 1976). However, Aron (1962) and Taylor (1968) considered aspects of the distribution of myctophids in eastern subarctic waters. Aron's (1962) results are qualitative due to the nature of the sampling gear used (unmetered, nonclosing nets of variable mesh size). Differences between results of our study and those of Taylor's (1968) comprehensive investigation are probably attributable to the different sampling gear employed rather than to fundamental variations in behavior of fish in different parts of the subarctic Pacific. For example, Taylor's use of very course-meshed nets probably accounts for both his finding of different relative abundances of myctophid species and for somewhat different patterns of vertical distribution of species. Thus in Taylor's study, carried out not far from Station Q, *P. thompsoni* and *D. theta* were more abundant than *S. leucopsarus*, but this was probably because Taylor's net either did not efficiently catch juvenile (<35 mm) *S. leucopsarus* which were the numerically dominant size class of that species in our samples (Figure 4), or they were much less abundant during the time he sampled. Further, Taylor obtained some of the largest catches of *D. theta* and *S. leucopsarus* below 90 m at night. This probably also reflects the sampling bias of his net for larger sizes of fish, which at night tend to be more broadly spread over the water column than smaller fish (Figure 5C; Table 6, night series). Unfortunately, Taylor did not report the sizes of fish captured. Except for probable sampling bias toward larger sizes of fish, Taylor's results on vertical distribution of the nonmigratory *P. thompsoni* and other species of fish agree with ours.

Pearcy et al. (1977) described patterns of vertical distribution of mesopelagic fishes and crustaceans off the coast of Oregon. The mesopelagic assemblage there is essentially subarctic in faunistic affinity and the vertical distributions of species are similar to those observed at Stations P and Q. The only notable departure from our results was the finding by Pearcy et al. that significant numbers of all sizes of *S. leucopsarus* did not participate, at least on a regular basis, in the diel vertical migrations. Our observations at both Stations P and Q indicate that virtually all *S. leucopsarus* smaller than about 80 mm performed extensive diel vertical migrations (Figure 5). However, in our studies, *S. leucopsarus* was also very rare below 400 m (Figure 5, Table 4), whereas Pearcy et al. found large concentrations below that depth. Thus there may be major differences in the vertical distribution and migration behavior of *S. leucopsarus* in different parts of its geographical range (Paxton 1967). Significantly, Pearcy et al. (1977) detected no seasonal variations in vertical distributions and migrations for any species, which may also be true for subarctic waters to the north (Taylor 1968).

Perhaps the most remarkable feature of the mesopelagic fauna of the area sampled was its simplicity. Only four species of myctophid fishes were abundant in the upper 700 m. Two of these species, *S. leucopsarus* and *D. theta*, undertook diel migrations of substantial vertical extent; the other two, *P. thompsoni* and *S. nannochir*, did not. Other taxonomic groups also showed low diversity. Among the micronektonic crustaceans there were single species of abundant euphausiid, *E. pacifica*, and decapod shrimp, *Sergestes similis*, and both were vertical migrators. The contrast between this relatively simple mesopelagic micronekton fauna and that, for example, in the subtropical North Pacific (Brinton 1962a; Clarke 1973; Walters 1977) or subtropical North Atlantic (Badcock 1970; Foxton 1970a, b) is striking, but not atypical. Low taxonomic diversity of the mesopelagic micronekton is found in other subpolar oceans, such as the Boreal Atlantic (e.g., Backus et al. 1971; Zahuranec and Pugh 1971).

Associated with the taxonomic simplicity of the mesopelagic fauna herein reported, was a relatively simple structure of the sound-scattering layers. Generally, both the number and depth of sound-scattering layers change with latitude in the deep ocean; fewer and shallower layers are found in subpolar oceans than in tropical-subtropical oceans (Haigh 1971; Cole et al. 1971; Donaldson and Pearcy 1972; Tont 1976). Our unpublished observations on deep sound-scattering layers (12-kHz echosounder), taken in September 1972 along long. 155°W between Alaska and Hawaii, showed this trend. Subarctic waters had the relatively simple sound-scattering structure illustrated in Figure 2, with single migratory and nonmigratory layers occurring shallower than 400 m. In the subtropical waters near Hawaii, at least three sound-scattering layers were observed in the daytime at depths ranging from 260 to 625 m, and three to four migratory layers were recorded.

