

Echo strength and density structure of Hawaiian mesopelagic boundary community patches

Kelly J. Benoit-Bird^{a)}

Hawaii Institute of Marine Biology and Department of Zoology, University of Hawaii, P.O. Box 1106, Kailua, Hawaii 96734

Whitlow W. L. Au^{b)}

Hawaii Institute of Marine Biology, P.O. Box 1106, Kailua, Hawaii 96734

(Received 18 September 2002; accepted for publication 4 August 2003)

A broadband sonar system and digital camera with strobe lights were mounted on a vertically profiling frame with a depth sensor. The echo strengths and densities of animals within individual mesopelagic boundary community patches were investigated as a function of depth. Time and distance from shore were also investigated. Simultaneous surface echosounder surveys permitted comparison of density estimates from two techniques. Echo strength values suggest nearshore boundary community animals are primarily myctophid fishes, which was confirmed by preliminary photographic evidence. Echo strength varied significantly as a function of distance from the shoreline and time. These measures of echo strength are important for estimating density from a surface echosounder. Density estimates from these revised echo strengths compare well with those made with echo highlight counting, which is independent of echo strength. These density measures suggest that previous density estimates were too low but do not change the conclusions of these studies. Vertical microstructure in density was apparent but animal size and compositional structure was not evident within a patch. Patch edges were abrupt, with no differences in the density or echo strength from patch interiors. These edges were generally straight, with a sharp drop in density to the background density of zero. Estimates of animal size as a function of time provide information about the diel migration patterns of these mesopelagic animals. © 2003 Acoustical Society of America. [DOI: 10.1121/1.1612484]

PACS numbers: 43.30.Sf, 43.30.Ft, 43.30.Vh [WMC]

I. INTRODUCTION

The mesopelagic boundary community in Hawaii is a land-associated sound-scattering layer of small fishes, shrimps, and squids (Reid *et al.*, 1991). This community undergoes diel vertical and horizontal migrations (Benoit-Bird *et al.*, 2001). Near its inshore boundary, the boundary community is heterogeneously distributed with discrete patches forming in areas with lower animal densities (Benoit-Bird and Au, 2003c). The boundary community serves as an important food resource to many predators whose foraging behavior is strongly affected by both the layer's migration patterns and its spatial distribution (Benoit-Bird and Au, 2003b). While patch microstructure, including density and composition, is known to affect the animals within the patch and its predators, previous work has been unable to observe microstructure because of methodological limitations.

Taxonomic composition is probably the most obvious form of microstructure. Because of the large differences in swimming ability of equivalent size fishes, shrimps, and squids (Cowles, 2001; Reid, 1994; Sambilay, 1990; Yatsu *et al.*, 1999), this could have important consequences for predators. The degree of compositional heterogeneity could also have significant effects on mating opportunities and competition for food. Previous work has implied that vertical

stratification in species composition and/or size classes is absent (Benoit-Bird and Au, 2003c). However, the composition of the nearshore component (within 3 km of shore) of the mesopelagic boundary community has not been directly observed.

The spatial distribution of mesopelagic animals by size is obviously important to its predators as it is correlated with the energy content (Benoit-Bird and Au, 2002) and swimming ability (Sambilay, 1990) of these prey items. The differences in swimming ability of mesopelagic animals also affect their potential migration range and consequently, their temporal distribution. In nearshore areas, migration rates of up to 1.6 km/h have been measured (Benoit-Bird and Au, 2003a). These speeds are not likely achievable by the entire size range (1–10 cm) of mesopelagic animals within the boundary community, or by all taxonomic groups. The swimming ability of animals also affects their foraging ability. In particular, the size of animals affects the size (Elnor and Hughes, 1978) and type of prey they can consume (Robinson and Motta, 2002), and how much prey they require to support themselves. Consequently, larger animals probably also produce more waste, which may have important ecosystem level effects (Benoit-Bird and Au, 2003a). Body size also affects the reproductive ability; as in many nektonic marine species, fecundity increases with body size (Gross and Sargent, 1985), and body size is correlated with male mating success (Howard, 1980). The distribution of mesopelagic animals of different sizes has implications for population

^{a)}Electronic mail: benoit@hawaii.edu

^{b)}Electronic mail: wau@hawaii.edu

level processes and for the role of the layer in the nearshore and pelagic ecosystems surrounding the Hawaiian Archipelago.

The density and distribution of mesopelagic animals also has consequences for individual animals, their predators, and their prey. The behavior of predators of mesopelagic boundary community animals can be directly affected by their prey's density and distribution (Benoit-Bird and Au, 2003b). Longer term, these density patterns determine the amount of food the predator can obtain, affecting its growth and survival (Beyer, 1995). The density of mesopelagic animals affects their predation risk (Walter *et al.*, 2000), particularly because some of their predators specifically forage on high densities of prey (Benoit-Bird and Au, 2003b). The impact of mesopelagic micronekton on the zooplankton on which it feeds and the competition experienced by mesopelagic animals are also likely density dependent.

Variability in animal density, size, and composition within a patch is often most noticeable near patch edges (Nakaoka and Izumi, 2000). Animals at patch edges are often different sizes from animals in the interior (Crawford and Jorgenson, 1996), and even sexes can be different within and at edges of patches (Bertiller *et al.*, 2000). Differences in behavior are also often observed in individuals near the edge of patches (Meadows, 2001). These differences in characteristics measured from a snapshot of a patch are probably caused by the influence of position within a group on fitness measures. Animals at the edges often have greater feeding opportunities (Black *et al.*, 1992; Romey, 1995), but also have greater predation risk (Cocroft, 2002; Hamilton, 1971). Grazers have been observed to feed most heavily on patch edges (Clarke *et al.*, 1995), which is also probably a factor with some predators of the boundary community (Benoit-Bird and Au, 2003b). Costs and benefits associated with living "on the edge" can be seen in territorial fish that grow slower and are smaller at group edges, but also have more matings and offspring (Meadows, 2001). In mobile prey, predation risk changes can affect spatial behavior and patch characteristics. For example, some nocturnally active animals avoided patch edges more at full moon when predation risk was higher (Bowers and Dooley, 1993). The need to balance hunger and predation risk affects the distribution of animals within a patch. Changes in characters such as patch shape and size can serve as indicators of changes in this tradeoff as they change the percentage of animals experiencing edge conditions.

