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Counterillumination and the upper depth limits of midwater animals

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Abstract—The maximum counterillumination intensities of three species of mesopelagic squids and one species of mesopelagic fish were determined in a shipboard laboratory. The values were compared with the intensity of downwelling irradiance in the ocean measured off Oahu, Hawaii. The upper depth limits of the mesopelagic fauna were determined by mid-day and moonlit-night trawling. The data support the hypothesis that limits on concealment from predation through counterillumination determine the upper depth limits of this fauna during the day. At night near full moon, however, animals may be found at light levels higher than those at which counterillumination seems to be an effective strategy.

INTRODUCTION

THE VERTICAL migration of oceanic micronekton into near-surface water by night and their descent during the day are well documented (e.g., FOXTON, 1970; CLARKE, 1973; ROPER and YOUNG, 1975). Occupation of surface waters coincides with increased feeding rates for many migrators (e.g., MERRETT and ROE, 1974; CLARKE, 1978; HU, 1978). Downward migration may be related to predator avoidance (e.g., MORGAN, 1903; BURCKHARDT, 1910; HUTCHINSON, 1967), although the hypothesis is still debated (see ENRIGHT, 1977, and ENRIGHT and HONEGGER, 1977, for arguments concerning zooplankton). Here we address the latter topic. Experimental evidence supports a predator-avoidance function for downward migration of some limnetic zooplankters (ZARET and SUFFERN, 1976). While such evidence is lacking for oceanic micronekton, the vulnerability of the animals to visual oceanic predators during the day in the well-lighted surface waters would seem to be considerable. ALVERSON (1961) documented intensive feeding by tunas on myctophid fishes that failed to descend during the day.

If micronekters descend into darker waters to avoid being eaten by epipelagic visual predators, at some depth this predation pressure must become greatly reduced or disappear altogether, a depth that should mark the upper limit of the micronekton during the day; it might be determined by light levels low enough for animals to conceal themselves by counterillumination (i.e., use of bioluminescence to obliterate the animal's silhouette; YOUNG and ROPER, 1977).

For the present study we restrict the definition of micronekton to sub-adult or adult mesopelagic fishes, decapod crustaceans and cephalopods that are consistently sampled by

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the ISAACS–KIDD midwater trawl (IKMT). We are concerned with whether or not limitations on concealment via counterillumination could be responsible for the upper depth limits of this fauna. We do not consider either (a) other hypotheses concerning the upper limit of the fauna or (b) hypotheses that bear on the various vertical distribution patterns of mesopelagic species.

We evaluate the concealment hypothesis by comparing laboratory measurements of the light levels under which counterillumination is effective with *in situ* measurements of the depth of light penetration at noon and under full moon. We discuss the results within the context of the upper vertical distribution limits of micronekton as determined by trawls taken during midday and under full moon.

MATERIALS AND METHODS

Most data were gathered aboard the R.V. *Kana Keoki* off Oahu, Hawaii (21°15 to 20'N, 158°15 to 30'W), 20–29 March 1978. The study consisted of three phases: (1) Underwater irradiance was measured during the 4-h period bracketing local apparent noon (LAN) and at the zenith of near-full moon to determine the characteristics of transmitted light at the upper faunal limits. (2) The abilities of midwater squid and fishes to counterilluminate at a variety of light intensities were examined in a shipboard laboratory. (3) Animals were collected by trawl near noon and moon zenith to define day and night upper limits of the fauna. During trawling surface irradiance was monitored.

Underwater light measurements

Levels of transmitted daylight and moonlight were determined to depths of 450 and 125 m, respectively, with the bathythermoirradiance meter described by KAMPA (1970). Seven interference filters (half-peak bandwidths, 10 nm) rotated into the light path allowed measurement of irradiance at 408, 438, 465, 471, 479, 501, and 542 nm. A shutter system afforded exposure of the entire photosensor, 0.001 of its area, or zero. This permitted measurement of light through six orders of magnitude, as well as routine monitoring of the dark current. For near-surface daylight measurements a 3.0 neutral density filter extended the instrument's range. Temperature was detected by thermistors; depth was measured by a Bourdon sensor coupled with a sliding-wire potentiometer. The depth sensor was calibrated with an Ashcroft deadweight gauge.

The irradiance sensor of the submersible meter was calibrated for absolute energy units. A U.S. National Bureau of Standards lamp run at constant voltage, an Eppley thermopile, and a Keithley nanovoltmeter were used to determine, for each color filter, the energy in $\mu W\ cm^{-2}$ striking the cosine collector. The calibration is valid for lights in which the spectral distribution of energy is broad compared with the narrow bands of transmission of the color filters. That relationship holds for the measurements reported here.

Approximately 2 h before LAN or moon zenith the submersible instrument was lowered as rapidly as possible, with its flat-plate cosine collector facing upward, to a depth greater than that at which it was anticipated that downwelling irradiance might be detected. The meter was held at this depth until the sensor had equilibrated to the temperature change. Downwelling irradiance was measured at each of the seven wavelengths and temperature and depth were recorded. The instrument was then raised in increments (approx. 50 m during the day and 25 m during the night) and measurements of all functions were

repeated. Two midday casts and one moonlight cast were made during the cruise in March. Loss of equipment prevented additional measurements.

Surface light measurements

A surface scalar irradiance meter (KAMPA, 1970) monitored light levels at 10 m above the sea surface to determine changes occasioned by variations in cloud cover and elevation of the sun and moon. No attempt has been made to calibrate it in absolute energy units. The instrument embodies the same principles as the light function of the submersible meter. The collector is a translucent sphere that is less susceptible to ship movements than a flat collector. A combination of Schott BG12 and GG5 filters provided maximum sensitivity at 470 nm with a 60-nm half-peak bandwidth, which encompasses the spectral range of the central five of the seven interference filters in the submersible meter. The shutter is identical with that in the underwater meter. The instrument operated continuously throughout the cruise; it was closely monitored during underwater light measurements and during trawling.

Counterillumination: capture and measurement techniques

Two capture techniques were used. Three species of squids and one species of myctophid were obtained in a 3-m IKMT that was shortened, fitted with a light-shielded cod-end bucket, and towed slowly to minimize damage to the animals (see YOUNG and ROPER, 1977). The same species of myctophid was also dip-netted at night. The trawling program for experimental animals ran continuously during periods when the trawling series designed to define the upper faunal limits was not in operation.

Experiments were conducted at sea in a laboratory-van equipped with running, refrigerated, filtered seawater and a light- and temperature-controlled environment at 1 atm pressure. A counterillumination chamber held the animal and contained an overhead light source and light sensors (Fig. 1). An animal was positioned in a close-fitting tube of thin, flexible, clear vinyl plastic connected to flowing seawater at a temperature appropriate to its habitat (approx. 6 to 8°C, day; 16 to 19°C, night). The animal was restricted in the tube by glass clamps. Light from a Kodak Carousel projector passed through one to six neutral density filters (N.D. range 0.5 to 2.5×10^{-11}) plus an interference filter (peak transmission 476 nm, 10-nm half-peak bandwidth) and entered the chamber horizontally at the top. The light was then reflected downward by a mirror at 45° onto a 30 × 30-cm diffuser 13 cm above the animal. A second 45° mirror below the animal provided a ventral view for an observer. Overhead light from the diffuser was measured using a 1.6-mm diameter fiberoptic probe with an EMI 9789 photo-multiplier tube (PMT). Bioluminescence was measured using a 3.2-mm diameter fiberoptic probe placed just beneath the animal and connected with an EMI 9558B PMT. Measurements were displayed on a two-channel Hewlett–Packard strip chart recorder. One probe-PMT system was calibrated on the same optical bench as the submersible irradiance meter; the second system was calibrated against the first while positioned in the chamber.

