

Nocturnal light and lunar cycle effects on diel migration of micronekton

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Abstract

The roles of nocturnal light and lunar phase in the diel migration of micronekton from a nearshore scattering layer were examined. Migration patterns were measured over six complete lunar cycles using moored upward-looking echosounders while nocturnal surface irradiance was recorded. We hypothesized that animals would remain at a constant isolume at night despite changes in nocturnal illumination between nights. The scattering layer migrated closer to the surface during dark nights than during well-lit ones. However, this movement was not enough to compensate for observed changes in light, and at night animals often remained at light levels higher than they experience at depth during the day. Light and lunar cycle were not completely coupled, allowing separation of the light and lunar phases. Contrary to the initial hypothesis, lunar phase accounted for substantially more of the variability in layer migration than surface irradiance, showing strong effects on the scattering layer's depth and animal density within the layer. Changes in layer depth and animal density were amplified a small amount by variations in light level but were minimized by the seafloor in shallow areas. The horizontal component of the scattering layer's migration was also affected by lunar phase, with animals remaining further offshore in deeper waters during nights near and during the full moon, even when these were not the nights with the highest light levels. These results suggest that moonlight may be a cue for an endogenous lunar rhythm in the process of diel migration rather than a direct cause.

Diel vertical migration of zooplankton and nekton, active movement from deep, dark waters where animals reside during the day to near-surface waters at night (Longhurst 1976), is thought to be ultimately driven by maximization of survival controlled by food, predators, and physiological costs (Zaret and Suffern 1976; Enright 1977). However, individual animals have limited means to follow predator and prey distributions in the water column. Therefore, environmental cues must be used as proxies. Light is one of the strongest environmental cues available to migrating animals and is hypothesized to serve as a proxy for the risk of predation by visual predators (*see a review in Forward 1988*).

Light is generally accepted as playing an important role in controlling the timing of diel vertical migration since most migrations occur at sunrise and sunset (Esterley 1911; *see a review in Ringelberg 1995*). Two mechanisms to explain how light may trigger vertical migration have been examined: absolute light intensity and rate of light change. One hypothesis about absolute light levels suggests that animals remain at an optimum light level, following this constant level, or isolume, up and down in the water column as the surface irradiance changes (Michael 1911; Longhurst 1976). Alternatively, animals may use an absolute threshold value of light to trigger upward movement when light becomes lower than the threshold (Esterley 1911; Pearre 1973). The absolute level of light may be difficult for animals to detect, however. Instead, animals may use the rate of the change in light intensity to cue migration (*reviewed in Ringelberg 1995*).

There have been many studies to examine the role of light changes at sunset and sunrise in initiating vertical

migration but relatively few examining the role of nocturnal light in determining the vertical position or behavior of migrators. Hardy and Bainbridge (1954) showed experimentally that individual zooplankton change their swimming direction during migration in responses to changes in light intensity at very short timescales, indicating that light can alter behavior and vertical position even after the onset of migration. In situ observations have shown similar short-term responses with upward migration of an acoustically detected layer after the set of a bright moon (Dietz 1962). Similar changes in the vertical migration timing and extent have been observed in layers of mesopelagic shrimp (Chiou et al. 2003) and myctophids (Linkowski 1996; Benoit-Bird et al. *in press*). Tarling et al. (1999) compared the behavior of vertically migrating euphausiids over several lunar phases and a lunar eclipse, concluding that euphausiid species can perceive moonlight and that this influences vertical migration, as animals migrated much closer to the surface during the eclipse than during the days immediately afterward. Vertically migrating zooplankton in a freshwater lake have been observed to occupy different nocturnal vertical positions in the water column depending on the relative timing of moonrise and sunset (Gliwicz 1986). This relative timing was correlated with predator-induced mortality, resulting in changes in zooplankton density with lunar phase (Gliwicz 1986). This study provided in situ evidence that vertical migrators respond to the moon and that this can alter their mortality; however, nocturnal light levels were not measured. Hernandez-Leon et al. (2001) similarly found a lunar cycle in zooplankton biomass that they attributed to changes in predation intensity caused by variation in illumination, but again, illumination was not directly measured. Dodson (1990) provided indirect evidence that lunar light might be

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a controlling factor in vertical migration, with both water clarity and moon phase serving as strong determinants of the extent of migration.

The lack of light measurements in many previous studies of lunar effects on diel migration make it impossible to separate the effects of lunar phase from nocturnal light. The lunar cycle provides a strong, predictable set of environmental cues including tidal water movement and moonlight. Many endogenous cycles including movement, feeding, and reproduction in marine fishes and invertebrates are cued to lunar phase (Neumann 1981; Taylor 1984; Parrish 1999). As suggested by Tarling et al. (1999), moonlight may be a cue for an endogenous lunar rhythm in the process of vertical migration. Thus, to separate the role of nocturnal illumination from lunar phase on diel migration, it is critical that light be measured. Despite the long-standing hypotheses about the role of light in vertical migration, few oceanic studies of migration have measured light levels either in situ (but *see* Kampa and Boden 1954; Roe 1983; Widder and Frank 2001) or at the sea surface (Clarke and Backus 1964; Boden and Kampa 1967; Currie et al. 1969). Previous efforts to measure light during migration have primarily been aimed at examining the effects of changes in sunlight during twilight. Measuring nocturnal light is typically much more challenging as light at the surface from a full moon can be four orders of magnitude lower than that measured at sunrise and sunset and six orders of magnitude lower than full sun (Kaul et al. 1994; Macy et al. 1998). Instruments for making the highly sensitive measurements required to measure nocturnal light are not readily available.

A sound-scattering layer with a unique species composition of myctophids and mesopelagic shrimp and squid is associated with land around the Hawaiian Islands (Reid 1994; Benoit-Bird and Au 2006). This layer undergoes diel migrations with both a vertical (~400 m) and horizontal component (~5 km) and as a result can be found in shallow waters close to shore (Benoit-Bird et al. 2001; Benoit-Bird and Au 2006). These active inshore-offshore migrations (McManus et al. 2008) have been shown to result in increased access to food resources relative to simple vertical migration (Benoit-Bird et al. 2008). It has been hypothesized that horizontal migrations in general, like the vertical migrations they typically accompany, are a strategy for avoiding visual predators while accessing food-rich waters (White 1998), and thus are also likely to be cued by light. The goal of this work was to examine the role of nocturnal light in the nearshore component of the diel migration behavior of the scattering layer surrounding the Hawaiian Islands. Applying models developed to explain the downward movement of animals in response to sunrise (Iwasa 1982), we hypothesize that at night animals attempt to maintain a constant level of light, regardless of nocturnal illumination. Therefore, we predict that animals will migrate substantially closer to the surface and into shallower nearshore waters on nights with low levels of nocturnal light, e.g., new-moon nights, than they will on nights with high levels of nocturnal light, e.g., clear, full-moon nights. To test this hypothesis, the vertical distribution and density of the nearshore component of the