The primary technique that has been used to study the distribution of the mesopelagic boundary community and other sound-scattering layers has been acoustics. Downward looking echosounders have been the principal tool employed because of their high spatial coverage with relatively high spatial and temporal resolution. Interpretation of this acoustic data requires information on the acoustic size, or target strength, of the animals. In order to estimate density from volume scattering, the mean target strength of individual animals within the study area must be known (MacLennan and Simmonds, 1992). Within the boundary community, target strength is most strongly affected by the taxonomic identity of the scatterer, i.e., whether the animal is a shrimp, a fish, or

a squid (Benoit-Bird and Au, 2001). A second important factor is the size of the animal; smaller animals have lower target strengths and larger animals have higher target strengths. To calculate animal density using a technique called echo-energy integration, the total volume scattering is divided by the mean target strength for an individual (MacLennan and Simmonds, 1992). Previous estimates of mesopelagic animal density have been conservative, using the highest scattering possible by an individual animal from the mesopelagic layer as the divisor. Differences in animal density might be masked by concurrent differences in animal size and composition, and the limited resolution of downward looking sonars makes observation of microstructure difficult.

The goals of this work were to (1) obtain estimates of the lateral aspect echo strength of mesopelagic boundary community animals; (2) determine how echo strength varies with sampling variables including depth, time, and location; (3) identify taxonomic groups of animals present in the boundary layer; (4) estimate the density of mesopelagic boundary community animals using echo highlight counting; and (5) observe the distribution of mesopelagic animals near patch edges.

II. METHODS

A. Surveys

Acoustic surveys were conducted using a 200-kHz calibrated echosounder system as in Benoit-Bird *et al.* (2001). On each night between 1 and 5 June 2001, one 18-km long transect off the Kona coast of Hawaii was surveyed for 1 h at 2100, 0000, and 0300, local time, from the National Oceanic and Atmospheric Administration vessel, R/V TOWNSEND CROMWELL. Sampling began well after twilight each night and ended before morning twilight. During the sampling, the moon was between 85% and 100% illuminated. Ongoing work has shown a minimal effect of lunar cycle on the overall migration patterns of the nearshore scattering layer (Benoit-Bird and Au, unpublished data). Two transects were located 1.5 km (inshore) from the shoreline and two were located 3.0 km from the shore (offshore). Transects were selected in this way because previous studies have indicated that the effects of distance from the shoreline were significant on the distribution of the scattering layer but bottom topography was not (Benoit-Bird *et al.*, 2001). The order of transects and the direction in which they were surveyed was randomized and no transect was surveyed more than once each night.

Twice along each transect, an acoustically identified patch was further investigated with a vertical transect using both a broadband sonar system and a digital still camera with strobe lights. The sonar transducer, the pressure-housed camera, two strobe lights, and a conductivity, temperature, depth (CTD) sensor were mounted to a profiling frame and lowered at a rate of 0.1 m/min to 70 m. The CTD sent real time depth information through a conductive cable to the surface. This information was simultaneously stored with digitized echo data collected every 0.33 m and still images every 1 m during the entire descent. Temperature and conductivity data in

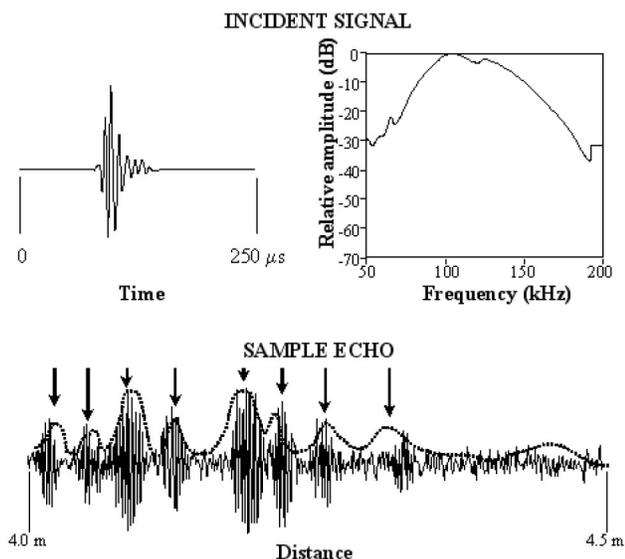


FIG. 1. Waveform and spectrogram of the incident sonar signal. The bottom shows a sample of a resulting echo waveform, solid line, and cross-correlation envelope, broken line. Arrows indicate echo highlights.

this well-mixed area were not found to significantly correlate with acoustic scattering and are not presented here.

B. Broadband sonar

The sonar used a 50- μ s, broadband signal (Fig. 1, bandwidth 35 kHz, center frequency 120 kHz), modeled after a dolphin echolocation click. The outgoing signal was produced using a function generator computer plug-in board. A Rapid System R1200 analog-to-digital (A/D) converter was used to digitize and store the data to hard disk. Sampling rates of 500 kHz were used for the function generator and the A/D converter. This system has a temporal resolution of 3 cm (Au and Benoit-Bird, 2003) and at the peak frequency of the signal, a 3-dB beamwidth of 8°.

C. Camera

A 3.3 mega pixel digital camera in a pressure housing was modified so that it could be controlled from the surface. The flash of the camera triggered two, digital strobe lights. Calibration of the camera system showed that it effectively sampled 0.3–1.3 m from the camera, with an angle of 32°, under these lighting conditions. The total effective sampling volume of the camera system was 0.18 m³.

D. Data analysis

1. Survey data

Survey data were utilized to select focal patches within the boundary layer and place them into a larger context. In particular, this information was utilized to compare the characteristics of the boundary layer to those observed in previous surveys. Echo energy integration (MacLennan and Simmonds, 1992) was utilized as in Benoit-Bird *et al.* (2001) to estimate animal density, and patch geometry was determined as in Benoit-Bird and Au (2003c).