It is unlikely that the correlation between taxonomic diversity of the mesopelagic micronekton and complexity of the sound-scattering structure in the water column was fortuitous. Attempts to causally relate deep sound-scattering layers to aggregations of mesopelagic organisms were stimulated by hypotheses advanced more than three decades ago (for a review see Hersey and Backus 1962). However, field studies based on net samples taken simultaneously with echosounder records tend to be inconclusive for a variety of reasons. A major difficulty is that different taxonomic groups tend to occur together at the same depths and may even show similar migratory behavior. For example, all four of the migratory mesopelagic species in our study (*Stenobrachius leucopsarus*, *D. theta*, *E. pacifica*, and *Sergestes similis*) ascended towards the surface layer after sunset, and only from fine temporal spacing of samples did it become apparent that some species were more closely associated with the scattering layer than others (Table 11). Similarly, in the daytime some of these migratory species cooccurred at the depth of the sound-scattering layer together with the nonmigratory *P. thompsoni*, and any or all could have contributed to the daytime sound-scattering layer. Despite extensive cooccurrence of several types of potential sound-scattering organisms, the most reasonable hypothesis is that myctophids were primarily responsible for both the migratory and nonmigratory sound-scattering layers in the eastern subarctic Pacific.

Taylor (1968), also working in the subarctic Pacific, found the best correlation between deep sound-scattering layers and those mesopelagic fish which possessed gas-filled swim bladders. Although Taylor grouped *Stenobrachius leucopsarus* and *D. theta* among fish with fat-invested swim bladders, gas is present in the swim bladders of immature individuals (<30 mm SL) of both species (Capen 1967). Taylor made no mention of the size of the fish caught in his study; however, in view of the very coarse-meshed nets he used, it is probable that he did not quantitatively sample immature fish. At Stations P and Q, some individuals of *S. leucopsarus* and *D. theta* were theoretically the right size to resonate at 12 kHz while at their daytime depths (Capen 1967), and the abundance of either species was probably sufficient to produce deep sound-scattering in the daytime (Hershey and Backus 1962). This presumably holds also for *P. thompsoni*, which has a gas-filled swim bladder throughout life (Taylor 1968; Butler and Pearcy 1972). Indeed, concentrations of either *D. theta* or *P. thompsoni* alone in Figure 12 were comparable with the concentration of *D. taaningi*, which Baird et al. (1974) believe was responsible for the migratory sound-scattering layer over the Cariaco Trench.

As pointed out above, *Sergestes similis* may be excluded as a potential sound scatterer; it was distributed too broadly and deeply in the daytime and lagged the ascent of the migratory sound-scattering layer at sunset (Figure 11, Table 11). Although *E. pacifica* (Figure 10) was about five times more abundant in the depth of the daytime sound-scattering layer than all myctophid fishes combined, it did not approach concentrations necessary for it to be an effective scatterer of 12-kHz sound (Hersey and Backus 1962; Bary 1966; Beamish 1971).

In conclusion, we suggest that the nonmigratory deep sound-scattering layer (Figure 2B) in the vicinities of Stations P and Q in the eastern subarctic North Pacific was caused by *P. thompsoni*, and that the migratory sound-scattering layer (Figure 2B) recorded the migrations of smaller size classes of *Stenobrachius leucopsarus* and *D. theta*. *Protomyctophum thompsoni* may have been largely responsible for the deep scattering layer observed in the daytime, with possible lesser contributions from the two migratory myctophid species. Pearcy (1977) found similar general correspondence between vertical distributions of the same three species of myctophids and deep sound-scattering layers off Oregon, but he pointed out that quantitative correlation between abundance of potential sound-scatterers and distribution of volume scattering was not always strong. A more definitive analysis, similar to that of Baird et al. (1974), is required; that is, simultaneous observations should be obtained on distribution of volume scattering and abundance and acoustical properties of suspected sound-scatterers.

