Energy: Converting from acoustic to biological resource units

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Acoustic backscattering strength is often used as an index of biomass; however, the relationship between these variables has not been directly validated. Relationships were investigated between acoustic cross section at 200 kHz, measured as part of a previous study, and measured values of length, biovolume, dry weight, ash-free dry weight, and caloric content of the same individual specimens. Animals were part of the Hawaiian mesopelagic boundary community and included shrimps, squids, and myctophid fishes. The strong relationships found between all the variables measured make it possible to approximate any one variable from the measured values of others within a class of animals. The data show that for these midwater animals, acoustic scattering can be used as an index of biomass. Dorsal-aspect acoustic cross section at 200 kHz predicted dry weight and ash-free dry weight at least as well as did body length, a standard predictor. Dorsal-aspect acoustic cross section at 200 kHz was also a strong predictor of total caloric content. The relationship between dorsal-aspect acoustic cross section and caloric content of Hawaiian mesopelagic animals was linear and additive. Consequently, it is possible to directly convert acoustic energy from these animals to organic resource units without having knowledge of the size distribution of the populations being studied.
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I. INTRODUCTION

The goal of the majority of population and community surveys has been to assess biomass and its distribution. Biomass is measured in many ways: wet weight, dry weight, ash-free dry weight, biovolume, chlorophyll α for primary production, protein for secondary production, carbon, ATP, and energy content (calories). In every case, biomass is a measure of organic resources or available energy. Acousticians and fisheries biologists attempt to assess biomass acoustically, some using acoustic volume backscattering as an index of biomass and sometimes attempting to convert acoustic units into measures of biomass more palatable to the biologists who use this information.

Converting acoustic measurements into biomass estimates requires samples of the population being measured (Claytor *et al.*, 1999). To estimate biomass, standard length–weight relationships (Kemper and Raat, 1997) for the taxa involved are often applied to the acoustic estimates of abundance obtained. The biological samples taken therefore need to represent the length distribution and taxonomic composition of the population examined in the acoustic survey (Bethke *et al.*, 1994). This requires that the collecting gear be unbiased in capturing the objects in the volume of water sampled (Bethke *et al.*, 1994). Such nonselective collection is difficult, if not impossible (Parkinson *et al.*, 1994). The problems associated with converting acoustic energy to abundance estimates have been amply discussed (see MacLennan and Simmonds, 1992). These problems can only be further compounded by using average length–weight relationships that are often plagued by collection biases, limited data, and spatial and seasonal variations. When biological samples of the population surveyed hydroacoustically are not available, volume backscattering is often used as a direct index of biomass (Liao *et al.*, 1999). However, studies directly validating the assumption that backscatter is an appropriate measure of biological energy are rare.

Ideally, we would like to assess biomass through a direct conversion of acoustic energy to units of organic energy without an intermediate step. The goal of this work was to assess the relationship between acoustic energy, measured as part of a previous study, and various measures of biomass taken on the same individuals, including biovolume, dry weight, ash-free dry weight, and caloric energy content. This was an attempt to directly validate the use of acoustic backscatter as a measure of biomass. We also attempted to determine if acoustic scattering can be directly converted to biomass without knowledge of the size distribution of the population being surveyed, at least for animals from the Hawaiian mesopelagic boundary community—a near-shore scattering layer community of small fish, shrimp, and squid (Reid *et al.*, 1991). This is a biological perspective on assessing biomass for this noncommercial animal community rather than a more traditional fisheries acoustics perspective. Ultimately, the units obtained are the same as those estimated in many fisheries acoustics studies; however, our method of converting between acoustic measures and biomass is novel and more direct.

II. METHODS

Trawling for micronektonic animals was conducted using a 2-m opening Isaacs–Kidd midwater trawl (IKMT) during two cruises in May and July of 2000 aboard the NOAA ship TOWNSEND CROMWELL. The trawl was towed obliquely

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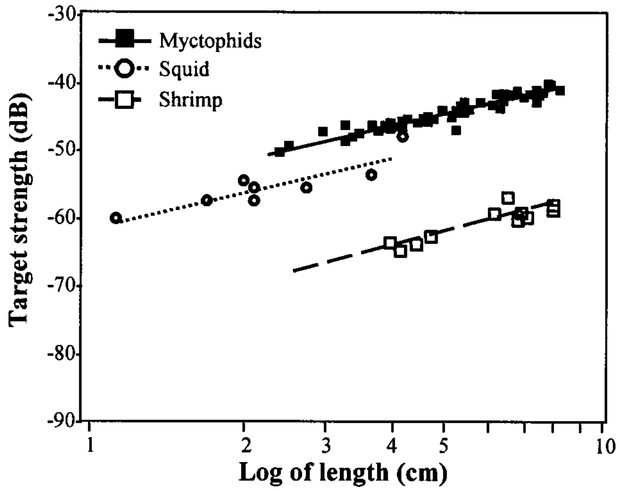

FIG. 1. The relationship between fish standard length, shrimp total length, squid mantle length, and animal target strength (redrawn from Benoit-Bird and Au, 2001).

for 20 to 30 min, reaching a maximum depth of 200 m. The ship was traveling between 3 and 4 knots with wire sent out at 25 m per min. The dorsal-aspect target strengths at 200 kHz, shown in Fig. 1, of the various live animals from the mesopelagic boundary community were measured as part of a previous study (Benoit-Bird and Au, 2001). The standard length of fish (the distance between the tip of the snout and the rear end of the caudal peduncle), the mantle length of the dorsal side of the squids, and the total length of the fish, squid, and shrimp species were measured with vernier calipers to the nearest 1 mm. Animals were then identified to species and frozen for later analysis.