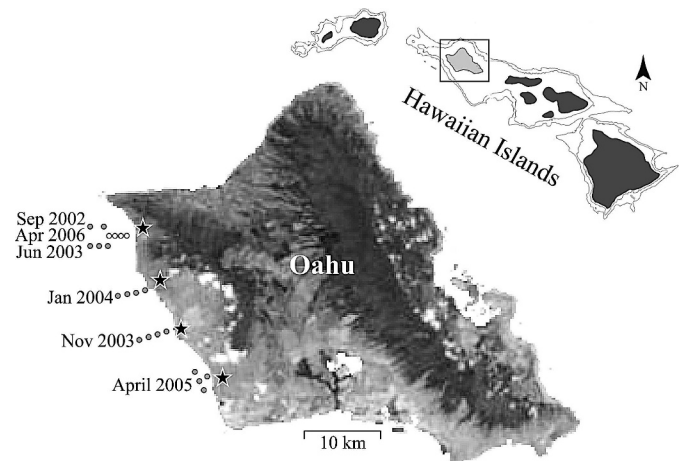


Fig. 1. Upward-looking echosounder moorings were deployed for a complete lunar month, six times over a 5-yr period in various locations off Oahu's leeward coast. The locations of these moorings are indicated by small circles, with filled circles representing custom-built instruments and open circles representing water column profilers. The positions of Nightlight sensors on the shoreline adjacent to each mooring deployment area are indicated by stars.

scattering layer around the Hawaiian Islands were measured using a series of moored, upward-looking echosounders while at the same time nocturnal surface irradiance was measured. Data were collected during six complete lunar months within a 5-yr period.

Methods

Addressing the hypothesis that nocturnal light affects the nearshore component of the diel migration of micronekton around the Hawaiian Islands requires that the previously identified effects of distance from shore and bottom depth (Benoit-Bird and Au 2004, 2006) be accounted for and that small differences in these variables between nights within a lunar month be detectable. To address both of these needs, the density and vertical distribution of the distinctive scattering layer of mesopelagic micronekton off Oahu's leeward coast were assessed from bottom-mounted, upward-looking echosounders deployed over six full lunar months distributed over approximately 5 yr (Fig. 1). During each deployment at least two and typically four of these moorings were deployed to allow the effects at several bottom depths to be examined simultaneously. Nocturnal light was measured near the sea surface using custom-developed and -calibrated light sensors. In addition, during the final two deployments, vertical profiles were made directly over each of the deployed moorings during several lunar phases to provide information on water clarity and the taxonomic and size composition of animals in the sound-scattering layer. Lunar phase information and moon and sun rise and set times for the study sites and times were obtained from the United States Naval Observatory, which is freely available at <http://aa.usno.navy.mil/data/>.

Table 1. Moored echosounder deployments.

Deployment dates	Site	No. of moorings	Deployment depths (m)
02 Sep–27 Oct 2002	Makua	2	75, 150
17 Jun–19 Jul 2003	Makua	3	40, 100, 150
07 Nov–09 Dec 2003	Maili	4	40, 75, 100, 150
17 Jan–19 Feb 2004	Makaha	4	40, 75, 100, 150
20 Apr–27 May 2005	Electric Beach	4	25, 40, 40, 40
09 Apr–16 May 2006	Makua	4	10*, 20, 25, 40

* No scattering layer detected over this mooring.

Echosounder moorings—2002–2005: Each custom-built moored echosounder (Benoit-Bird and Au 2004) consisted of an echosounder circuit board, a microcontroller with an analog-to-digital converter and memory, a clock, and batteries within a pressure housing and an upward-looking transducer. The circuit board from a Computrol Tournament Master Fishfinder NCC 5300 was modified to read the envelope of the echo directly into the microcontroller. The echosounder used a 200-kHz signal with a pulse length of 130 μ s, resulting in a vertical resolution of approximately 20 cm. This signal (200 kHz) was selected as it is the standard fishery frequency most correlated with micro-nekton density in this habitat (Benoit-Bird 2009). A Persistor CF1 microcontroller was programmed to sample 10 echoes (over a total of 5 s) from the sounder every 15 min, from an initial “wake-up” trigger at 18:00 h until 07:00 h local time. Digital alarm clocks, synchronized with each other, triggered the microcontroller within each mooring to begin the sampling regime. An Ocean Embedded Systems CF1 analog-to-digital converter was used to digitize the envelope of the echo at a sampling rate of 10 kHz and saved onto a compact flash memory card. The transducer was mounted on top of a pressure housing, looking upward with a 10° conical beam. The buoyant pressure housing surrounded by syntactic foam was attached to a sacrificial anchor with two acoustic releases (SubSea Sonics AR-60). Each echosounder had an effective range of 156 m, limiting our study to only the shallowest nearshore component of the scattering layer’s migration.

2006: For the 2006 deployment, autonomous 200-kHz echosounders made by ASL Environmental (Acoustic Water Column Profiler) were used in a similar physical setup. All echosounders in 2006 collected one echo every 4 s during the deployment with an effective range of 200 m, but other signal characteristics were identical to the instruments deployed in previous years. For comparative analyses, only the first 10 echoes in each 15-min interval were used.

Calibration—Each echosounder was calibrated using an indirect procedure incorporating a 38.1-mm-diameter tungsten carbide reference sphere as prescribed by Foote et al. (1987). The sphere was held at least 10 m from the transducer to ensure calibration in the far field. Calibrations were conducted once before and once after each deployment. Calibration at a range of distances validated

the accuracy of the hardware-based 40 log R time varying gain in each echosounder. The echosounders were determined to have a threshold of between –85 and –80 dB, well above the minimum volume scattering at 200 kHz from the micronekton scattering layer measured in this area of approximately –50 dB (Benoit-Bird 2009).

Deployment—Moorings were deployed at six different times between 2002 and 2006 for a period of at least 32 d per deployment (Table 1, Fig. 1). These deployments covered four sites along Oahu’s leeward coast ranging from the northernmost beach along this shoreline (Makua) to the southernmost (Electric) beach.