2. Broadband sonar data

The total echo energy in each 0.5-m interval from 2.0 to 6.0 m from the transducer was calculated by taking the ratio of the frequency spectrum of the echo signals referenced to 1 m and the frequency spectrum of the incident signal. The transmitted signal was measured by directing the transducer toward an acoustic mirror made of a 0.64×45×45 cm sheet of aluminum covered with closed-cell neoprene.

The envelope of the cross-correlation between each echo and the incident signal was examined to determine basic time-domain characteristics. The cross correlation function was determined by the Fourier transform technique using the equation

$$c(t) = \mathcal{F}^{-1}[E(f)U(f)] \quad (1)$$

(Brigham, 1988), where $E(f)$ and $U(f)$ are the Fourier transform of the echo and incident signals, respectively, and \mathcal{F}^{-1} denotes the inverse Fourier transform of the terms in the brackets. The envelope of the cross-correlation function was calculated by converting $c(t)$ into an analytic signal using the Hilbert transform method where the absolute value of the analytic signal represents the envelope of the signal (Barr, 2001; Burdic, 1968). Individual highlights, or glints, in the echo waveforms represent distinct surfaces from which sound is reflected. The broadband signal had temporal resolution of 3 cm (Au and Benoit-Bird, 2003), larger than the structures within a single boundary community animal (Benoit-Bird and Au, 2001). Individual highlights probably represent reflections from different animals. At the highest animal densities estimated in previous studies (Benoit-Bird *et al.*, 2001), mesopelagic animals within the boundary community would have an average spacing of 12 cm, much larger than the resolution of the sonar signal. Highlights most likely represent reflections from distinct individuals from within the boundary community permitting echo highlight counting estimates of mesopelagic animal density (MacLennan and Simmonds, 1992). Animal density was calculated in each 0.5-m interval from the transducer.

The average backscatter cross-section in each 0.5-m interval from the transducer was calculated by dividing the total energy within the distance class by the number of individual echo highlights. These values were converted to echo strength for easier presentation. The effects of time, distance from the shoreline, depth, and range from the transducer on echo strength and animal density estimates were analyzed using two univariate analyses of variance (ANOVAs).

3. Camera data

The digital camera produced limited results because of focusing difficulties. This limited the identification of animals in most of the images. However, the number of animals in each digital photo could be analyzed. The rough calibration of the sampling volume of the camera permits approximate estimates of density to be made.

III. RESULTS

Patches observed with the echosounder surveys were not significantly different from those observed during previous

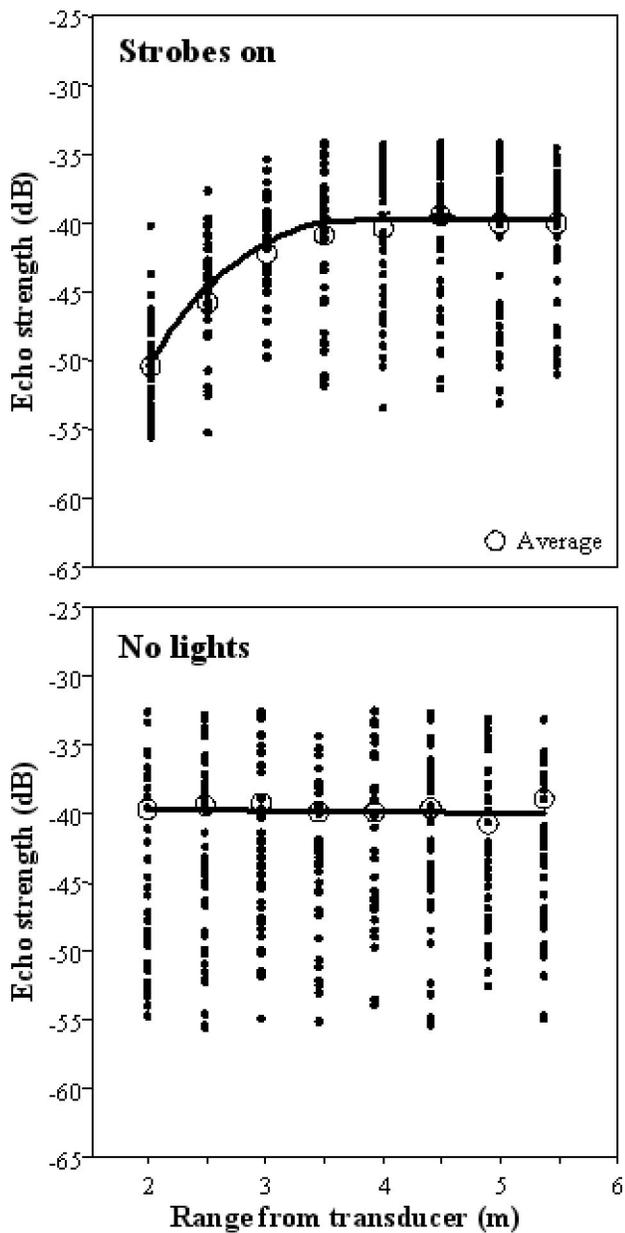


FIG. 2. Echo strength of individual highlights within each 0.5-m interval from the transducer from transects during which the strobe were lights on, top, and those during which strobe lights were not used, bottom.

surveys of the same transects. Both in their geometry and density characteristics, the patches surveyed with the vertical transects were typical of the patches in the remainder of each transect. Patches ranged in horizontal extent from 20 to 110 m. The vertical extent of patches matched the distribution of layer reported in this location by Benoit-Bird *et al.* (2001), ranging from 70 to 100 m. No differences were observed in surface echosounder results when the broadband, dolphin-like signal was used and at other times suggesting there is no strong effect of the signal on the animals in the layer.