Two methods were used to insure that the probe beneath the animal received only the animal's light. When squids were examined, the overhead light was frequently turned off for brief periods, usually less than 1 s. The moment of darkness generally had little effect on the squids but allowed positive separation of bioluminescence from overhead light. The myctophid fish responded too quickly to the overhead light for this technique to be useful. For this fish, therefore, the probe was positioned posterior to the head where the tube could

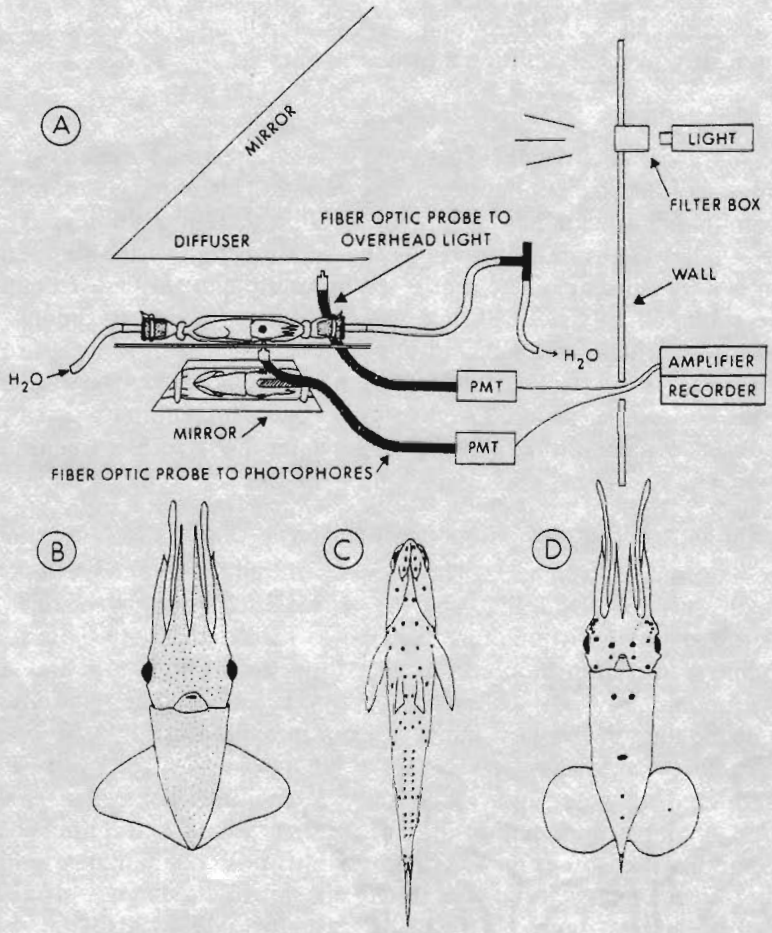

FIG. 1. (A) Experimental apparatus. (B) *Abraliopsis* sp. B. Ventral view showing approximate photophore pattern. *Abraliopsis* sp. A has a similar pattern. (C) *Myctophum obtusirostrum*. Ventral view showing photophore pattern. (D) *Pterygioteuthis giardi*. Ventral view showing photophore pattern (flashing photophores deleted). PMT = photo-multiplier tube.

be covered by black tape without affecting the animal's responses (see YOUNG, ROPER and WALTERS, 1979), thus insuring that only bioluminescence reached the probe.

After capture, an animal was placed in a light-shielded container, transported to the laboratory van, and transferred into the vinyl tubing where it was allowed to acclimatize for one to several hours. Experiments began at low light levels, and intensity was increased in steps by changing the combination of neutral density filters in the light path. The overhead light was held constant at each step for 5 min, and intensities of bioluminescence were taken as an average of the last 30 s of measurements of that time. The highest light level to which an animal was exposed depended on the animal's response: if the animal no longer increased its light when the overhead light was increased, the experiment was terminated. Prior observations and our initial results (see Results) indicated that midwater animals would respond to high light levels by decreasing their luminescence (CASE, WARNER, BARNES and LOWENSTINE, 1977; YOUNG and ROPER, 1977).

In estimating an animal's counterillumination potential in the ocean, we assumed that the maximum intensity of bioluminescence recorded was a better estimator than the maximum intensity of bioluminescence recorded when the animal was still matching the overhead light. The former measure reveals a potential that may not have been realized under stressful laboratory conditions. In most cases the values were similar (see Figs 6–9). The "water depth" equivalent to the laboratory-measured bioluminescent intensity for each animal was calculated from our underwater irradiance measurements. We made no attempt to measure the lowest light intensity at which the animals could counterilluminate.

Trawl series

The general vertical distribution of the micronekton off Oahu, Hawaii is known from previous trawling (CLARKE, 1973, 1974; AMESBURY, 1975; MAYNARD, RIGGS and WALTERS, 1975; ZIEMANN, 1975; WALTERS, 1976; YOUNG, 1978). Our program was designed to determine the depth distribution of the upper faunal limits under known light conditions during midday and midnight (full moon) periods. A maximum of two horizontal tows per day were made with a standard 3-m IKMT, one bracketing LAN and one near moon zenith. Although they were open tows, contamination from shallower depths was minimal because we were fishing into increased animal density as sampling depth increased and because setting and retrieval were rapid. Contamination between tows was greatly reduced by removing animals entangled in the netting after each tow. Missed animals deteriorated sufficiently during the 12 h or more between tows to be recognized as contaminants in the subsequent catch. Each day tow was at depth for about 2 h and each night tow for about 100 min at speeds of about 7.4 km h^{-1}. Depth was recorded on a Benthos 0 to 500-m time–depth–recorder (TDR). For day tows an AMF acoustic depth telemeter was mounted on the trawl vane and monitored continuously; ship speed was adjusted to maintain the trawl's depth. The TDR and telemeter were calibrated on the same dead-weight tester as the submersible irradiance meter and gave depth records that agreed within 10 m.

Midwater fishes, squids, and decapod shrimps (excluding larvae and post-larvae) were identified from formalin-preserved trawl catches. The groups comprised 88% of the individuals and 82% of the biomass (wet weight) of midwater animals collected by the IKMT during a study of the micronekton off Oahu, Hawaii (MAYNARD *et al.*, 1975).

RESULTS

Underwater light measurements

Measurements of the mid-water photoenvironment were made at midday on 21 and 23 March 1978 (Fig. 2). Total irradiance at 400 m, extrapolated from a curve based on measurements at seven wave-lengths at 380 m, was 2.3×10^{-2} μW cm^{-2} (6×10^{10} quanta s^{-1} cm^{-2}). Mean midday attenuation coefficients (K_λ) between depths of 205 and 380 m were (standard deviation in parentheses): 408 nm—0.039 (0.002); 438 nm—0.033 (0.001); 465 nm—0.034 (0.001); 471 nm—0.035 (0.002); 479 nm—0.035 (0.002); 501 nm—0.035 (0.002); 542 nm—0.039 (0.002). Transmitted moonlight of equivalent intensity but different spectral distribution was calculated to occur at about 100 m at night during full moon. Composite curves that represent the attenuation of irradiance with depth (Fig. 2) are relatively smooth; the curves are corrected for differences in the incoming scalar irradiance at the sea surface and for fluctuations in depth during the 8-min interval required