Nightlight sensors—During each echosounder mooring deployment, two small, self-contained sensors called Nightlights capable of detecting the low levels of light found at night were deployed on land to measure the incident light at the ocean’s surface. The sensor consisted of an 8-bit data logger (HOBO H8 4 External Channel Data Logger, Onset Computer), a photodiode (CL705HL, Clairex Electronics), and a 10-M Ω resistor to scale the output range of the diode. The data logger provided power to the photodiode and digitized and stored the output voltage from the diode. The photodiode is sensitive between 400 and 600 nm, with a peak spectral sensitivity at 550 nm, similar to the peak of nocturnal light, which is centered between 550 and 560 nm (Hobson et al. 1981; Kaul et al. 1994). The logger and small circuit board were housed in a small waterproof box with a clear, polycarbonate lid (Otter Box). The photodiode was held securely against the lid with custom-shaped black foam. A small area surrounding the photodiode in the lid was left clear but the surrounding area was painted flat black to minimize reflections.

Nightlight sensors were calibrated against the 554-nm band of a factory-calibrated radiometer (OCR-507-1CSA, Satlantic). However, because the radiometer was not as sensitive as the Nightlight there was only a very short time period, about 15 min at dusk and 15 min at dawn, where there was any overlap between the radiometer and the Nightlight. A tungsten-bulb flashlight with a spectral response curve measured by the radiometer to be very similar to the response curve of sunlight was used as a standard light. On the darkest nights of the study, the flashlight was rigidly mounted 17.8 cm above the sensor of the Nightlight or the radiometer. Various numbers of 2-mm-thick sheets of gray polyethylene were affixed firmly to the head of the light source to provide variable source light

levels, a process that did not change the shape of the radiometer's spectral response curve while it decreased the amplitude of the measured flux. The light attenuation function for the polyethylene sheets at 554 nm was developed using the radiometer and then applied to each Nightlight. The relationship between light level and voltage from the Nightlight sensor was fitted with an exponential function for each sensor, resulting in R^2 values greater than 0.97, allowing the measured voltage to be converted to light in units of $\mu\text{W cm}^{-2}$ with a high confidence. The measured dynamic range of the Nightlight sensor was 1.7×10^{-9} to $12.34 \mu\text{W cm}^{-2}$. The resolution of the Nightlight sensor varied exponentially, with the highest resolution at the lowest levels of light. The saturation value occurred during all daylight hours until approximately 30 min after sunset, providing enough sensitivity and dynamic range for measurements of most nocturnal light conditions.

The Nightlight sensors were deployed on top of the nearest point of land where light from human activities would not contaminate the measurements and instrument security was high, for example the U.S. Air Force Satellite Tracking Station at Makua Beach and Maili Point Beach Park. Light sensors were placed at two distinct sites within these areas to minimize the effect of tampering. Each sensor was mounted to a camouflaged tripod that was anchored with a sandbag. The surface of each sensor was leveled using a circular bubble level. The Nightlights sampled data at 30-s intervals for approximately 1 wk each when they were replaced by duplicate sensors during daylight hours to provide complete coverage during nighttime hours of mooring deployment periods. During the 2005 and 2006 sampling, a single Nightlight was placed on top of the survey vessel. The mean and maximum light levels measured from the shipboard sensor were identical to the land-based sensors during these time periods, confirming the applicability of the land-based sensor data to the entire mooring line over which ship-based sampling was conducted.

In situ profiler measurements—During the 2005 and 2006 deployments, a high-resolution profiler was lowered from the surface to 3 m off the bottom in the areas over each mooring. The profiler was equipped with an SBE-25 CTD (temperature, salinity, pressure), a SBE-43 dissolved oxygen sensor, a WET Labs 530-nm, 25-cm path-length WetStar Transmissometer, a Biospherical photosynthetically active radiation sensor, an optical plankton counter and Tracor acoustic profiling system for assessing zooplankton, and a low-light camera system to identify micronekton and measure animal size as well as the numerical density of animals (Benoit-Bird and Au 2006). During both 2005 and 2006, sampling was conducted continuously from 20:00 h to 03:00 h local time. Vertical casts with the profiling package were carried out over each of the four mooring sites repeatedly throughout the night. The location of the first profile each night was randomized.

During the 2005 deployment, four 3-night shipboard surveys were conducted in the area of the mooring array coinciding with a full moon (23–25 April; 22–24 May), new

moon (07–09 May), and first-quarter moon (15–17 May). During the 2006 deployment, three 3-night shipboard surveys were conducted in the area of the mooring array. The overnight shipboard surveys coincided with a full moon (13–15 April), new moon (26–28 April), and third-quarter moon (12–14 May).

Data analysis—The 10 echoes collected in each 15-min interval were averaged for each mooring before they were thresholded at a value of -80 dB. The edges of the scattering layer were then defined by using the Webster (1973) sliding window technique described in Benoit-Bird and Au (2003). Briefly, the mean scattering intensity in two 1-m vertical windows were compared using a one-tailed t -test before sliding the windows deeper in the water column and repeating, progressively changing the α level using the Bonferroni method (Legendre and Legendre 1998). This approach defines the edges of discontinuities in scattering intensity, marking the top and bottom edges of the scattering layer. It should be noted that the scattering features were typically highly distinct from the surrounding water column and could be easily identified by eye. However, this approach allows automated detection, which is important in a large data set.

The minimum depth of the scattering layer each night at each mooring was identified. The time this minimum was achieved ranged from 22:30 h to 01:45 h local time. The maximum depth, area scattering, and mean density were also measured at the time the minimum layer depth was observed. Density of micronekton in the scattering layer was calculated using an echo-integration approach (MacLennan and Simmonds 1992) using the acoustic cross-section of a 4.5-cm myctophid, the mean size of the most abundant animal observed in the camera profiles between 22:30 h and 01:45 h during the 2005 and 2006 studies.

To determine if the scattering layer's vertical movement was adequately described by data collected at 15-min intervals, the 2006 data were reanalyzed using the entire data set, collected at 4-s intervals rather than only the first 10 echoes in each 15-min interval. Data were averaged over 10 echoes to provide true volume scattering estimates before the minimum depth was determined. The maximum depth, area scattering, and mean density for the interval each night that the minimum scattering-layer depth was achieved were also analyzed. These values were then compared with those obtained at 15-min intervals using paired t -tests.

Data from the Nightlight sensors were visually analyzed for any anomalies that might be caused by man-made light sources, typically visible as sharp spikes above the instrument's ceiling of $12.34 \mu\text{W cm}^{-2}$. These data and data from before sunset and after sunrise were removed before further analysis. The maximum light value each night was identified and the mean light value from 30 min after sunset to 30 min before sunrise was calculated for each night.