In single hauls, we observed concentrations of myctophids, all species combined, which regularly exceeded 100 fish/10^4 m^3 in the region of the deep sound-scattering layer in the daytime and in the surface layer at night. Similar concentrations of myctophids are found in other oceans (e.g., Kashkin 1967). Further, the maximum concentrations of myctophids observed by us in the surface layer at night (365 fish/10^4 m^3, Table 8) and at depth in the daytime (874 fish/10^4 m^3, horizontal haul at 327-333 m, Station Q) equal or exceed maximum concentrations inferred from the apparently high catch rates of single hauls reported by Halliday (1970) and Backus et al. (1971) for the western Boreal Atlantic, where one species of myctophid, *Benthosema glaciale*, predominates. The very low concentrations of myctophids found by Pearcy et al. (1977), using a 2.4 m Isaacs-Kidd midwater trawl, are puzzling and seem to indicate that myctophids are about 1/10 as abundant off the Oregon coast as in the open subarctic Pacific. However, the data of Pearcy et al. (1977) differ from the earlier results of Pearcy and Laurs (1966), in which reported concentrations of myctophids were much higher and similar to concentrations observed by us; the difference could be due to year-to-year variability (Pearcy 1977).

There is relatively little variability between years in our estimates of abundance of myctophid fishes (the three most abundant species, Table 2) in the water column extending to 385-460 m. We estimate 0.61-1.24 myctophid fish/m² based on averaged day and night series (Table 10). No quantitative study comparable to ours has been made in the open subarctic Pacific, but Pearcy and Laurs (1966) provided data on the abundance of mesopelagic fish near the Oregon coast. In two cruises (August 1963), Pearcy and Laurs found about 0.78 myctophid fish/m² in the 0-500 m water column at night; this estimate is based upon the three numerically dominant myctophid fish captured (Pearcy and Laurs 1966, fig. 4), two of which ranked 1 and 3 in abundance among myctophids in our study. The average standing stock of all mesopelagic fish found by Pearcy and Laurs (1966) was 2.9 g wet weight/m² in the 0-500 m water column at night. Using a factor of 0.3 to convert wet weight to dry weight, the average nighttime standing stock is 0.87 g/m², a value probably not significantly different from our estimates based on night samples (Table 9), especially since the Pearcy and Laurs estimate is based on all mesopelagic fish captured. Similar concentrations of myctophids (about 0.6-0.8 fish/m²) are found in the subtropical Pacific near Hawaii (Clarke 1973; Maynard et al. 1975). However, many more species of myctophids (47) occur there, and the standing stock of myctophids (about 0.3-0.7 g wet weight/m²) is somewhat less than our estimates (0.23-0.53 g dry weight/m², Table 9), probably because the fish are considerably smaller in average size (Clarke 1973).

With regard to sampling bias, we found no evidence of light-aided avoidance of the nekton trawl by either myctophids or other types of micronekton occurring in the upper 385-460 m during the daytime (Table 3). Consistent day-night differences in catches of organisms, such as those observed for the largest size class (>80 mm SL) of *S. leucopsarus* and for *Sergestes similis*, were probably due to migration of these organisms below the depth range of daytime sampling. The results of the single very deep vertical series at Station P (Table 4) support this interpretation. Furthermore, very deep vertical migrations of both species are well documented in other parts of their geographical ranges in the North Pacific (Omori et al. 1972; Pearcy et al. 1977).

In addition to determining vertical distributions and vertical migrations of myctophid fishes, on each cruise we also sampled zooplankton with a smaller trawl (Frost and McCrone 1974). Analyses of the zooplankton samples, together with data on stomach contents of the three most abundant myctophids, are the subject of a report (in preparation) on the feeding behavior of myctophids in relation to their vertical distribution and the vertical distribution of their zooplankton prey.