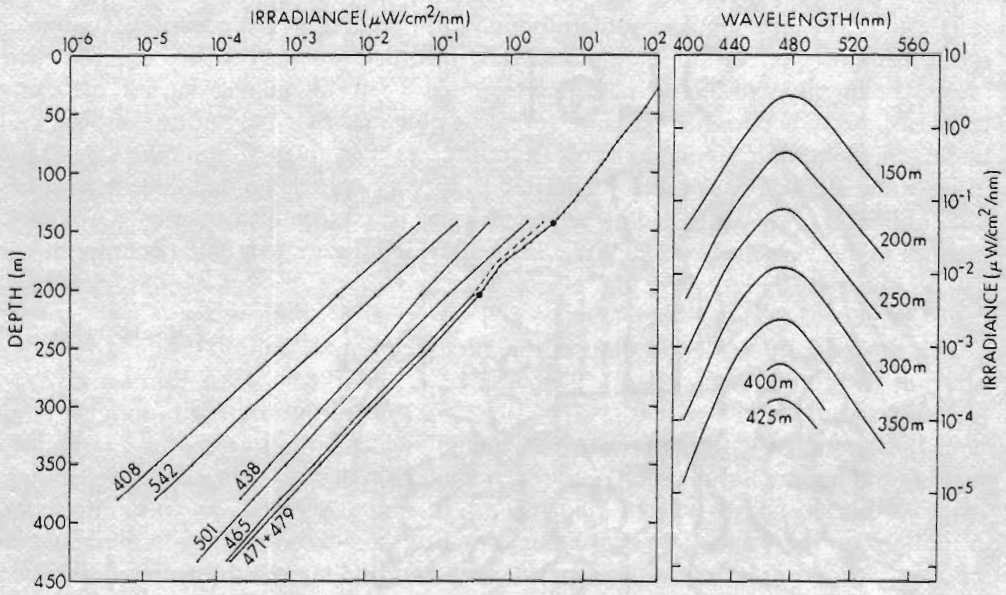

FIG. 2. Left: relation between depth and midday irradiance at various wavelengths in the mid-waters southwest of Oahu, Hawaii, 21 to 23 March 1978. Numbers at the ends of the curves indicate wavelengths (nm) of maximum transmission of the interference filters used. The upper portion (small dots) of the 479-nm curve was obtained with a 3.0 neutral density filter in the light path. Points of coincidence of the records obtained with and without the neutral density filter are indicated by large dots. Right: spectra of light at each depth sampled, derived from the attenuation curves at the left.

for the scan of the 408- to 542-nm spectrum at each depth. Attenuation coefficients calculated for seven wave lengths at depths from 140 to 450 m are consistent with those for coastal islandic areas (JERLOV, 1968). Attenuation of irradiance at 479 nm in near-surface layers was examined on 21 March (Fig. 2).

Moonlight penetration was measured between 2245 hours and midnight on 22 March, two days before full moon (moon zenith = 2319 h; Fig. 3). Surface scalar irradiance was about 2/3 that at full moon zenith on 24 March. Attenuation of moonlight at 479 nm corresponds well with that of midday light in the near-surface layers. There was a rapid increase in attenuation of all wavelengths of moonlight between 100 and 120 m.

Measurements of counterillumination

A. *Initial experiments and calibration assumptions.* A preliminary experiment was run to confirm that animals reduce the intensity of their bioluminescence at high light levels. Several squids were tested. The results of one test are presented here.

A squid, *Abraliopsis* sp. A. was exposed to light of increasing intensity in a series of steps. The first 12 steps (Figs 4, 5) correspond to changes in underwater daylight over a depth range of 285 m off Oahu, Hawaii. The animal's increase in luminescent output was nearly equal to the intensity change in the overhead light although the difference between the observed slope (0.94, $r = 0.999$) and the expected slope (1.0) was significant ($P < 0.001$). A record of four intermediate steps is shown in Fig. 5. The response to a step was usually completed in about 10 s or less. At high intensities the animal continued to increase its

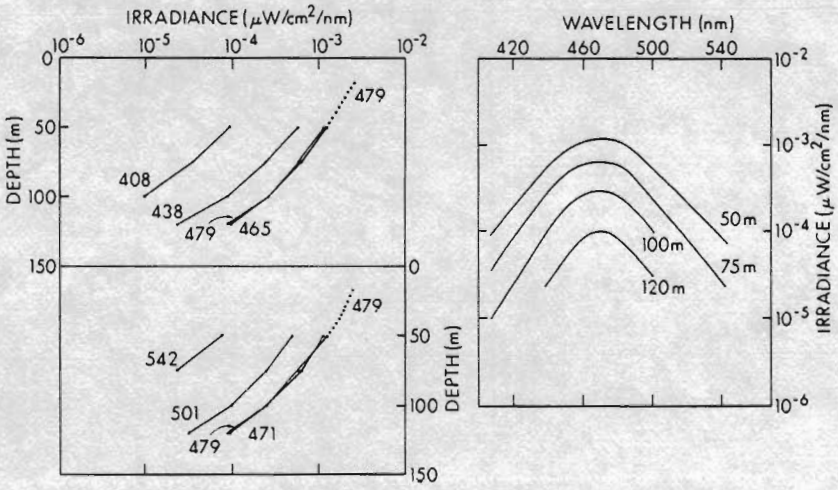

FIG. 3. Left: relation between depth and near-full moonlight in the waters off southwest Oahu, 22 March 1978. Numbers at the ends of the curves indicate wavelengths of maximum transmission of interference filters used. Dotted part of the 479-nm curve was obtained with a 3.0 neutral density filter in the light path. Right: spectra of moonlight at the depths of observation derived from the attenuation curves at the left.

luminescence but the magnitude of bioluminescent increase was less than that of the overhead light increase. Finally, a level was reached at which the squid reduced its bioluminescence in response to an increase in overhead light, and the bioluminescence continued to drop in subsequent steps. By the termination of the experiment, the squid had decreased its bioluminescence to about 0.08% of its maximum intensity (Fig. 4). Apparently there is an upper limit of overhead light intensity beyond which this squid and others tested no longer increase their bioluminescence. The exposure to high light levels had no subsequent effect on the ability to counterilluminate at intermediate light levels but did impair ability at low light levels. The initial experiments were made before fully calibrating our system.

The calibration for subsequent experiments involves several assumptions. First, the animals and the probe must "view" the overhead light similarly. The animals rely on a complex system to determine downwelling light intensity, a system that involves input from both the eyes and the extraocular photoreceptors (YOUNG *et al.*, 1979). The acceptance angles of the latter have not been measured, but at most they could receive a light intensity 1.5 to 2 times that of the probe as determined by the area of the diffuser. The second assumption is that the radiance distribution of the bioluminescence and of daylight in the sea are comparable. The match has been demonstrated for several midwater animals (DENTON, GILPIN-BROWN and WRIGHT, 1972; HERRING, 1976). If the assumptions are valid, the probe detects luminescence as it detects overhead light provided the probe is close to the animal's ventral surface and that photophores are small, numerous, and closely spaced. Of the four species tested these conditions were met only for one squid, *Abraliopsis brevis*. Due to the photophore size or arrangement or the position of the animal in the three other species, the probe measured light from a non-diffuse source, and bioluminescence measurements could not be compared with overhead light intensity on an absolute scale. So long as relative changes in bioluminescent intensity matched relative changes in the

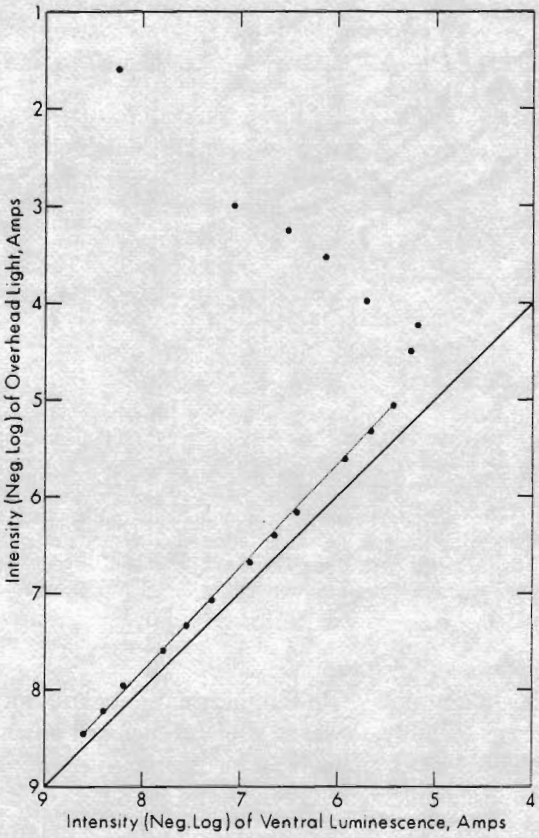

FIG. 4. *Abraliopsis* sp. A. Effect of increasing overhead light intensity beyond the animal's ability to match this light with its bioluminescence. The regression line ($x = 0.94y + 0.65$) is derived from the lower 12 points (i.e., steps 1–12). Solid line is expected value if calibration assumptions are valid.

overhead light intensity and an observer confirmed that the animal's luminescence was similar to that of the background, we concluded that the animal was matching the overhead light. We also assumed that the probe detects the overhead light in the same manner that the submersible irradiance meter detects downwelling light. The acceptance angles of the two are approximately the same.