Predictions about the minimum depth of the scattering layer over the lunar cycle were made relative to the depth achieved during the night of the new moon at the same mooring using the equation derived from Beer's law

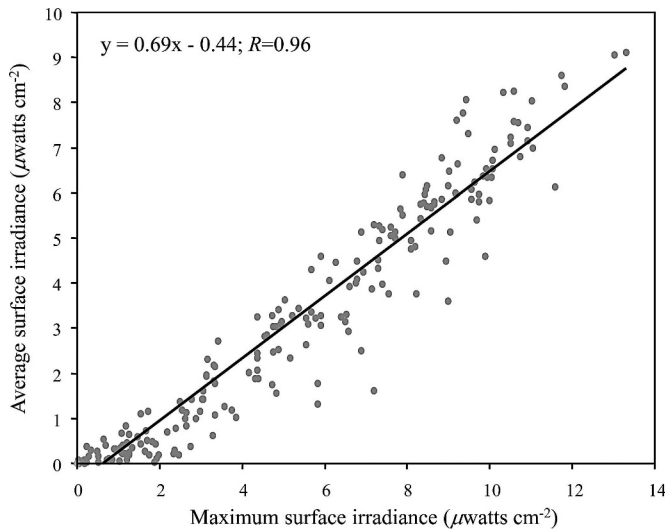


Fig. 2. The relationship between average and maximum nocturnal surface irradiance on each night of the mooring deployments as measured with the Nightlight sensors.

$$\Delta z = (\ln[I_0/I_x])/K \quad (1)$$

where Δz is the predicted change in the depth of the scattering layer, I_0 is the maximum (or mean) measured surface irradiance during the night of the new moon, I_x is the maximum (or mean) measured surface irradiance during the night to be predicted, and K is the diffuse attenuation coefficient. For the analysis here, K was conservatively estimated as the maximum value of beam attenuation measured by the 530-nm transmissometer from the surface to the maximum depth of the scattering layer in the area of the moorings during the 2005 and 2006 study periods (0.05 m^{-1}). An ANOVA showed no significant effect of study year (and its covariate site), mooring depth, or lunar phase on mean or maximum beam attenuation measured from the surface to the bottom of the scattering layer ($p > 0.05$ for all comparisons), supporting the use of a constant value for K . Because it is likely that the selection of K in this way underestimates the predicted depth change, this is a minimum prediction of the depth change expected on the basis of light. These predictions were compared with the measured difference in the minimum depth of the scattering layer at each mooring over the lunar cycle. Because of the uncertainty in K , this equation was rearranged to use the measured depth change and the measured surface light values to predict the K necessary to account for the observed changes in scattering-layer depth if it were driven primarily by light as hypothesized.

Results

Surface irradiance was quantified using two different parameters: peak light level on a given night and mean light level between 30 min after sunset and 30 min before sunrise. These two levels of light were highly correlated (Fig. 2), with the mean surface light level averaging about 66% of the peak surface light level. Because of this strong

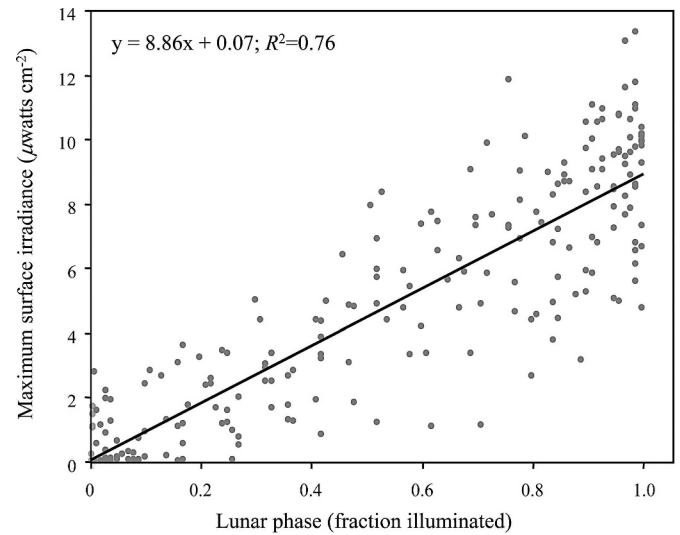


Fig. 3. Maximum nocturnal surface irradiance measured by the Nightlight during each night of the mooring deployment as a function of lunar phase, which is represented as fraction of the moon's face illuminated. Lunar phase data are from the U.S. Naval Observatory.

relationship, either value could be used to examine light effects. Light level was also correlated with lunar phase. Peak surface light level is shown as a function of the fraction of the moon illuminated, a graded measure of moon phase, in Fig. 3. Lunar phase explains about 76% of the variability in peak surface light level and about 70% of the variability in average light level. The remaining variability is likely explained by a combination of cloud cover, moonrise and -set times, changes in moon azimuth and range from the earth, and similar changes in bright stars and other celestial bodies. Variability in light that is not accounted for by lunar phase permits the effects of light and lunar phase to be separated and provides an estimate of the effect size that should be expected.

Data from the low-light camera system during the 2005 and 2006 study periods showed that the scattering layer over the moorings was composed of myctophid fishes with densities measured with the camera system ranging from 2 to 194 fish m^{-3} with a mean individual length of 4.5 cm. These densities compare well with density estimates from the acoustic moorings during the same time intervals, which ranged from 1 to 235 fish m^{-3} . There was a strong, positive correlation between the densities measured with the two techniques, with $R = 0.94$ ($p < 0.01$) providing validation that the acoustic scattering is being correctly attributed to mesopelagic micronekton. Density, species composition, and mean animal size are consistent with acoustic and image data reported from several other months of the year off Oahu's leeward coast (Benoit-Bird and Au 2006; Benoit-Bird 2009).

Paired analysis of the 2006 data using t -tests revealed that there was no significant difference at the $p = 0.05$ level in minimum layer depth ($t = -0.25$, $df = 703$), maximum layer depth ($t = 0.97$, $df = 703$), area scattering ($t = 1.03$, $df = 703$), or mean density ($t = -0.76$, $df = 703$) between full-resolution data and data sampled at 15-min intervals.

This suggests that for these parameters, 15-min intervals adequately sample the migration of this scattering layer. For all further analyses, only the 15-min interval data are included.

An ANOVA showed that there was a significant ($p < 0.05$) effect of bottom depth on layer minimum depth ($F_{5,687} = 3529$), layer depth change ($F_{5,687} = 23$), layer maximum depth ($F_{5,687} = 15,142$), layer thickness ($F_{5,687} = 819$), area scattering ($F_{5,687} = 942$), and animal density ($F_{5,687} = 384$). There were no significant effects of deployment ($df = 5,685$; $p > 0.05$ for all comparisons), nor were there significant interaction effects between bottom depth and deployment site ($df = 7,685$; $p > 0.05$ for all comparisons). For further analyses, deployments were pooled; however, depth was considered a separate independent variable.