Strong light-avoidance effects were observed on the echo strength of mesopelagic animals (Fig. 2). During several transects, no strobe lights were utilized because of equipment failure providing a no-light condition for comparison. The strongest avoidance effects were observed nearest to the transducer with the effect apparently lost at around

TABLE I. Analysis of variance (ANOVA) of between-subject effects on mean echo strength. SS=sum of the squared deviations of scores from their mean (a measure of variability or dispersion), df=degrees of freedom (the number of independent pieces of information available in the estimation of population parameters), MS=mean square (a calculated variance estimate), $F=F$ ratio (an index permitting assessment of the statistical significance), and p =probability where ns=non significant at the 0.05 level.

Source	SS	df	MS	F	p
Time	2576	2	1288	7625	<0.05
Depth	73	69	1	1	ns
Range	15	4	4	34	ns
Distance	1368	1	1368	20484	<0.05
Time*Depth	145	138	1	14	ns
Time*Range	16	8	2	6	ns
Depth*Range	294	276	1	3	ns
Time*Distance	563	2	282	3804	<0.05
Depth*Distance	355	69	5	20	ns
Range*Distance	10	4	3	5	ns
Error	6	1	6		
Total	298 815	1680			

4 m. When the first 4 m from the transducer were ignored, no significant effects of range were observed on mean echo strength (Table I). There was also no significant effect of depth on echo strength ($p>0.05$). Both time and distance from the shoreline had significant effects on echo strength (Fig. 3). There was also a significant interaction of time and distance on echo strength.

The mean echo strength values were relatively high for micronektonic animals. The lateral aspect length-target strength relationships established for these mesopelagic animals by Benoit-Bird and Au (2001) were used to estimate the average size of animals with these echo strengths oriented randomly in the lateral plane relative to the transducer. The variance in target strength in this orientation measured for other fish by Benoit-Bird and Au (Benoit-Bird *et al.*, 2003)

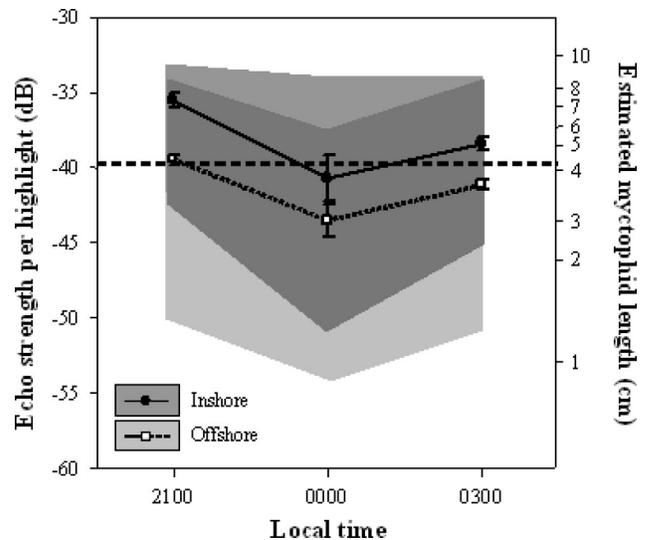


FIG. 3. Mean echo strength from 4 to 6 m from the transducer at each sampling time for inshore and offshore sampling times. Error bars represent the standard error of the mean of the entire vertical range for each of four replicates. Gray areas show the entire range of echo strengths observed with the overlap zone between inshore and offshore in the darkest shade. The dashed line represents the average of all the samples. On the right axis is the estimated length of a myctophid randomly oriented in the lateral plane.

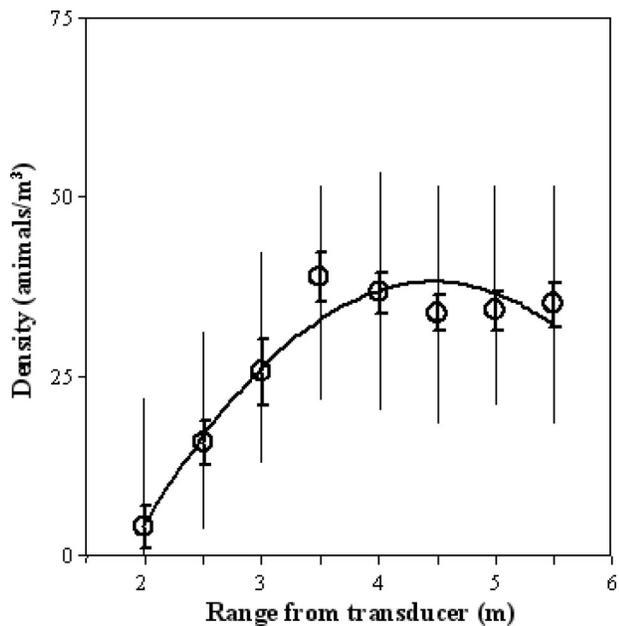


FIG. 4. Mesopelagic animal density at midnight, inshore as a function of distance from the transducer when strobe lights were on. Like echo strength, no range effect was observed when the lights were off. Similar patterns were observed both inshore and offshore at other sampling times. Error bars represent the standard error of the mean while vertical lines show the entire range of each sample.

was used as an estimate of the expected change for myctophids. The measured variation for squid (Arnaya *et al.*, 1989) and shrimp (Imazeki *et al.*, 1989) was utilized. All of the mean lateral aspect echo strengths were too high to have come primarily from mesopelagic shrimps. Only the largest squids in the boundary layer could have produced the echo strengths measured at midnight inshore. All other echo strengths measured were too strong for backscattering primarily from squid. The mean echo strengths measured are estimated to be equivalent to myctophids between 2.9 and 7.3 cm long. While limited, the photographic results support the conclusion that the scattering layer was primarily comprised of fish. Of the nearly 1700 photographs taken, 880 of which were within the acoustically identified layer, only 27 had animals identifiable to taxonomic class. All of the identified animals were myctophid fishes.

Light avoidance was also observed in the density of mesopelagic animals estimated from echo highlight counting (Fig. 4). When the first 4 m were ignored, no significant effect of range from the transducer was observed (Table II). Depth, distance from the shoreline, and time all significantly affected density. Significant interactions between time and depth, time and distance, and distance and depth on echo strength were also observed. The effects of depth, time, and distance from the shoreline on density are shown in Figs. 5 and 6. The mean echo strength at each depth is also shown.