If the calibration assumptions are correct and the animal's bioluminescence matches the overhead light, all data points should fall on line $x = y$ (the calibration line). In most cases the points were well off this line. The errors arise from a breakdown in the geometry required for calibration due to small animal size, distance from the light guide or the arrangement of photophores.

B. *Final experiments.* All specimens examined could follow changes in the overhead light regime closely (Figs 6–9). Judgments by an observer concerning the animal's ability to match the overhead light agreed well with the recorded data.

The linear regressions for seven of nine specimens, however, had slopes less than one. The observed slope for five specimens was significantly different from 1.0 (see below). In most cases the low slopes resulted from a gradual failure of the animal's bioluminescence to keep exact pace with increases of overhead light at the higher light levels. The general trend

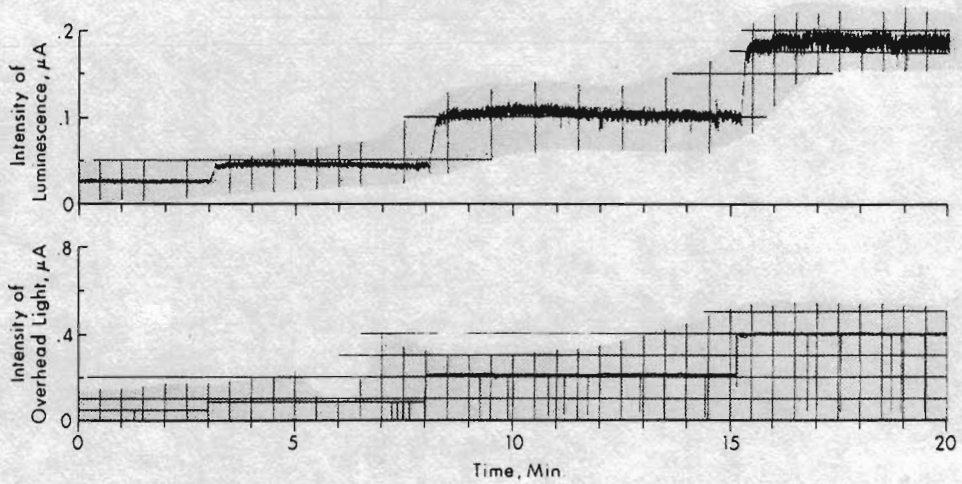

FIG. 5. *Abraliopsis* sp. A. Example of records from which data in Fig. 4 were extracted. Upper record: squid's bioluminescence. Lower record: overhead light. The recording pens were offset slightly to allow overlap. Thus, the apparent slight delay between increase in overhead light and bioluminescence is an artifact. In the lower record the vertical lines (not the grid lines) that approach the abscissa result from momentarily turning off the overhead light.

is apparent in Fig. 10 in which all curves are superimposed. The animals, therefore, are slightly underilluminated at higher light levels. We have no explanation for this trend.

In the following species accounts, the calculated ocean depth corresponding to the intensity of overhead light in the laboratory has been rounded to the nearest 5 m. Maximum intensities of counterillumination are summarized in Table 1.

Abraliopsis sp. A (Fig. 6). The species has numerous small photophores covering its ventral surface. The regression line slope (0.98, $r = 0.997$) was not significantly different from 1 ($P = 0.5$). The offset of the data points from the calibration line is probably due to the small size of the individual, which makes proper alignment of the probe difficult. YOUNG (1978) recorded the species from depths of 475 to 700 m during the day and 20 to 200 m at night. The specimen is similar in size to those taken in Trawl 3 (403 m max., day) and Trawl 7 (44 m max., night) (see Appendix).

Abraliopsis sp. B (Fig. 7). Size and configuration of photophores in the species were ideal for our measurement techniques; data points for all three squid were close to the calibration line. The squid performed best at middle light intensities and somewhat less well at the lower ones. At high levels they tended to be slightly underilluminated. As a result, in two of the three specimens the slopes of the linear regressions were significantly different from 1.0 (specimen 1: slope = 1.015; $r = 0.999$, $P = 0.1$; specimen 2: slope = 0.86, $r = 0.999$, $P < 0.001$; specimen 3: slope = 0.94, $r = 0.999$, $P < 0.001$). The luminescence of specimen 3 became erratic at steps 12 ($\approx$ 415 m depth) and 13 ($\approx$ 385 m) but recovered considerably on the following step ($\approx$ 360 m). During the day the species has been caught as shallow as 390 m (R.E.Y. unpublished observations) but more commonly at 500 to 600 m; during the night it occupies depths of 15 to 100 m (YOUNG, 1978). No specimens were taken in the 10 trawls of the upper-faunal-limit study.

Pterygioteuthis giardi (Fig. 8). Several factors complicated luminescence measurements of this species. It has a few large photophores on the head, viscera, and tentacles, and thus

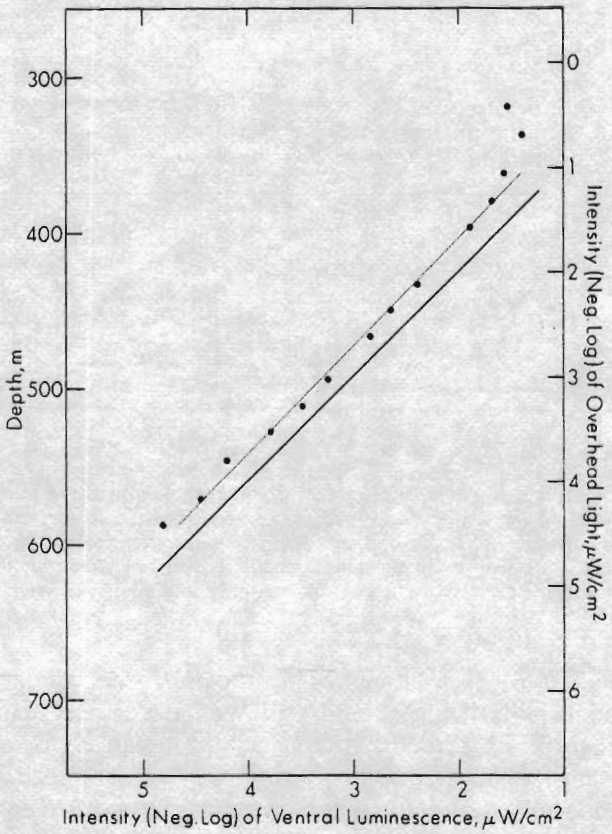

FIG. 6. Counterillumination measurements of the squid *Abralia opsis* sp. A. One immature male, 15 mm. mantle length (ML). Dot = data point. Thick line = calibration line. Thin line = regression line for steps 1–12 ($x = 0.98y + 0.36$). Depth scale refers to noon-time depths in the ocean with light intensity corresponding to that of the overhead light.