The hypothesis posed in this study, that migrating animals maintain themselves at a constant level of light from one night to the next, can be examined by using surface light levels and a simple estimate of light transmission in the water column to predict the depth change of the scattering layer at each mooring location over a lunar cycle and comparing the predicted depth change with the observed depth change. Figure 4 shows this relationship using the maximum surface illumination. Although the predicted depth change explains 40% of the variability in the observed change in depth using the peak light level and 44% of the variability using mean light level (not shown), the observed depth changes are approximately an order of magnitude less than those predicted. An alternative way of examining this relationship is to determine the value of K that would be needed for surface illumination to explain the observed depth changes. Excluding the new-moon days used as a baseline for migration measurements, these predicted K -values ranged from 0.4 to about 400, with a mean of 5.1, orders of magnitude higher than the maximum measured beam attenuation coefficient during the 2005 and 2006 studies. These data show that the scattering layer occurred at higher levels of nocturnal light than expected from the depth of the layer observed during the new moon.

A more general form of the hypothesis is that animals migrate substantially closer to the surface and into shallower nearshore waters on nights with low nocturnal light levels than they do on nights with high levels of nocturnal light. Support for this hypothesis in relation to the horizontal component of the diel migration of the nearshore scattering layer comes from moorings at bottom depths of 20 and 25 m. At the 25-m moorings deployed in 2005 and 2006, the scattering layer was not observed on the night of the full moon or the nights immediately preceding or following it, despite being observed at the 40-m moorings during these studies. The full moon was observed twice during each of these study periods. During the 2006 study, the only one including a 20-m mooring, the scattering layer was not observed on the seven nights surrounding the first full moon observed in the study or on six nights surrounding the second full moon observed during the study. Again, the scattering layer was observed at the 40-m mooring during all nights of the study.

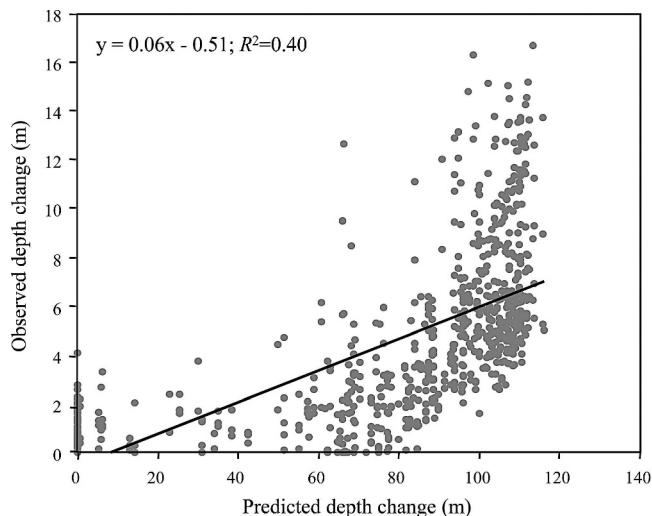


Fig. 4. Predicted vs. observed depth change of the scattering layer. The minimum depth of the scattering layer measured over each mooring during the new moon was used as a baseline value and was compared with the minimum depth achieved by the scattering layer at the same location on nights during other moon phases. The predicted depth change was calculated by combining the maximum nocturnal surface irradiance during the new moon with the maximum surface irradiance on nights of other moon phases and an estimate of the diffuse attenuation coefficient from measurements of beam attenuation during the 2005 and 2006 at-sea sampling.

The role of light in changing the extent of the vertical migration of the scattering layer in nearshore waters is examined in Fig. 5. The minimum observed depth of the scattering layer was 3.1, 3.0, 4.7, 9.3, 17.2, and 47.3 m at 20, 25, 40, 75, 100, and 150 m, respectively. The shallowest depth of the scattering layer at a given location was always achieved on the night of the new moon, though often the scattering layer had a similar minimum depth on the nights around the new moon. In Fig. 5, peak light level is shown on the x -axis, whereas the y -axis shows the difference in the minimum depth of the scattering layer on a given night compared with the minimum depth of the scattering layer on the night of a new moon at the same mooring in the same lunar month. This normalizes the data to the depth of the scattering layer at a given location to examine the change in migration rather than its absolute depth. The maximum surface light level predicts between 64% and 78% of the variance in the change in the scattering layer's depth, depending on the depth of the mooring. Because of the strong correlation between maximum and mean surface irradiance, the relationships are quite similar for mean surface light levels (not shown).

To support the hypothesis that light is the cause of the changes in vertical migration observed, it is necessary to examine the relationship between lunar phase and changes in the scattering layer's depth. On the basis of the relationship between lunar phase and light shown in Fig. 3, we expect that lunar phase will explain variance in scattering-layer depth changes about 75% as well as light, resulting in explanatory power between 48% and 59%. The relationship between lunar phase and scattering-layer depth

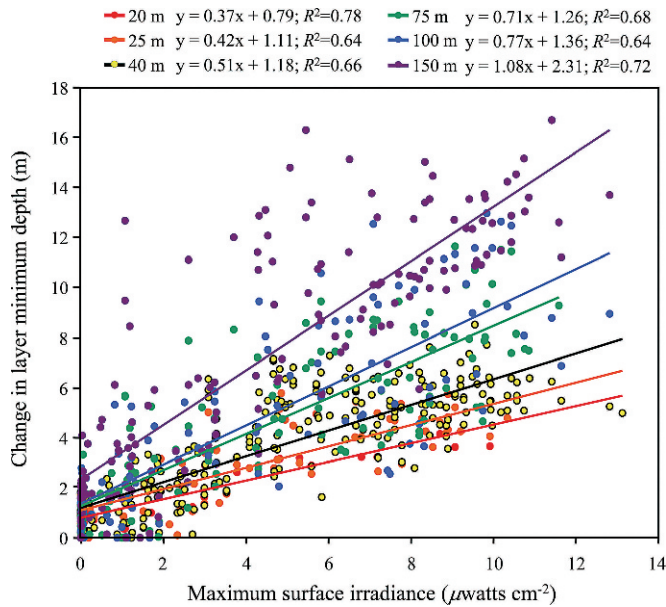


Fig. 5. Change in layer depth relative to the minimum depth of the layer achieved during a new moon as a function of maximum nocturnal illumination. Each seafloor depth where moorings were deployed is indicated by a separate linear regression.

changes is shown in Fig. 6. Contrary to our predictions, lunar phase explains between 74% and 92% of the variance in layer depth change. The variance explained by lunar phase is higher than that explained by maximum surface irradiance for all bottom depths, with an improvement in explanatory capability of 4% to 26%.