ACKNOWLEDGMENTS

We extend special thanks to David Thoreson for his assistance in all phases of the research. Bruce Davies participated in the cruises and was primarily responsible for nearly flawless operation of the trawl. We were fortunate to obtain help and advice on systematics of myctophid fishes from Richard McGinnis. Karl Banse made many useful suggestions on the manuscript. Others whom we wish to thank for participating in the cruises or assisting with the analysis include Gene Anderson, Arthur Griffiths, Louise Hirsch, Jeffrey Napp, Bruce Nesset, Mary Nirini, Layne Nordgren, Scott Ralston, Wesley Rowland, Gary Shigenaka, and Steve Spyker.

This research was supported by the Office of Naval Research (Contract N00014-75-C-0502, Project NR 083-012). Early development of the trawl was supported by National Science Foundation Grant GA-25385.

LITERATURE CITED

AHLSTROM, E. H.
1959. Vertical distribution of pelagic fish eggs and larvae off California and Baja California. U.S. Fish Wildl. Serv., Fish. Bull. 60:107-146.

ARON, W.
1962. The distribution of animals in the eastern North Pacific and its relationship to physical and chemical conditions. J. Fish. Res. Board Can. 19:271-314.

BACKUS, R. H., J. E. CRADDOCK, R. L. HAEDRICH, AND D. L. SHORES.
1971. The distribution of mesopelagic fishes in the equatorial and western North Atlantic Ocean. *In* G. B. Farquhar (editor), Proceedings of an international symposium on biological sound scattering in the ocean, p. 20-40. Maury Center for Ocean Science, Wash., D.C.

BADCOCK, J.
1970. The vertical distribution of mesopelagic fishes collected on the SOND Cruise. J. Mar. Biol. Assoc. U.K. 50:1001-1044.

BADCOCK, J., AND N. R. MERRETT.
1976. Midwater fishes in the eastern North Atlantic - I. Vertical distribution and associated biology in 30°N, 23°W, with developmental notes on certain myctophids. Prog. Oceanogr. 7:3-58.

BAIRD, R. C., D. F. WILSON, R. C. BECKETT, AND T. L. HOPKINS.
1974. *Diaphus taaningi* Norman, the principal component of a shallow sound-scattering layer in the Cariaco Trench, Venezuela. J. Mar. Res. 32:301-312.

BARHAM, E. G.
1966. Deep scattering layer migration and composition: observations from a diving saucer. Science (Wash., D.C.) 151:1399-1403.

BARY, B. MCK.
1966. Back scattering at 12 kc/s in relation to biomass and numbers of zooplanktonic organisms in Saanich Inlet, British Columbia. Deep-Sea Res. 13:655-666
1967. Diel vertical migrations of underwater scattering, mostly in Saanich Inlet, British Columbia. Deep-Sea Res. 14:35-50.

BEAMISH, P.
1971. Quantitative measurements of acoustic scattering from zooplanktonic organisms. Deep-Sea Res. 18:811-822.

BEAUCHAMP, J. J., AND J. S. OLSON.
1973. Corrections for bias in regression estimates after logarithmic transformation. Ecology 54:1403-1407.

BRINTON, E.
1962a. The distribution of Pacific euphausiids. Bull. Scripps Inst. Oceanogr., Univ. Calif. 8:51-269.
1962b. Variable factors affecting the apparent range and estimated concentration of euphausiids in the North Pacific. Pac. Sci. 16:374-408.

BUTLER, J. L., AND W. G. PEARCY.
1972. Swimbladder morphology and specific gravity of myctophids off Oregon. J. Fish. Res. Board Can. 29:1145-1150.

CAPEN, R. L.
1967. Swimbladder morphology of some mesopelagic fishes in relation to sound scattering. U.S. Navy Electron. Lab., Res. Rep. 1447, 32 p.

CLARKE, M. R.
1969. A new midwater trawl for sampling discrete depth horizons. J. Mar. Biol. Assoc. U.K. 49:945-960.

CLARKE, T. A.
1973. Some aspects of the ecology of lanternfishes (Myctophidae) in the Pacific Ocean near Hawaii. Fish. Bull., U.S. 71:401-434.

COLE, H. P., G. M. BRYAN, AND A. L. GORDON.
1971. The deep scattering layer: patterns across the Gulf Stream and the Sargasso Sea. *In* G. B. Farquhar (editor), Proceedings of an international symposium on biological sound scattering in the ocean, p. 281-293. Maury Center for Ocean Science, Wash., D.C.