was probably not a diffuse light source. The animal orients at an angle oblique to the horizontal in the water and directs its luminescence anteroventrally (personal observation). Therefore, the tube holding the animal was tilted. As a result, the animal was at some distance from the probe and luminescence could be measured only during momentary periods when the overhead light was turned off. The slope of the linear regression was not significantly different from 1.0 in one specimen (slope = 0.98, $r = 0.998$, $P = 0.4$) but was significantly different in the other (slope = 0.86, $r = 0.990$, $P < 0.001$). The small size of the latter animal combined with the tilt of the tube prevented close confinement; apparently the squid moved slightly relative to the probe in the middle of the measurements (see Fig. 7). If the data for this squid are analyzed in segments, the slope is not significantly different from 1.0 for the first 9 steps (steps 1–6: slope = 0.97, $r = 0.999$, $P = 0.1$; steps 7–9: slope = 1.00, $r = 0.999$, $P = > 0.80$). In steps 10–12 the light from the animal clearly lagged behind the overhead light in intensity (slope = 0.82, $r = 1.000$, $P = < 0.05$). Differences between specimens are probably due to difference in animals' sizes and distances from the probe. YOUNG (1978) recorded this animal from depths of 390 to 525 m

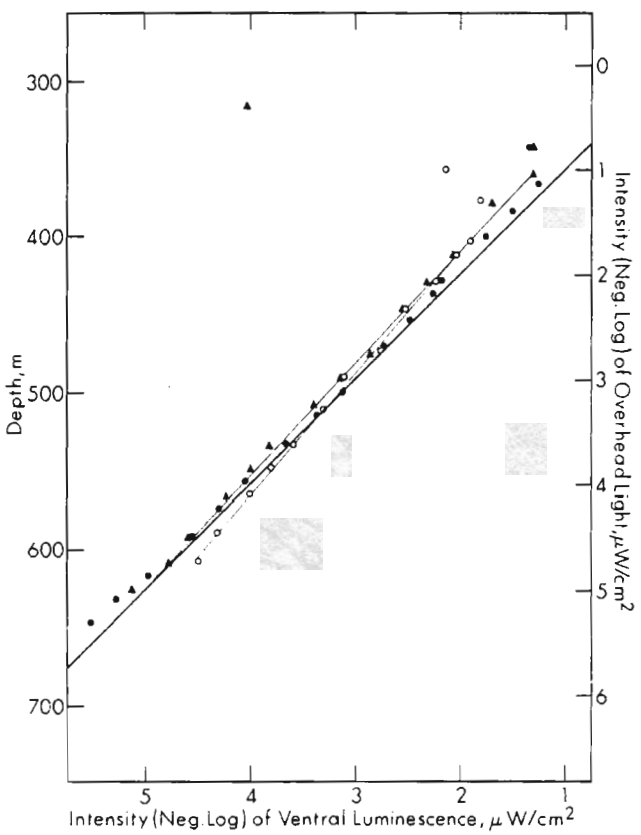

FIG. 7. Counterillumination measurements of the squid *Abraliopsis* sp. B. Dots = data points for specimen 1, 22 mm ML, male (regression line for steps 1–16: $x = 1.015y + 0.03$). Circles = data points for specimen 2, 26 mm ML, male (regression line for steps 1–12: $x = 0.86y + 0.48$). Triangles = data points for specimen 3, 17 mm ML, male (regression line for steps 1–14: $x = 0.94y + 0.35$). Thick line = calibration line. Thin lines = regression lines. For clarity the regression line for specimen 1 was not drawn. It lies very close to the calibration line.

during the day and 15 to 180 m at night. This was the most common squid captured in the present trawl series at the upper faunal limits both day and night.

Myctophum obtusirostrum (Fig. 9). The regression line slope for specimen no. 1 was 0.93 ($r = 1.00$), which differed significantly from 1.0 ($P < 0.001$). At light step 13 (= 405-m depth) specimen 1 began flashing its photophores then suddenly decreased its luminescent output to less than 8% of the previous value. The fish then began flashing again and slowly increased the intensity to its final value at step 13, which was close to matching the overhead light. At step 14 the animal flashed its photophores for a short period then abruptly reduced its luminescence to less than 4% of the previous value; the fish maintained this level for the full 5 min. Because of the large, broadly-spaced photophores of the species, the apparent close match of the specimen's response to the calibration line may be accidental. The different positions of the curve (Fig. 9) between specimens 1 and 2 could be due to different positions or distances of the probe relative to the photophores. Specimen 2 gave a peculiar response at low light levels—reason unknown (see Fig. 9); however, the

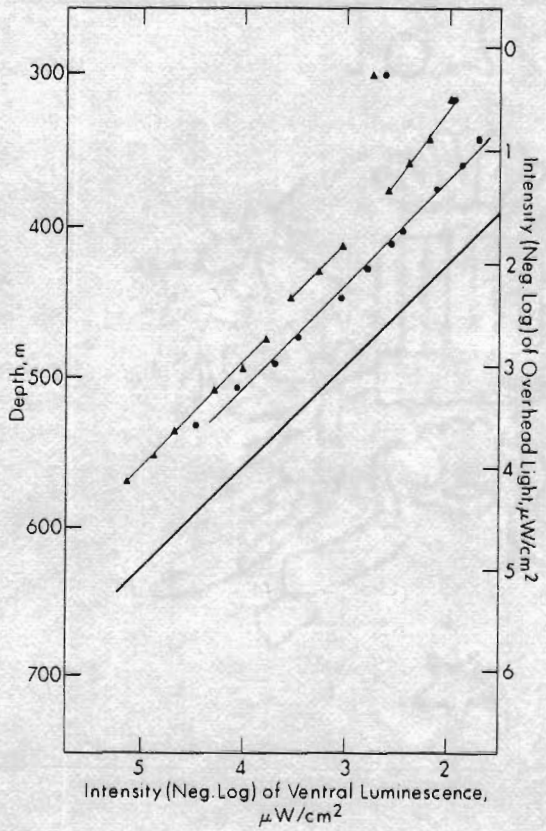

FIG. 8. Counterillumination measurements of the squid *Pterygioteuthis giardi*. Dots = data points for specimen 1, 21 mm ML, female (regression line for steps 1–11: $x = 0.98y + 0.85$). Triangles = data points for specimen 2, 14 mm ML, male. The break in the regression line indicates probable movement of squid (regression line for steps 1–6: $x = 0.97y + 1.14$; regression line for steps 7–9; $x = y + 1.21$; regression line for steps 10–13: $x = 0.73y + 1.64$). Thick line = calibration line. Thin lines = regression lines.

linear regression was not significantly different from 1.0 (slope = 1.04, $r = 0.994$, $P \approx 0.2$). The behavior of specimen 2 paralleled that of specimen 1 at high light levels. At step 18 ($\approx$ 395 m) it rapidly increased then abruptly decreased the intensity of its luminescence. Thereafter, its luminescent output gradually increased to the initial level but with fluctuations (Fig. 11). Figure 12 shows the capability of specimen 2 to follow changes in the overhead light.

CLARKE (1973) recorded the species from 500 to 700 m during the day and from 0 to 15 m at night but suggested that it may avoid the trawl and occur in well-lighted depths during the day and at night. This fish, therefore, like the squid is found near the upper faunal limits.