Multiple linear regression was used to examine the relative roles of nocturnal light and lunar phase on changes in the vertical positions of Hawaii's nearshore scattering layer. The results are summarized in Table 2A. The R^2 -values show the predictive capability of a linear regression model containing the variable in that row combined with the variables in the preceding rows. The R^2 change shows the contribution to predictive capability of adding that variable. Values of the standardized regression coefficient, β , show how strongly each predictor value influences the changes in the scattering-layer depth within the complete regression model, with higher values representing a stronger effect. Probability values of these coefficients are indicated. Finally, a backward selection approach was utilized and the effects of removal of each variable in the model on predictive capability tested. The variable "mean surface light" can be removed without significantly affecting the predictive capability of the regression model, but the removal of all other variables has a significant effect.

Multiple linear regression was similarly used to examine the effects of nocturnal light and lunar phase on other characteristics of the scattering layer's migration. These results are summarized in Table 2B–E. These can all be interpreted in the same manner as described for Table 2A. For scattering layer thickness and mean animal density, both maximum and mean light could be removed as an effect without significantly affecting the predictive capability

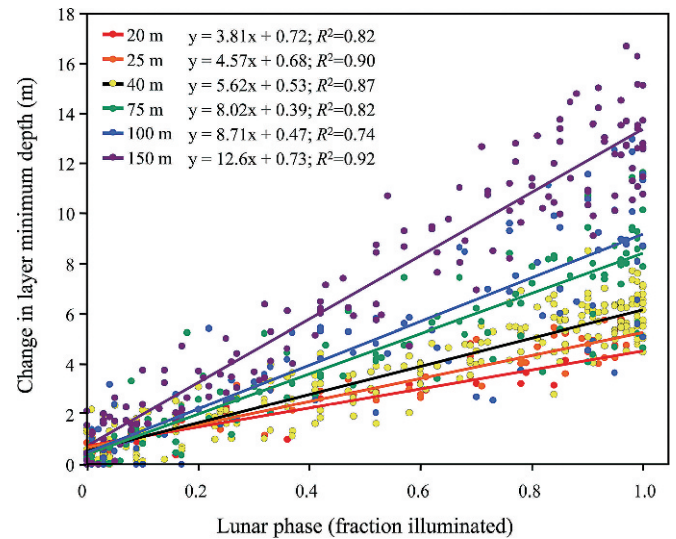


Fig. 6. Change in layer depth relative to the minimum depth of the layer achieved during a new moon as a function of lunar phase. Lunar phase is represented by the fraction of the moon's face that was illuminated. Each seafloor depth where moorings were deployed is indicated by a separate linear regression.

ity of the regression model while lunar phase and depth added significantly to predictive capability. The maximum layer depth and layer area scattering, however, were affected only by bottom depth. These factors are all interrelated as shown in an example from a single mooring in Fig. 7. Because the depth of top edge of the scattering layer changes significantly over the lunar cycle while the bottom edge of the scattering layer does not, scattering-layer thickness decreases with increasing fraction of moon illuminated. Layer area scattering, a water-column integrated measure of acoustic scattering, is not affected by lunar phase, suggesting that the number of animals in the layer does not change with lunar phase. However, because layer thickness changes with lunar phase, the volume the individual animals are found in does change, resulting in an increasing density of animals with increasing fraction of moon illuminated despite a lack of change in animal numbers. This relationship between layer thickness and mean animal density within the layer is shown for each mooring depth in Fig. 8. Only at 150 m was the relationship between layer thickness and layer density not significant at a probability level of 0.05. At all other depths, there was a strong and significant negative correlation between layer thickness and animal density.

Discussion

The goal of this work was to examine the role of nocturnal light and lunar phase in the nearshore component of the diel migration of the scattering layer surrounding the Hawaiian Islands. To address this, we used a series of upward-looking echosounder moorings to observe the scattering layer and sensitive yet inexpensive light meters to measure the nocturnal illumination just above the sea surface. During two of the six full lunar cycle deployments,

Table 2. Results of multiple linear regressions for changes in scattering layer characteristics.

Factor	R^2	R^2 change	Standardized β for factor in complete model	p -value of β	Backward criterion of F
(A) Change in scattering-layer minimum depth					
Seafloor depth	0.18	0.18	0.43	<0.01	<0.05
Maximum surface light	0.69	0.51	0.11	0.05	<0.05
Average surface light	0.69	0.00	-0.07	0.28	>0.1*
Lunar phase	0.80	0.12	0.75	<0.01	<0.05
(B) Scattering-layer maximum depth					
Seafloor depth	0.93	0.93	0.97	<0.01	<0.05
Maximum surface light	0.93	0.00	-0.05	0.27	>0.1*
Average surface light	0.93	0.00	-0.03	0.31	>0.1*
Lunar phase	0.93	0.00	0.02	0.49	>0.1*
(C) Scattering-layer thickness					
Seafloor depth	0.79	0.79	0.89	<0.01	<0.01
Maximum surface light	0.83	0.04	-0.09	0.18	>0.1*
Average surface light	0.83	0.00	0.05	0.36	>0.1*
Lunar phase	0.84	0.01	-0.20	<0.01	<0.01
(D) Layer area scattering					
Seafloor depth	0.16	0.16	-0.40	<0.01	<0.01
Maximum surface light	0.16	0.00	-0.03	0.84	>0.1*
Average surface light	0.15	0.00	-0.04	0.77	>0.1*
Lunar phase	0.16	0.00	0.11	0.14	>0.1*
(E) Layer mean animal density					
Seafloor depth	0.52	0.54	-0.72	<0.01	<0.01
Maximum surface light	0.57	0.49	-0.12	0.25	>0.1*
Average surface light	0.57	0.00	0.05	0.6	>0.1*
Lunar phase	0.60	0.03	0.33	<0.01	<0.01

* Does not contribute significantly to the model and can be removed.

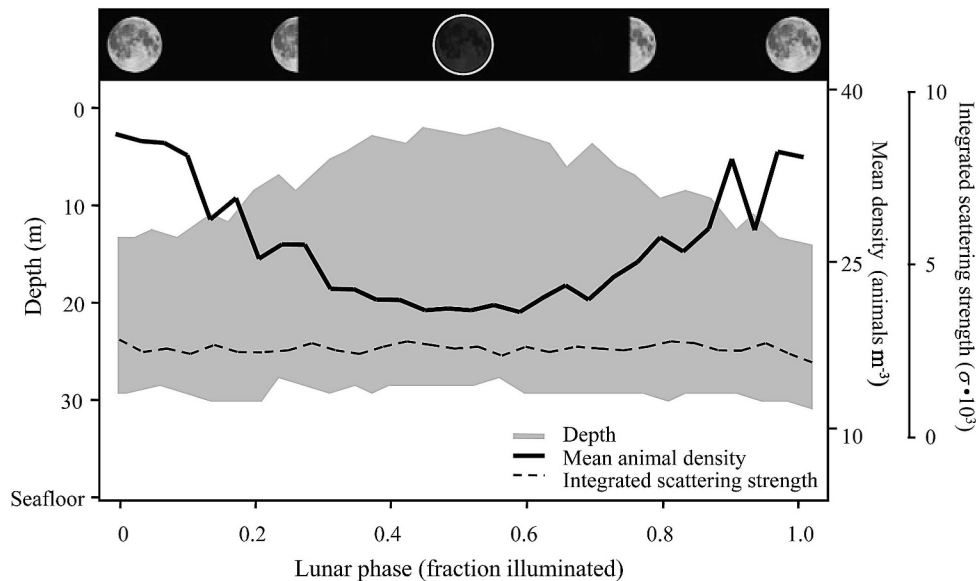


Fig. 7. An example from the 40-m mooring during the 2006 study showing layer depth, area scattering, and mean animal density as a function of lunar phase. A multiple linear regression on the full data set showed that layer minimum depth, thickness, and density were significantly affected by lunar phase, whereas layer maximum depth and area scattering, a measure of the total number of animals, were not.