Figure 7 shows the mean density of mesopelagic animals estimated through echo highlight counting as a function of time. Also shown are the mean densities of the same patches measured from the surface using echo energy integration. The target strength value used as the average for the population was -37 dB, the same as that used in previous studies (Benoit-Bird and Au, 2003a, c; Benoit-Bird *et al.*,

TABLE II. Analysis of variance (ANOVA) of between-subject effects on density (all abbreviations are the same as those in Table I).

Source	SS	df	MS	F	p
Time	8903	2	4452	13425	<0.05
Depth	7671	69	111	456	<0.05
Range	68	4	17	29	ns
Distance	874	1	874	1981	<0.05
Time*Depth	6712	138	49	303	<0.05
Time*Range	107	8	13	21	ns
Depth*Range	981	276	4	13	ns
Time*Distance	1873	2	937	1593	<0.05
Depth*Distance	4098	69	59	87	<0.05
Range*Distance	67	4	17	27	ns
Error	8	1	8		
Total	423 931	1680			

2001). Differences in both the density values and the patterns in density were observed between the two estimates. The mean lateral aspect echo strengths measured here were converted to the equivalent dorsal aspect target strength of myctophid fishes (measured by Benoit-Bird and Au, 2001) and used to reestimate the density by echo energy integration. Both the values of the revised density estimates and their patterns fit the echo highlight counting estimates more closely than those based on the fixed target strength from previous studies. The density calculated by echo energy in-

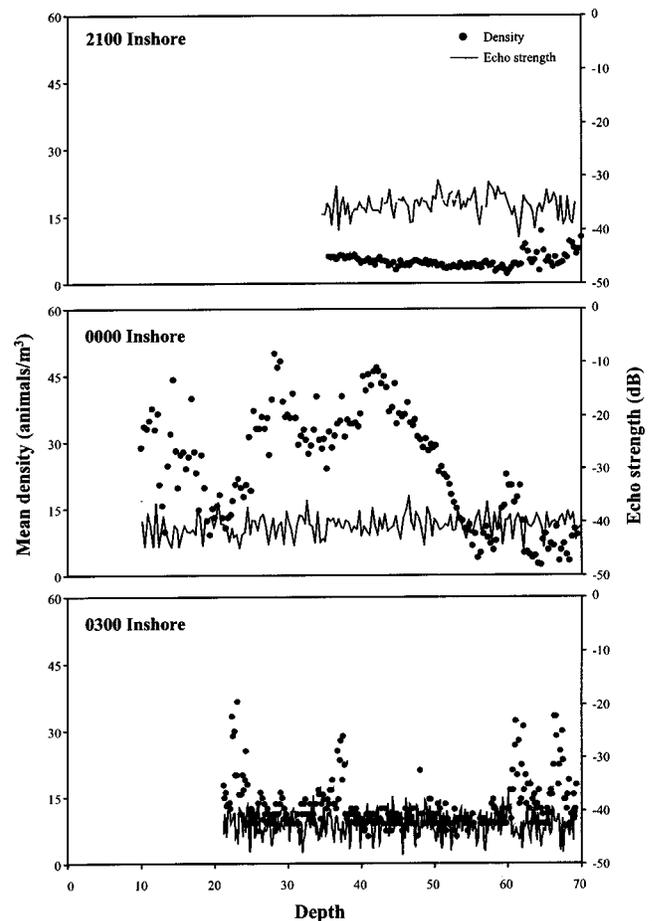


FIG. 5. Mean density from 4 to 6 m from the transducer of mesopelagic animals as a function of depth at inshore sites measured with echo highlight counting. The mean echo strength at each depth is also shown.

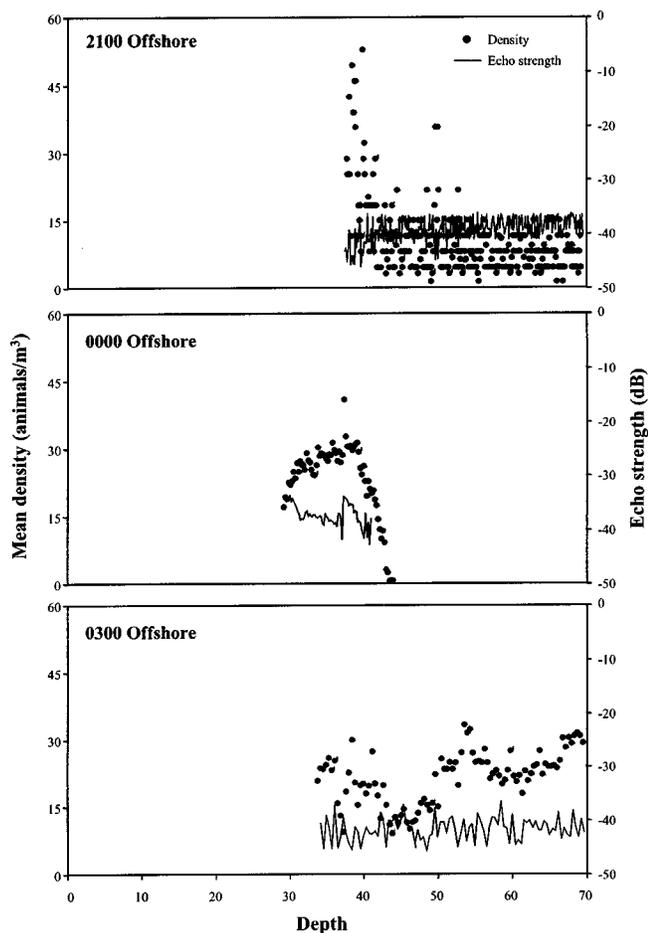


FIG. 6. Mean density from 4 to 6 m from the transducer of mesopelagic animals as a function of depth at offshore sites measured with echo highlight counting. The mean echo strength at each depth is also shown.