Trawling series

The daytime upper depth boundary of the midwater fauna is not abrupt (see Table 2; Appendix). Although all of our daytime tows captured midwater animals, micronekton

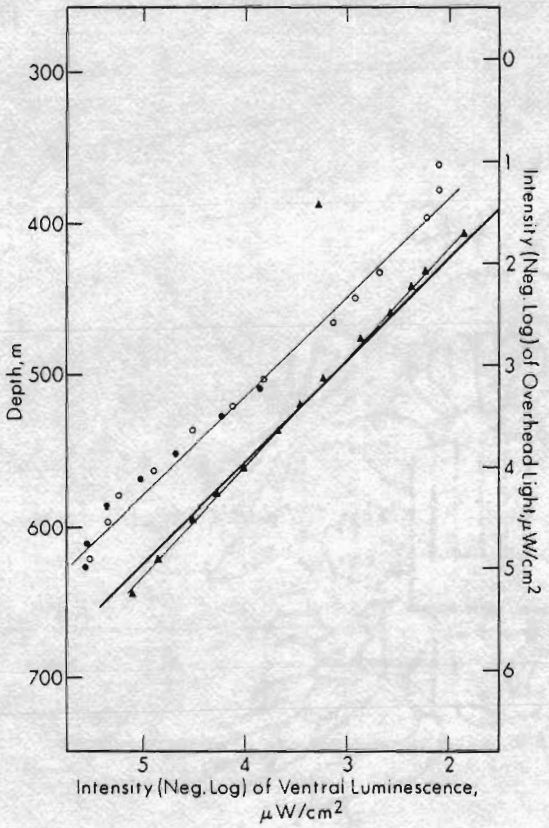

FIG. 9. Counterillumination measurements of the fish *Myctophum obtusirostrum*. Triangles = data points for specimen 1, 67 mm standard length (SL), female (regression line for steps 1–13: $x = 0.93y + 0.27$). Dots = data points for specimen 2, 63 mm SL, female (regression line for steps 1–19: $x = 1.04y + 0.58$). Circles = first run; dots = second run. Thick line = calibration line. Thin lines = regression lines.

above 400 m were sparse; small squid dominated. Of the three species of fishes captured above 400 m, one lacked obvious photophores. This fish, a macrurocyttid, was opaque, rather large (30 mm SL), and had a relatively broad silhouette. However, faint luminescence was recorded from a recently-dead specimen, which indicates that the species may have counterilluminating capabilities. Between 400 and 420 m the catches consisted of more individuals and were dominated by small fishes, many of which were partially transparent (e.g., *Cyclothone*, *Valencienellus*). A few small semitransparent squid and decapod shrimps were also present. By 450 m the catch was relatively large and varied (Table 2; Appendix).

The night catches were quite different in composition (Table 2; Appendix). The shallowest tow (44 m max.) was at a light intensity comparable to that of the shallowest day tow (Fig. 13). The catch consisted of numerous large myctophid fishes (almost exclusively *Hygophum proximum*) plus a few small squid and decapod shrimp. The next deepest night tow (80 m max.; daytime light-equivalent depth ≈ 385 m) contained a wide variety of large fishes, small sergestid shrimp, and a few squid. It was similar to the day

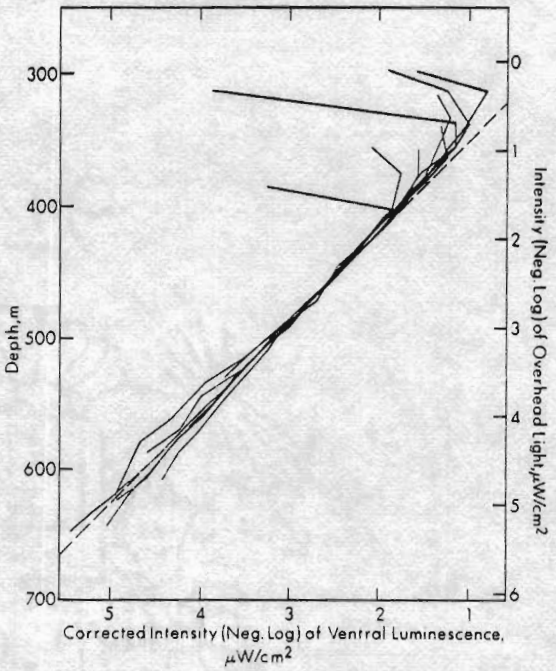

FIG. 10. Composite curves from counterillumination measurements of all animals. Curves shifted on horizontal axis to minimize calibration error and differences between individuals. Corrected for movement by *Pterygioteuthis giardi*, specimen no. 1. Dashed line has slope of 1.0.

Table 1. Estimated upper limits of counterillumination for species examined in the laboratory

Species	Adjusted maximum intensity of luminescence* ($\mu W\ cm^{-2}$)	Corresponding depth (m)		Minimum depth of capture (m)†	
		Day	Night	Day	Night
Abraliopsis sp. A	6.6×10^{-2}	370	70	385	44
Abraliopsis sp. B	7.8×10^{-2}	370	70	NC	NC
No. 1	7.8×10^{-2}	370	70	NC	NC
No. 2	2.3×10^{-2}	400	100	NC	NC
No. 3	6.6×10^{-2}	365	60	NC	NC
Pterygioteuthis giardi					
No. 1	9.3×10^{-2}	360	55	366	44
No. 2	1.8×10^{-1}	340	40		
Myctophum obtusirostrum					
No. 1	1.7×10^{-2}	410	105	NC	NC
No. 2	2.8×10^{-2}	395	90	NC	NC

* Curves were shifted on the horizontal axis onto the calibration line. The value of the maximum intensity of bioluminescence recorded during counterillumination was located on the calibration line and the corresponding value of the overhead light was found. The latter was used as the adjusted maximum intensity of luminescence.

† Maximum depth of the shallowest trawl which captured the species in our noon and full moon trawls. NC—no captures.

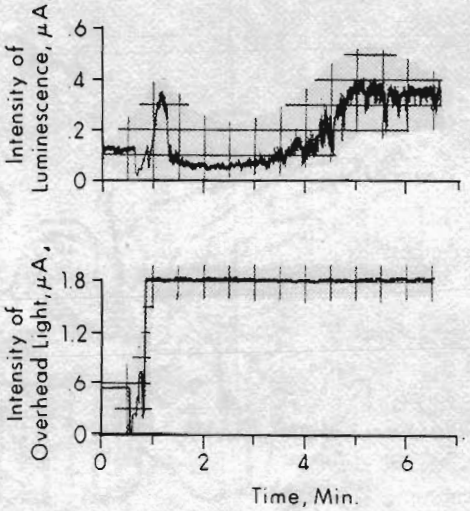

FIG. 11. Record of counterillumination in *Myctophum obtusirostrum*, specimen 2 near its brightest luminescence. Changes in the lower record result from changing neutral density filters in the path of the overhead light. At this step a number of filters must be changed to reach the desired intensity. Sequential changes in the filters had corresponding effects on the fishes' bioluminescence (upper record). See text for explanation of upper record.

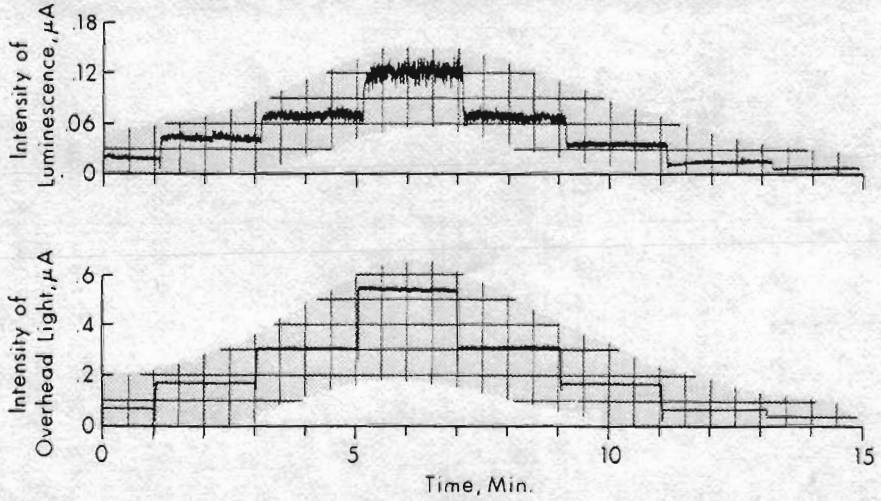

FIG. 12. Record of counterillumination in *Myctophum obtusirostrum*, specimen 2. The record was made subsequent to data gathered for Fig. 9 and demonstrates the animal's rapid and accurate bioluminescent response to changes in the overhead light intensity. Upper record: bioluminescence from fish. Lower record: overhead light. The two pens simultaneously recording the data were offset slightly. Thus, the slight delay seen in the animal's response is not real.