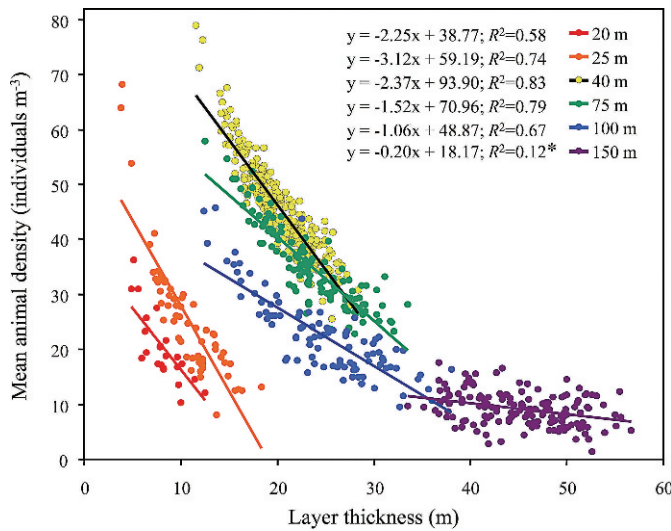


Fig. 8. Layer mean density and layer thickness at each mooring depth were negatively related. All relationships were significant at $p = 0.05$ except at 150 m, highlighted by an asterisk.

a transmissometer was used to assess water clarity while a low-light imaging system was used to confirm the identity of animals in the scattering layer. The photodiode in the light sensor and the transmissometer were selected to match the peak wavelength of moonlight, which is also quite similar to the peak visual sensitivity of myctophids (O’Day and Fernandez 1976) and many other fish species (Lythgoe 1988). This matching of optical wavelength is critical for the interpretation of the effects nocturnal light on diel migration. Important for the separation of light from lunar phase was the observation that significant variation in light level could not be accounted for by lunar phases alone (Fig. 3).

The first hypothesis examined in this work was that migrating micronekton attempt to remain at a constant level of light or isolume regardless of nocturnal illumination. This was tested by examining the change in the layer’s minimum depth at each mooring each night relative to the night when the shallowest layer depth was achieved, the night of the new moon. This was complemented by measurements of the light level incident at the sea surface and an estimate of the water’s attenuation coefficient from transmissometer measurements to predict the depth change of the scattering layer if the animals were to remain at a constant light level throughout a lunar month. On the basis of the maximum light levels measured each night, changes in depth of up to 116 m were predicted. Observed changes in scattering-layer depth were correlated with predicted changes; however, the observed changes were an order of magnitude smaller than predicted, with a maximum change of about 16 m.

The way light level was predicted throughout the water column might be responsible for the mismatch between the observed and predicted values. Ideally, the light level would be directly measured in situ at the depths of interest (Frank and Widder 1997). However, this was impractical because of the long deployment periods necessary to quantify the effects of lunar cycle and the extremely low levels of light

Table 3. Predicted light decrease experienced by animals at the top edge of the scattering layer due to their downward movement at a full moon relative to a new moon.

Bottom depth (m)	Depth change (m)	Light decrease
20	3.8	17%
25	4.5	20%
40	5.6	24%
75	8.1	33%
100	8.8	36%
150	13.0	48%

present at the surface and thus the high light sensitivity required in a submerged instrument. In the predictions made here, the choice of the attenuation coefficient was made from light transmission measurements during only two of the six mooring deployments and was held at a fixed level, the maximum measured, for all predictions, despite variability in water clarity over the water column. However, predicted depth changes made using actual beam attenuation values from the transmissometer at individual moorings in the 2005 and 2006 studies predicted even greater depth changes because of the conservative choice of the attenuation coefficient used for the predicted depths shown in Fig. 4. An alternative way to quantify the effect of the choice of attenuation coefficient is to identify the value of the attenuation coefficient that would be necessary to account for the observed depth changes if the constant light-level hypothesis were to hold. These values ranged from 0.44 to 442 m⁻¹, with a mean of 5.1 m⁻¹, orders of magnitude higher than the maximum attenuation coefficient measured here. Most of these values are far above the maximum diffuse attenuation coefficient expected in oceanic waters. It is not likely that the choice of attenuation coefficient is responsible for the mismatch between the expected and observed depth changes in the scattering layer’s vertical position.

It is clear that some animals in the scattering layer were found much too close to the surface to be choosing a constant light level throughout the lunar cycle. However, animals did migrate closer to the surface and into shallower nearshore waters on nights with low levels of nocturnal light than they did on nights with high nocturnal light levels (Fig. 5). As a result of these movements, animals decreased the light level around them by 17–48% relative to remaining at the same depth they reached during a dark night (Table 3). We estimate that the light at the top edge of the scattering layer ranged from 1.6×10^{-4} to $8 \mu\text{W cm}^{-2}$ with a mean of $2 \mu\text{W cm}^{-2}$. On the basis of the average values of irradiance for sunlight, the light experienced by these animals at their minimum daytime depth of 400 m (Benoit-Bird and Au 2006) is about $10^{-3} \mu\text{W cm}^{-2}$, about the level at which many visual predators become ineffective (Blaxter 1970). To remain below the threshold light level for visual predation, micronekton would need to remain at about 200 m during a clear night with a new moon. Even in deep waters further offshore, previous studies off Oahu’s leeward coast have shown a minimum

depth of the scattering layer of 75 m during a full moon (Benoit-Bird and Au 2006). During many nights, animals in the scattering layer are exposed to light levels higher than this predation threshold and to levels higher than they experience at depth during the day. However, the observed downward movement of animals during nights with high light levels may provide some protection from visual predators while balancing the need to access food found in shallow water and perhaps the illumination needs of myctophids as visual predators themselves (Salvanes and Kristoffersen 2001).