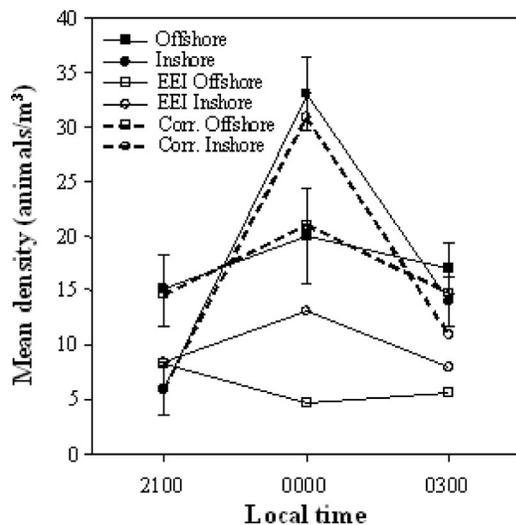


FIG. 7. Mean density of animals as a function of sampling time, measured from 4 to 6 m from the transducer using echo highlight counting from the broadband sonar is shown by the solid lines and filled symbols. Error bars show the standard error of the mean. Open symbols and solid lines show the mean density for the upper 70 m of the same patches estimated with echo energy integration (EEI), using the target strength estimates from previous studies (Benoit-Bird *et al.*, 2001). Utilizing the mean lateral aspect echo strengths measured in this study converted to equivalent dorsal aspect echo strengths to estimate density with echo energy integration greatly improved the density estimates made from the surface (dashed lines).

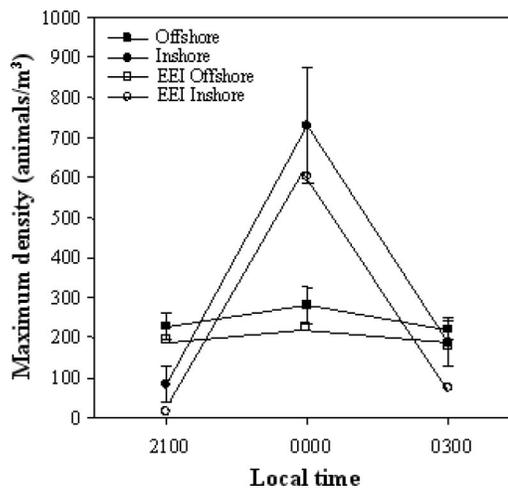


FIG. 8. Maximum density of mesopelagic animals as a function of sampling time and location estimated through echo highlight counting (filled symbols). Error bars represent the standard error of the mean. Open symbols show the maximum density estimated by echo energy integration (EEI) using the fixed target strength from previous studies.

tegration (using the measured echo strengths converted to dorsal aspect) and that calculated from echo highlight counting in each 1-m depth interval for all the vertical transects were compared. The correlation was significant ($p < 0.01$), with a coefficient of 0.81. An F -test revealed that the slope of the relationship was not significantly different from 1 ($p > 0.05$, observed power = 0.85). Figure 8 shows the effect of time on the maximum density of mesopelagic animals. Echo energy integration estimates of maximum density using the fixed target strength value from previous work were more similar to the echo highlight counting estimates than the fixed estimate-based estimates of mean density. Information from underwater photographs was limited. However, preliminary confirmation of the acoustic estimates of density was made by comparing the number of animals predicted from each photograph with the observed number of animals (Fig. 9). The number of expected animals was calculated from the density of animals observed between 2.0 and 2.5 m from the transducer (closest to the range photographed) at the same depth as each photograph. The observed and predicted number of animals were significantly correlated (Pearson correlation coefficient = 0.52, $p < 0.01$).

In seven patches, the edges of patches were observed with the sonar. An example from the patch edge observed for the greatest distance is shown in Fig. 10. Patch edges were very distinct, that is the change in density from within the patch to outside of it dropped dramatically, even over half a meter. Figure 11 shows the density of mesopelagic animals as a function of distance from the edge of the patch both within and outside its boundary. One-tailed t -tests were utilized to compare the density of animals in the 0.5 m nearest the patch edge to their density in the 0.5 m furthest from the edge. Density of mesopelagic animals was not significantly less near the edge of the patch than in the interior of the patch for any of the seven edges observed ($p > 0.05$ for all comparisons).

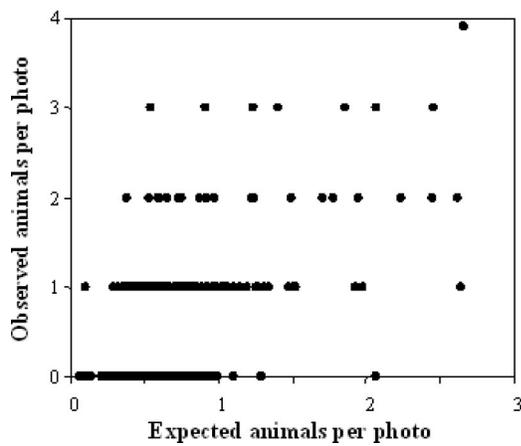


FIG. 9. Number of mesopelagic animals expected based on echo highlight counting density estimates from 2 to 3 m from the transducer, the range closest to that photographed, is shown on the x-axis. The y-axis shows the number of animals counted from a photograph at the same depth. The two variables were significantly correlated (Pearson correlation coefficient = 0.52, $p < 0.01$).

IV. DISCUSSION

Strong light avoidance was observed in mesopelagic animals. Future sampling devices will need to reduce this effect by eliminating light or otherwise reducing its effects. Reduced echo strength for the first 4 m from the transducer was evident. This could be accounted for by a change in animal orientation as animals started to move away from the light source. The end-on echo strength of animals, where their cross-section is smallest, is decreased relative to all other orientations (Benoit-Bird *et al.*, 2003; Martin Traykovski *et al.*, 1998). The decreases in animal density near the transducer suggest that animals are able to respond rapidly enough to move away from the transducer and the lights. However, the continuous increase in density with range from the lights suggests that some animals are able to move further away from the source in the same amount of time. The corresponding increase in echo strength with range from the lights indicates that larger animals are able to make it further. While questions about the orientation of the animals make it impossible to measure the size of the animals within the range of the light effect, this information suggests that animals from a range of sizes are present within the scattering layer, even at one depth. This supports previous conclusions that the mesopelagic boundary community off the Kona coast is not vertically stratified by animal size (Benoit-Bird and Au, 2003c). Further evidence to support this conclusion is provided from the echo strength values from 4 to 6 m from the transducer, where a range effect was no longer detected. No significant effects of depth were observed on echo strength in echoes from this range.