Table 2. Summary of station and catch data. Catch data expressed as numbers of individuals, with numbers of species in parentheses

	Trawl No.	Day, March '78	Time trawl at depth	Time of LAN or moon zenith	Moon phase rel. to full moon	Maximum trawl depth (m)	Fish: Myctophidae	Gonostomatidae	Sternoptychidae	Photichthyidae	Melanostomiatidae	Idiacanthidae	Nemichthyidae	Macrurocyttidae	Opisthoproctidae	Shrimp: Sergestidae	Oplophoridae	Squid: Enoploteuthidae	Histioteuthidae	Cranchiidae	Totals
Day	1	29	1226–1406	1238	—	366	0	1	1	0	0	0	0	1	0	0	0	8 (2)	1	0	12 (6)
	2	27	1206–1346	1238	—	385	0	0	0	0	0	0	0	0	0	1	0	3 (3)	0	—	4 (4)
	3	24	1132–1312	1239	—	403	10 (2)	2 (1)	3(1)	0	0	0	0	1	0	3 (2)	0	2 (2)	0	0	21 (9)
	4	26	1223–1403	1239	—	413	3 (1)	18 (1)	8 (1)	3 (1)	0	0	0	0	0	3 (2)	4 (2)	3 (1)	0	0	42 (9)
	5	22	1206–1346	1240	—	417	3 (1)	85 (1)	9 (1)	1	0	0	0	0	0	3 (3)	5 (2)	5 (2)	0	0	111 (11)
	6	28	1219–1359	1238	—	453	26 (6)	439 (3)	18 (5)	14 (2)	0	1	0	0	2 (1)	6 (4)	7 (2)	2 (2)	0	1	516 (27)
Night	7	27	0056–0236	0236	+3	44	32 (3)	0	0	0	0	0	0	0	0	5 (2)	0	4 (3)	0	0	41 (8)
	8	26	0009–0149	0144	+2	80	46 (10)	0	0	4 (2)	0	0	1	0	0	14 (6)	0	2 (2)	0	0	67 (21)
	9	23–24	2302–0042	0007	0	92	124 (11)	1	0	0	1	0	0	0	0	14 (7)	0	3 (1)	0	0	143 (21)
	10	25	0001–0141	0055	+1	110	66 (9)	0	0	2 (2)	2 (1)	0	0	0	0	19 (6)	0	3 (2)	0	0	92 (20)

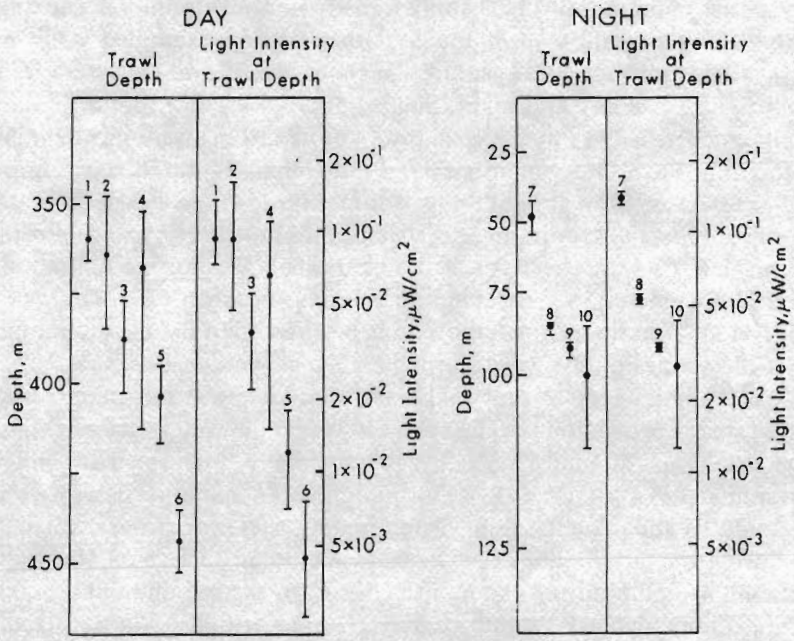

FIG. 13. Comparisons of trawl depths and the light intensities at the trawl depths for all tows taken to examine the upper faunal limits during the day and night. Numbers above bars refer to trawl number. Dots = mean of trawl depth or light intensity. Vertical bars = vertical depth range of trawl once at trawling depth or corresponding range of light intensity while trawl at depth.

catch at 450 m in the large number of species although different in species composition. The two subsequent and slightly deeper night tows resembled the 80-m tow.

DISCUSSION

Four species of the micronekton can counterilluminate under the light conditions found at the upper limits of the midwater fauna during the day. The squid *Pterygioteuthis giardi* could match the overhead light at an intensity comparable with that at a depth of 340 m during the day. All species tested were capable of matching the light present at 400 m, the approximate upper limit of the fauna. Although counterillumination above 400 m is clearly possible for at least short periods in some species examined, high visual acuity operates strongly against effective counterillumination at high light levels: if individual photophores can be resolved by a potential predator, the silhouette remains visible. High visual acuity of predators ultimately may be responsible for the small size of the animals occurring near the upper faunal limits and for the partially transparent nature of many of the animals (see also AMESBURY, 1975): small, semitransparent animals offer less contrast with the background and are more easily concealed. Only in the 435- to 453-m deep daytime tow did our trawl return an abundant catch of mesopelagic animals. To the human observer, the counterillumination strategy appeared effective at those light levels at close range.

The composition of the fauna in the shallow day tows differed dramatically from that in the shallow night tows. Of the 23 species of fishes taken at night, only seven were common to both groups. The differences were caused primarily by the large number of non-vertically

migrating species captured during the day (mostly non-myctophids). The different species composition alone does not affect the hypothesis being examined. One might expect, however, similar morphological features such as small size and semitransparency at comparable light levels day and night. Such similarity was not found.

The night catches in the three deeper tows (80 to 110 m) were most similar to the day catch at 450 m in the number of species and individuals captured (excluding *Cyclothone*), but the 80-m tow was taken at light levels 10 times those of the 450-m day catch. The night tow at 44 m contained a large number of myctophids mostly *Hygophum proximum*. CLARKE (1973) found this species to be atypical: it occurs shallower during full moon than during new moon. Unfortunately, we obtained no suitable specimen of *H. proximum* for testing. The light level at 44 m under the full moon is brighter than the maximum bioluminescent intensity of the species of myctophid tested (*Myctophum obtusirostrum*).

MARSHALL (1954) suggested that midwater animals move into near-surface waters at night to feed under protection of darkness. However, the waters are not completely dark, and numerous visual predators occupy the surface waters at night and will feed on midwater animals (WATANABE, 1958). During much of the month downwelling light levels at night should be adequate to allow visual predation in near-surface waters. The isolume at 400 m during the day should occur beneath the ocean surface off Hawaii for over one-third of the night hours during the month (based on surface illumination data in SIMON, 1974). The isolume reached a depth of about 100 m at full moon during this study and would occur at about 25 m at quarter moon (see SIMON, 1974).

Off Oahu, Hawaii many midwater animals inhabiting the upper 150 m at night during new moon are found 50 to 75 m deeper during full moon (CLARKE, 1973; ZIEMANN, 1975; WALTERS, 1976). This "moonlight depression" may be analogous to the downward migration during the day and could result from the threat of visual predation on moonlit nights. The moonlight depression, however, does not result in the lowering of the upper faunal boundaries to the same light levels as those frequented at midday.

Of the 14 species of myctophids captured in the night tows at least six feed predominantly or exclusively at night (CLARKE, 1978). The higher light levels encountered by the myctophids at night may be related to night feeding. However, myctophids do not occur during the day at comparable light levels where food is also abundant (CLARKE, 1978). There are, of course, differences in the day and night habitats: for example, in near-surface waters the downwelling light regime is much more variable, temperatures and O_2 concentrations are higher, and hydrostatic pressure is lower. These and other differences may affect prey–predator strategies either directly (i.e., light) or indirectly through possible effects on metabolism.

During the day, light levels at the upper limits of the midwater fauna correspond well with the upper limits for bioluminescent concealment as determined by our observations. If our full moon data prove to be typical, however, many midwater animals occur during moonlit nights at light levels higher than those at which counterillumination seems to be effective for concealment.