DODIMEAD, A. J., F. FAVORITE, AND T. HIRANO.
1963. Salmon of the North Pacific Ocean. Part II. Review of oceanography of the subarctic Pacific region. Int. North Pac. Fish. Comm. Bull. 13, 195 p.

DONALDSON, H. A., AND W. G. PEARCY.
1972. Sound-scattering layers in the northeastern Pacific. J. Fish. Res. Board Can. 29:1419-1423.

FARQUHAR, G. B. (editor).
1971. Proceedings of an international symposium on biological sound scattering in the ocean. Maury Center for Ocean Science, Wash., D.C., 629 p.

FOXTON, P.
1970a. The vertical distribution of pelagic decapods [Crustacea: Natantia] collected on the SOND Cruise 1965. I. The Caridea. J. Mar. Biol. Assoc. U.K. 50:939-960.
1970b. The vertical distribution of pelagic decapods [Crustacea: Natantia] collected on the SOND Cruise 1965. II. The Penaeidea and general discussion. J. Mar. Biol. Assoc. U.K. 50:961-1000.

FROST, B.W., AND L. E. MCCRONE.
1974. Vertical distribution of zooplankton and myctophid fish at Canadian weather station P, with description of a new multiple net trawl. Proceedings of the International Conference on Engineering in the Ocean Environment, Vol. I, p. 156-165. Halifax, N.S.

HAIGH, K. K. R.
1971. Geographic, seasonal, and annual patterns of midwater scatterers between latitudes 10° and 68° North in the Atlantic. *In* G. B. Farquhar (editor), Proceedings of an international symposium on biological sound scattering in the ocean, p. 268-280. Maury Center for Ocean Science, Wash., D.C.

HALLIDAY, R. G.
1970. Growth and vertical distribution of the glacier lanternfish, *Benthosema glaciale*, in the northwestern Atlantic. J. Fish. Res. Board Can. 27:105-116.

HARDING, D., E. SHREEVE, D. S. TUNGATE, AND D. MUMMERY.
1971. A net-changing mechanism for the Lowestoft multipurpose sampler. J. Cons. 33:483-491.

HARRISSON, C. M. H.
1967. On methods for sampling mesopelagic fishes. Symp. Zool. Soc. Lond. 19:71-126.

HART, J. L.
1973. Pacific fishes of Canada. Fish. Res. Board Can., Bull. 180, 740 p.

HERSEY, J. B., AND R. H. BACKUS.
1962. Sound scattering by marine organisms. *In* M. Hill (editor), The sea: Ideas and observations on progress in the study of the seas, Vol. 1, p. 498-539. Interscience, N.Y.

HOLTON, A. A.
1969. Feeding behavior of a vertically migrating lanternfish. Pac. Sci. 23:325-331.

KASHKIN, N. I.
1967. On the quantitative distribution of lantern fishes (Myctophidae s.l.) in the Atlantic Ocean. *In* T. S. Rass (editor), The pelagic and bathypelagic fishes of the world oceans, p. 206-264. Tr. Inst. Okeanol. Akad. Nauk SSSR 84. (Translated from Russ. by the Translation and Interpretation Division, Institute of Modern Languages, Inc., 1969.)

KULIKOVA, E. B.
1957. Growth and age of deep-water fishes. *In* B. N. Nikitin (editor), Marine biology, p. 284-290. Tr. Inst. Okeanol. Akad. Nauk SSSR 20. (Translated from Russ. by Am. Inst. Biol. Sci., 1959.)

LAVENBERG, R. J., AND A. W. EBELING.
1967. Distribution of midwater fishes among deep-water basins of the southern California shelf. *In* R. N. Philbrick (editor), Proceedings of the symposium on the biology of the California Islands, p. 185-201. Santa Barbara Botanic Garden, Inc., Santa Barbara, Calif.

MARSHALL, N. B.
1954. Aspects of deep sea biology. Hutchinson's Scientific and Technical Publications, Lond., 380 p.