The consistency of echo strength as a function of depth also supports the conclusion that there is no vertical stratification in the species assemblage in the upper 70 m of the nearshore component of the boundary layer. While the low animal densities near the transducer because of light avoidance and photographic difficulties limited the number of images containing taxonomically identifiable animals, all discernable images were of myctophid fishes. In addition, all

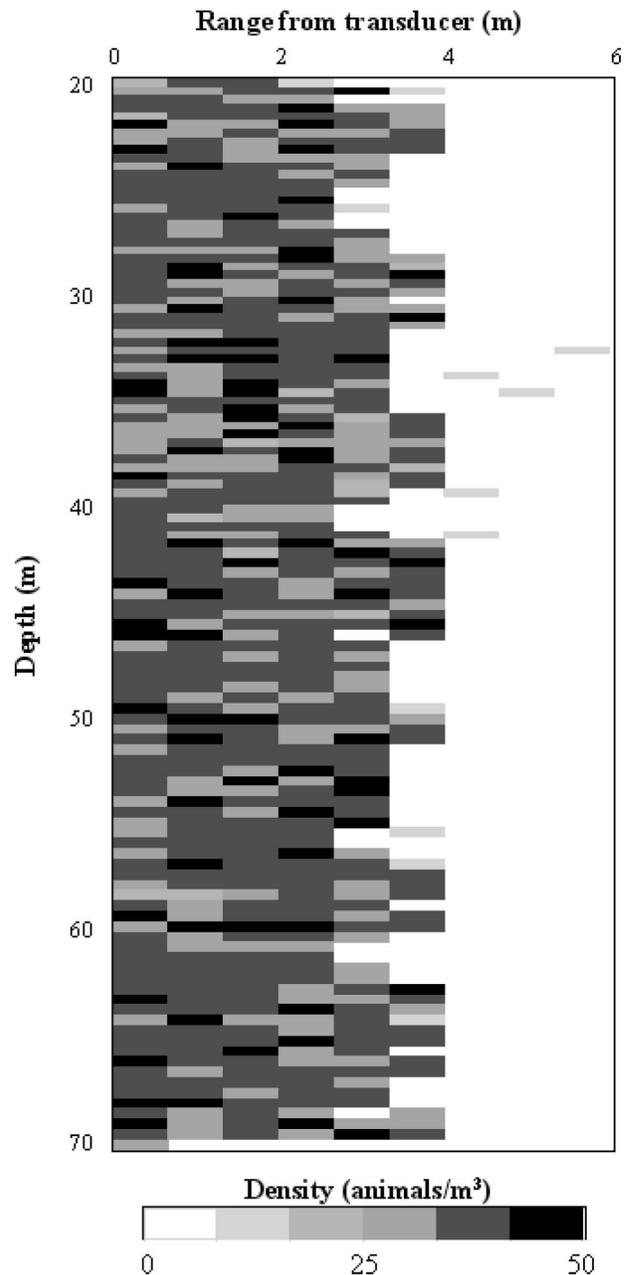


FIG. 10. Sample of animal density estimates from the edge of an inshore patch observed at midnight. The edge of the patch is relatively straight and very distinct in the 50-m depth range over which it was observed.

mean echo strengths were relatively high for micronektonic animals. These echo strengths could only have come from an assemblage of animals primarily composed of fish. While direct observation of composition of the layer was not possible, this is the first evidence of composition of this nearshore boundary layer component. Further offshore, net samples of the boundary layer's upper depths were also primarily comprised of myctophids (Reid, 1994).

While all mean echo strengths were relatively high, echo strength was significantly affected by time and distance from the shoreline. Animals with higher echo strengths, presumably larger animals, migrated inshore and upwards early in the night, before 2100 hours, and were followed by midnight by smaller animals with lower echo strengths. Smaller animals migrated down and away from shore before 0300

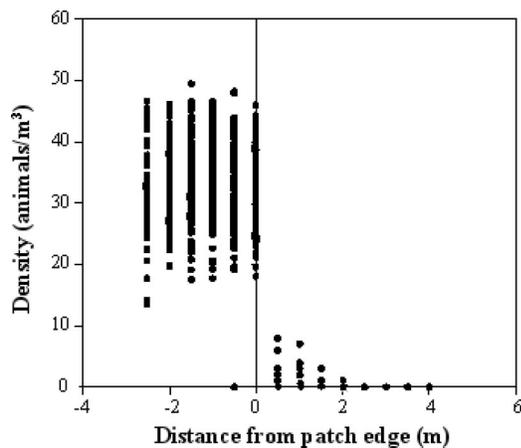


FIG. 11. Density of animal density in each 0.5-m interval near the edge of the midnight inshore patch shown in Fig. 10. Density drops dramatically at the patch's edge. A one-tailed *t*-statistic revealed no significant differences in density between the 0.5 m nearest the patch edge and the 0.5 m furthest from the edge.

hours. The larger, higher echo strength animals migrated down and away from shore later in the morning. Mean echo strength, and presumably animal size, decreased at midnight both inshore and offshore. The variance in echo strength also increased at midnight. This suggests that the mean size of animals near the beginning and end of the migration were larger than those near the midpoint of the diel migration near midnight. Further, animal sizes were larger inshore than offshore at all sampling times. The migration rates of the leading and trailing edges of the boundary layer have been measured at greater than 1.6 km/h. Based on the fin dimensions of myctophids, the smaller animals observed inshore at midnight are not likely capable of sustaining this swimming speed (Sambilay, 1990) while neither the largest mesopelagic shrimps or squids are likely capable of these speeds (Cowles, 2001; Yatsu *et al.*, 1999). The animals of the mean size predicted from echo strengths inshore at 2100 and 0300 hours could easily maintain this rate. The range of estimated animal sizes and the variance of estimated sizes also increased at midnight while the mean size of animals decreased. This suggests that the larger animals that migrated inshore first, before 2100 hours, were still present but were later joined by more, smaller animals. The increase in the density of animals from 0900 to 0000 hours supports this.