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APPENDIX

Species captured in trawl series. Arranged in order of increasing maximum trawl depth. Depth given is maximum depth. Following each species the number of individuals and size range in millimeters are given. Standard length, mantle length, carapace length used for fish, squid and shrimp respectively.

Day

Trawl 1 (366 m)—FISH: *Margrethia obtusirostra* (1 : 23), *Valencienellus tripunctulatus* (1 : 14), *Macrurocyttidae* (1 : 30). SQUID: *Pterygioteuthis giardi* (6 : 13–23), *Pyroteuthis addolux* (2 : 22–30), *Histioteuthis dofleini*? (1 : 10). DECAPOD SHRIMP: None.

Trawl 2 (385 m)—FISH: None. SQUID: *Pterygioteuthis giardi* (1 : 12), *Pyroteuthis addolux* (1 : 22), *Abraliopsis* sp. A (1 : 13). DECAPOD SHRIMP: *Sergestes cornutus* (1 : 3.5).

Trawl 3 (403 m)—FISH: *Valencienellus tripunctulatus* (3 : 18–19), Macrurocyttidae (1 : 25), *Cyclothone alba* (2 : 19–20), *Diaphus anderseni* (9 : 13–19), *Myctophum selenoides* (1 : 30). SQUID: *Pterygioteuthis giardi* (1 : 13.5), *Abraliopsis* sp. A (1 : 15). DECAPOD SHRIMP: *Sergestes cornutus* (2 : 4–5), *S. armatus* (1 : 8).

Trawl 4 (413 m)—FISH: *Valencienellus tripunctulatus* (8 : 16–28), *Cyclothone alba* (18 : 19–21), *Ichthyococcus ovatus* (3 : 18–37), *Diaphus anderseni* (3 : 13–15). SQUID: *Pterygioteuthis giardi* (3 : 15–18). DECAPOD SHRIMP: *Sergestes sargassi* (1 : 4.5), *S. pectinatus* (2 : 3.5), *Oplophorous spinosus* (2 : 5.5–6), *O. gracilirostris* (2 : 7–8).

Trawl 5 (417 m)—FISH: *Valencienellus tripunctulatus* (9 : 16–27), *Cyclothone alba* (85 : 16–22), *Ichthyococcus ovatus* (1 : 24), *Diaphus anderseni* (3 : 27–37). SQUID: *Pterygioteuthis giardi* (4 : 14–20), *Pyroteuthis addolux* (1 : 25). DECAPOD SHRIMP: *Sergestes cornutus* (1 : 5), *S. sargassi* (1 : 6), *S. pectinatus* (1 : 4), *Oplophorous spinosus* (4 : 4.5–5.5), *O. gracilirostris* (1 : 9).

Trawl 6 (453 m)—FISH: *Valencienellus tripunctulatus* (1 : 29), *Danaphos oculatus* (11 : 23–39), *Sternoptyx* sp. (1 : 11), *Argyropelecus hemigymnus* (4 : 9–28), *A.* sp. (1 : 10), *Vinciguerria nimbaria* (13 : 17–28), *V. poweriae* (1 : 23), *Idiacanthus fasciola* (1 : 58), *Cyclothone alba* (435 : 14–28), *C. pseudopallida* (3 : 17–19), *Gonostoma atlanticum* (1 : 43), *Diaphus brachycephalus* (1 : 13), *D. mollis*, type A (14 : 15–33), *D. mollis*, type B (1 : 17), *D. perspicillatus* (6 : 40–54), *Lobianchia gemellari* (2 : 45–47), Ceratoscopelus warmingi (2 : 23–25), *Opisthoproctus soleatus* (2 : 30–35). SQUID: *Pterygioteuthis microlampas* (1 : 15), *Pyroteuthis addolux* (1 : 13), *Sandalops melancholicus* (1 : 30). DECAPOD SHRIMP: *Sergestes cornutus* (1 : 5), *S. sargassi* (3 : 6.5–8.5), *S. pectinatus* (1 : 3), *S. orientalis* (1 : 6), *Oplophorus spinosus* (1 : 14), *O. gracilirostris* (6 : 7.5–15).

Night

Trawl 7 (44 m)—FISH: *Hygophum proximum* (30 : 26–49), *H. reinhardti* (1 : 33), *Diogenichthys atlanticus* (1 : 20). SQUID: *Pterygioteuthis giardi* (2 : 14–22), *P. microlampas* (1 : 18), *Abraliopsis* sp. A (1 : 13.5). DECAPOD SHRIMP: *Sergestes cornutus* (1 : 4.5), *S. orientalis* (4 : 5.5–6).

Trawl 8 (80 m)—FISH: *Hygophum proximum* (12 : 25–45), *H. reinhardti* (2 : 16–40), *Diogenichthys atlanticus* (2 : 19), *Diaphus mollis*, type A (2 : 18–28), *D. perspicillatus* (2 : 45–49), *D. schmidti* (1 : 30), *Ceratoscopelus warmingi* (21 : 22–37), *Benthosema fibulatum* (2 : 65–70), *B. suborbitale* (1 : 14), *Lampanyctus steinbecki* (1 : 21), *Vinciguerria nimbaria* (1 : 17), *V. poweriae* (2 : 14–16), *Photostomias guernei* (1 : 47), *Nemichthys larseni* (1 : 400). SQUID: *Pterygioteuthis giardi* (1 : 17), *Abraliopsis* sp. A (1 : 31). DECAPOD SHRIMP: *Sergestes pectinatus* (2 : 3.5), *S. armatus* (4 : 8–8.5), *S. erectus* (1 : 6.5), *S. orientalis* (3 : 5.5–6), *S. atlanticus* (3 : 4–5), *S. vigilax* (1 : 6).

Trawl 9 (92 m)—FISH: *Hygophum proximum* (19 : 14–47), *H. reinhardti* (3 : 22–34), *Diogenichthys atlanticus* (12 : 15–21), *Diaphus fragilis* (1 : 14), *D. mollis*, type A (14 : 13–33), *D. schmidti* (3 : 19–37), *Lobianchia gemellari* (3 : 19), *Ceratoscopelus warmingi* (52 : 12–38), *Benthosema fibulatum* (1 : 73),

B. suborbitale (2 : 12–13), *Notolychnus valdiviae* (14 : 14–20), *Gonostoma atlanticum* (1 : 23), *Bathophilus kingi* (1 : 47). SQUID: *Pterygioteuthis giardi* (3 : 15–16). DECAPOD SHRIMP: *Sergestes sargassi* (3 : 4–5.5), *S. pectinatus* (3 : 3.5–4), *S. armatus* (1 : 7), *S. consobrinus* (1 : 5.5), *S. erectus* (4 : 7–7.5), *S. orientalis* (1 : 6), *S. atlanticus* (1 : 4.5).

Trawl 10 (110 m)—FISH: *Hygophym proximum* (5 : 16–45), *H. reinhardti* (1 : 41), *Diogenichthys atlanticus* (4 : 15–20), *Diaphus mollis*, type A (5 : 12–22), *D. schmidti* (4 : 13–34), *Ceratoscopelus warmingi* (44 : 13–35), *Benthosema suborbitale* (2 : 14), *Symbolophorus evermanni* (1 : 34), *Notolychnus valdiviae* (3 : 20–21), *Vinciguerria nimbaria* (1 : 16), *V. poweriae* (1 : 16), *Bathophilus kingi* (2 : 72–95). SQUID: *Pterygioteuthis giardi* (2 : 13–15), *Pyroteuthis addolux* (1 : 21). DECAPOD SHRIMP: *Sergestes cornutus* (2 : 4–5), *S. sargassi* (1 : 3.5), *S. pectinatus* (4 : 3.5–5.5), *S. armatus* (4 : 6.5–8.5), *S. consobrinus* (2 : 5.5), *S. erectus* (6 : 6–8).