Nocturnal light does not appear to be the primary factor influencing the diel migration of the scattering layer in nearshore waters. Contrary to our predictions, lunar phase predicted the depth change in the scattering layer significantly better than surface illumination (Fig. 6). This was consistent across all six deployments, suggesting that the pattern is independent of location along Oahu's leeward coast or time of year, as sampling was across nearly all seasons. Multiple regression analysis showed that bottom depth and both lunar phase and maximum light level contributed significantly to the depth change observed in the scattering layer; however, the correlation coefficient for lunar phase was substantially greater than that for maximum light. The maximum observed effect of light independent of lunar phase can be estimated using these correlation coefficients. At the highest light levels measured, light amplified the observed lunar phase effect by approximately 2 m. This represents a 20% increase in scattering-layer depth over the depth change caused by lunar phase alone, indicating that animals in the scattering layer are indeed sensitive to nocturnal illumination. Overall, changes in scattering-layer depth were most pronounced in deeper water and appeared to be suppressed in shallower waters, potentially by the seafloor as the bottom edge or maximum depth of the scattering layer remained the same at a given bottom depth regardless of lunar phase or light level.

As a result of the bottom edge of the scattering layer remaining constant while the top edge or minimum depth changed with lunar phase, the thickness of the scattering layer also changed with lunar phase, with the layer much thinner during the full moon than during the new moon. However, the area scattering, an integrated measure of acoustic scattering, remained constant, suggesting that the number of animals migrating remained constant throughout the lunar cycle at all light levels. With the same number of animals found over each mooring over the lunar phase but a change in layer thickness with lunar phase, the density of animals also showed a strong lunar phase effect. During the full moon, the scattering layer was significantly thinner vertically and had a higher density of animals than during a new moon. This "packing effect" is likely caused by animal avoidance of the seafloor and the surface, similar to the packing observed as the layer moves into shallow water from offshore (Benoit-Bird and Au 2004). This effect is indicated by the significant effect of bottom depth on both layer thickness and density; however, with increasing lunar illumination, the avoidance of the surface increases, further concentrating animals in mid-water (Figs. 7, 8).

Neither layer thickness nor mean density was significantly affected by either mean or maximum light levels.

Lunar phase was also observed to have an effect on the inshore extent of the horizontal component of the diel migration of the scattering layer. At the shallow moorings deployed in 2005 and 2006, the scattering layer was absent on nights surrounding the full moon, whereas it was observed at moorings further from shore. The scattering layer was absent on more nights near and during the full moon at 20 m than at 25 m. This suggests that animals in the scattering layer are abbreviating their inshore migration on nights when there is a full moon. However, although the nights during which no scattering layer was observed in shallow water had high levels of light, similarly high values were also observed on other nights, suggesting a correlation of this abbreviated migration with lunar phase but a less tight coupling with surface irradiance.

The lunar cycle showed strong effects on the scattering layer's migration, which was amplified a small percentage by variations in light level and minimized by the seafloor. However, contrary to our initial hypotheses, the observed changes in scattering-layer migration did not appear to be directly caused by nocturnal light levels. This supports the idea proposed by Tarling et al. (1999) that moonlight may be a cue for an endogenous lunar rhythm in the process of vertical migration rather than a direct cause. One advantage of coupling horizontal migration patterns with the lunar cycle could be correlation with tides to maximize movement by advection, minimizing swimming effort. However, diel migration was not correlated with the timing or direction of the tides during the 2005 and 2006 study periods (McManus et al. 2008). Many reef animals in Hawaii show strong lunar cycles in their behavior and reproduction (Lobel 1978). As the nearshore component of Hawaii's deep scattering layer migrates directly over a coral reef, the coupling of migration to the lunar phase may maximize access to food or dilute predators on nights with high light levels, reducing predation risk. The lunar cycle may also be coupled with changes in predation risk for diel migrators in other ways. For example, spinner dolphins are more abundant in shallow waters during nights with a full moon than during a new moon (Benoit-Bird et al. in press). Risk of predation by these micronekton specialist nonvisual predators would not be affected by light level but is likely to be affected by their abundance. Alternatively, the coupling of migration pattern with the lunar cycle might just be a way to cope with the high variability in light caused by changes in the relative timing of the rise of the moon and sun that has been observed to cause high mortality when not accounted for by diel migrators (Gliwicz 1986).

The observed lunar phase and light effects on migration were relatively small. It is likely that these effects would be difficult to detect from a ship-based sampling program. Because bottom depth was such an important factor, slight displacements of the vessel on repeat transects would cause variability that was not related to lunar phase or light. Shadowing by the vessel and artificial lighting aboard might cause changes in the vertical behavior that would not be expected from the bottom-mounted instruments. A

reanalysis of the 2006 data at 60-min intervals shows that sampling at this rate would be inadequate to describe changes in the scattering layer. Even 60-min interval sampling is highly ambitious for a ship-based program, making it highly likely that the peak of the layer's migration would be missed. Finally, the costs of studying lunar and light effects on migration from a ship have limited many previous studies to a single lunar month or replicates of distinct lunar phases (e.g., full moon, new moon, quarter moon). The use of relatively inexpensive moored sensors that could be deployed at several depths simultaneously using just a few hours of boat time for deployment and recovery solved many of these challenges.

In summary, diel migrators from Hawaii's nearshore scattering layer did not follow isoluminescence in shallow waters at night. A strong effect of lunar phase was observed on the vertical movement, vertical extent, and density of the scattering layer, whereas surface irradiance was only weakly correlated with vertical movement. Limitation of horizontal migration was also associated with lunar phase. This suggests that the pattern observed may represent an endogenous rhythm with the lunar cycle that is amplified by variations in nocturnal light level. However, in shallow water areas, variation in vertical migration is also minimized by the proximity of the seafloor. Despite increased avoidance by the scattering layer of the sea surface during a full moon, the same number of animals migrated near shore each night, resulting in substantial packing of animals through the loss of effective vertical habitat. The loss of vertical habitat has been previously hypothesized to account for the high densities of these micronektonic animals in shallow waters as a result of bottom topography (Benoit-Bird and Au 2004). Packing of animals appears to have both a temporal (lunar cycle) and spatial (bottom depth) component. Movement into shallow, nearshore areas appears to be a critical part of the diel behavior of these micronektonic animals despite the high densities of animals and likely intensified competition that occurred during the full moon and the high levels of light and presumably predation risk that diel migrators were exposed to in this habitat. This is likely because of the greater access to food that these animals experience nearshore relative to offshore at night (Benoit-Bird et al. 2008). The consistent migration of these animals into nearshore waters despite the potentially increased costs associated with high light levels and high densities of potential competitors during the full moon indicates the importance of these nearshore areas to mesopelagic micronekton in Hawaii's nearshore scattering layer.

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