Analysis of echo strength provides information about the biological processes at work within the boundary layer. It also provides significant practical information for estimating density. To estimate density with downward looking echosounders requires information on the average acoustic size of targets within the study area. Accounting for all sources of target strength variance such as time, depth, and location is difficult, particularly when animal densities are high and target strength cannot be determined using a split-beam echosounder. While dorsal aspect target strengths cannot be directly measured from the techniques employed here, the effects of sampling variables on echo strength can be assessed. Depth was not found to significantly affect echo strength. However, time and distance from the shoreline did significantly affect echo strength. This means that a single

estimate of target strength can be applied to the upper 70 m of the water column at a specific time and location. However, the static estimate of target strength utilized to estimate density in previous studies introduced error. The lateral aspect echo strengths measured can be converted into estimates of equivalent dorsal aspect echo strengths to estimate the effect of previous methods on the results. Utilizing the revised echo strength measurements confirms that previous density estimates were conservatively low both inshore and offshore, at all sampling times. The changes in echo strength as a function of time also suggests that previous estimates of density differences between midnight and the other sampling times were not large enough. However, these new analyses of density do not affect the major conclusions of these studies, instead they provide further support of the high abundance of animals in this layer.

Animal density was also measured utilizing echo highlight counting, which is independent of echo strength. Preliminary photographic measures confirm these estimates. Echo highlight counting density estimates were remarkably close to those obtained with data from the echosounder at the surface analyzed using dorsal-aspect equivalent echo strengths applied to echo-energy integrations. This method of obtaining *in situ* estimates of patterns in mean echo strength over space and time can be useful for interpreting volume scattering data from an echosounder. The echo highlight density estimates are significantly higher than those obtained previously using fixed-target strength echo-energy integration, however, the conclusions from the estimates are the same. The density patterns as a function of time and distance from the shoreline show the diel, horizontal migration of the mesopelagic boundary community (Benoit-Bird *et al.*, 2001).

Animal density, measured with echo highlight counting, changed not only as a function of time and distance from the shoreline as in previous studies (Benoit-Bird *et al.*, 2001), but also with depth. These animal density patterns were consistent among the four replicates of each treatment. Abrupt spikes in animal density, covering narrow depth zones, were sometimes observed, primarily when the overall animal density was low. When overall animal density was higher, animal density peaks tended to cover a greater range of depths and the changes in animal density were much more gradual. As the entire layer migrated upward from 2100 to 0000 hours, the depths of animal density peaks also moved upward. While vertical microstructure in echo strength was not observed, fine-scale vertical microstructure in animal density was apparent.

Edge effects were not observed in the mesopelagic boundary community. Neither echo strength, related to animal size, nor animal density varied significantly between the patch's edge and the patch's interior for any of the seven patch edges observed. Variance in these characteristics also remained the same. In all cases the density dropped dramatically at the patch edge to an average of zero outside the patch. For all seven patches, the vertical patch edge was nearly straight as observed in previous work (Benoit-Bird and Au, 2003c). This is unusual when compared with studies of other scattering communities (see, for example, Greene *et al.*, 1994). The reasons for this sharp change between the

patch and the background are not clear; however, the result is that the perimeter of each patch is as low as possible for its size. This might reduce the number of animals exposed to edge risks but also reduces the number of animals experiencing its potential foraging benefits. Off the coast of Oahu, a sharp delineation between a high animal density mesopelagic layer and lower density patches was observed (Benoit-Bird and Au, 2003c). Because distinct patches are only found in sites with low animal density while high animal density sites have continuous layers, the distinct edges also suggest a density threshold for mesopelagic animal distribution. These animals could disperse into a continuous layer, reducing the overall density and eliminating edge effects except at the top and bottom of the layer. Maintenance of a threshold density appears to be more important than the avoidance of edge effects.

The microstructure observed within the mesopelagic boundary layer off the coast of Hawaii was similar to that predicted from echosounder surveys (Benoit-Bird and Au, 2003c). Most animals in this nearshore boundary layer appear to be myctophid fishes. Strong effects of time, distance from shore, and depth were observed on density. However, no vertical effect on echo strength was evident, suggesting a lack of stratification in animal size and composition. Depth-dependent animal density patterns provide important information for assessing the impact of the boundary layer and the behavior of its predators. Finally, revision of echo strength values reveals the underestimates of animal density estimates from previous studies, but supports the conclusions of these studies. High animal density sites with continuous layers show strong vertical stratification in echosounder surveys and may produce different results with respect to echo strength and density microstructure. The technique of utilizing a high-resolution, relatively short-range system could provide important information to explain the differences between these sites and assist in the interpretation of echosounder data from these, and other locations.

ACKNOWLEDGMENTS

We thank the National Marine Fisheries Service, Honolulu Laboratory, especially Robert Humphreys for collaborating and providing ship time. The crew of the TOWNSEND CROMWELL, especially Phil White, was instrumental in conducting this research. Christopher Bird assisted in the construction of the underwater camera housing and with field work. K. Benoit-Bird was partially supported by a Leonida Family Fisheries Research Scholarship and an ARCS Foundation award. This work was supported in part by Office of Naval Research Grant No. N00014-98-1-068, Dr. Robert Gisiner, Program Manager. This work was also funded by a grant from the National Oceanic and Atmospheric Administration, Project No. R/FM-7, which is sponsored by the University of Hawaii Sea Grant College Program, SOEST, under Institutional Grant No. NA86RG0041 from NOAA Office of Sea Grant, Department of Commerce. The views expressed herein are those of the authors and do not necessarily reflect the views of NOAA or any of its subagencies. UNIH-SEAGRANT-JC-02-17. This is HIMB contribution 1154.

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