MAYNARD, S. D., F. V. RIGGS, AND J. F. WALTERS.
1975. Mesopelagic micronekton in Hawaiian waters: Faunal composition, standing stock, and diel vertical migration. Fish. Bull., U.S. 73:726-736.

MCCARTNEY, B. S.
1976. Comparison of the acoustic and biological sampling of the sonic scattering layers: R.R.S. "DISCOVERY"

SOND Cruise, 1965. J. Mar. Biol. Assoc. U.K. 56:161-178.

MCGOWAN, J. A.
1971. Oceanic biogeography of the Pacific. *In* B. M. Funnell and W. R. Riedel (editors), The micropaleontology of oceans, p. 3-74. Camb. Univ. Press, Camb.

NAFPAKTITIS, B. G.
1968. Taxonomy and distribution of the lanternfishes, genera *Lobianchia* and *Diaphus*, in the North Atlantic. Dana Rep. Carlsberg Found. 73, 131 p.

OMORI, M., A. KAWAMURA, AND Y. AIZAWA.
1972. *Sergestes similis* Hansen, its distribution and importance as food of fin and sei whales in the North Pacific Ocean. *In* A. Y. Takenouti (editor), Biological oceanography of the northern North Pacific Ocean, p. 373-391. Idemitsu Shoten, Tokyo.

PAXTON, J. R.
1967. A distributional analysis for the lanternfishes (Family Myctophidae) of the San Pedro Basin, California Copeia 1967:422-440.

PEARCY, W. G.
1977. Variations in abundance of sound scattering animals off Oregon. *In* N. R. Anderson and B. J. Zahuranec (editors), Oceanic sound scattering prediction, p. 647-666. Plenum Press, N.Y.

PEARCY, W. G., E. E. KRYGIER, R. MESECAR, AND F. RAMSEY.
1977. Vertical distribution and migration of oceanic micronekton off Oregon. Deep-Sea Res. 24:223-245.

PEARCY, W. G., AND R. M. LAURS.
1966. Vertical migration and distribution of mesopelagic fishes off Oregon. Deep-Sea Res. 13:153-165.

SMOKER, W., AND W. G. PEARCY.
1970. Growth and reproduction of the lanternfish *Stenobrachius leucopsarus*. J. Fish. Res. Board Can. 27:1265-1275.

TATE, M. W., AND R. C. CLELLAND.
1957. Nonparametric and shortcut statistics in the social, biological, and medical sciences. Interstate Printers and Publishers, Inc., Danville, Ill., 171 p.

TAYLOR, F. H. C.
1968. The relationship of midwater trawl catches to sound scattering layers off the coast of northern British Columbia. J. Fish. Res. Board Can. 25:457-472.

TONT, S. A.
1976. Deep scattering layers: patterns in the Pacific. Calif. Coop. Oceanic Fish. Invest., Rep. 18:112-117.

TUCKER, G. H.
1951. Relation of fishes and other organisms to the scattering of underwater sound. J. Mar. Res. 10:215-238.

VINOGRADOV, M. E.
1968. Vertical distribution of the oceanic zooplankton. Inst. Okeanol. Akad. Nauk SSSR, Moscow, 339 p. (Translated from Russ. by A. Mercado and J. Salkind, Isr. Program Sci. Transl., Jerusalem, 1970.)

WALTERS, J. F.
1977. Ecology of Hawaiian sergestid shrimps (Penaeidea: Sergestidae). Fish. Bull., U.S. 74:799-836.

WIEBE, P. H., AND W. R. HOLLAND.
1968. Plankton patchiness: effects on repeated net tows. Limnol. Oceanogr. 13:315-321.

WISNER, R. L.
1976. The taxonomy and distribution of lanternfishes (Family Myctophidae) of the eastern Pacific Ocean. Navy Ocean Res. Dev. Act., Rep.-3, U.S. Gov. Print. Off., Wash., D.C., 229 p.

ZAHURANEC, B. J., AND W. L. PUGH.
1971. Biological results from scattering layer investigations in the Norwegian Sea. *In* G. B. Farquhar (editor), Proceedings of an international symposium on biological sound scattering in the ocean, p. 360-380. Maury Center for Ocean Science, Wash., D.C.