After returning to the laboratory, the displacement volume to the nearest 0.5 ml of each individual animal was measured in a graduated cylinder of appropriate size for the individual. Animals were then homogenized in a small blender with distilled water added to facilitate even mixing. Homogenized samples were freeze-dried to remove all water without allowing the loss of volatile substances (Paine, 1971). Dry weight of the entire sample was then measured and the sample was further homogenized using a mortar and pestle.

Two 10–20-mg subsamples of each fully homogenized animal were compressed into pellet form with a Parr pellet press. Calorie values of the two subsamples were determined using a Kipp and Zonen BD40 Gentry microbomb oxygen calorimeter attached to a chart recorder, using standard methods (Paine, 1966). The samples were run in random order along with three 10–20-mg benzoic acid standards. If two subsamples disagreed by more than 3%, a third sample was run.

The percent of ash of each animal was also determined. Glass filters were heated to 500 °C for 4 h to remove any biological residues, cooled in a dessicator, and then weighed. Two freeze-dried subsamples of each animal were weighed and placed on these preweighed glass filters in aluminum foil dishes. The samples were then heated for 4 hours at 500 °C, cooled in a dessicator, and the sample and filter were weighed. The weight of the filter was then subtracted from

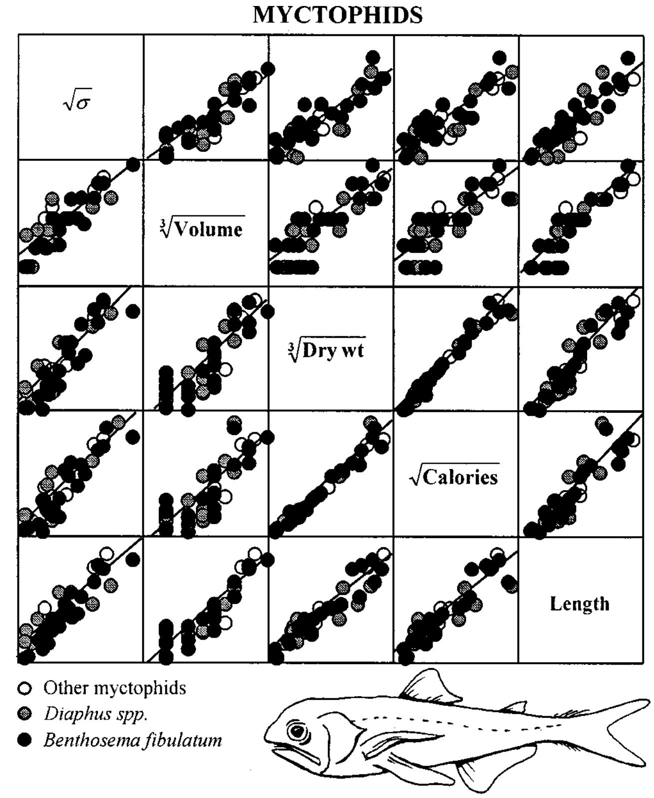

FIG. 2. Matrix of regressions for standardized measures of biomass, fish standard length, and the square root of dorsal-aspect acoustic cross section (σ) of myctophid fish. All possible combinations are shown with each variable as both the x and y axis.

the sample plus filter weight, and the percent of the sample that remained after ashing was calculated.

To examine the relationships between the variables measured, each was standardized into a one-dimensional variable. Acoustic cross section is closely related to the square of the mesopelagic animal's length (Benoit-Bird and Au, 2001); therefore, the square root of acoustic cross section was used for comparison between variables. Because the shapes of animals change roughly the same as length, the cube root of both volume and weight was taken. Calorie content, generally, has between a square and a cubic relationship with animal length (Golley, 1961; Slobodkin and Richman, 1961). To determine which exponent was more appropriate, the relationships of the square root and cube root of caloric content for each group against length were tested. Length predicted the square root of calories better than the cube root of calories in all three animal groups, so the square root was used for comparisons.

III. RESULTS

There was strong colinearity between standardized measures of dorsal-aspect acoustic cross section (σ), volume, dry weight, ash-free dry weight, length, and calories for myctophid fishes (Fig. 2), mesopelagic shrimps (Fig. 3), and mesopelagic squids (Fig. 4). Plots of linear, pairwise relationships of all these standardized variables, except ash-free dry weight, are found in the matrices of these three figures. For example, looking at the box labeled ''Volume,'' the graph above this box shows the cube root of volume on the x axis

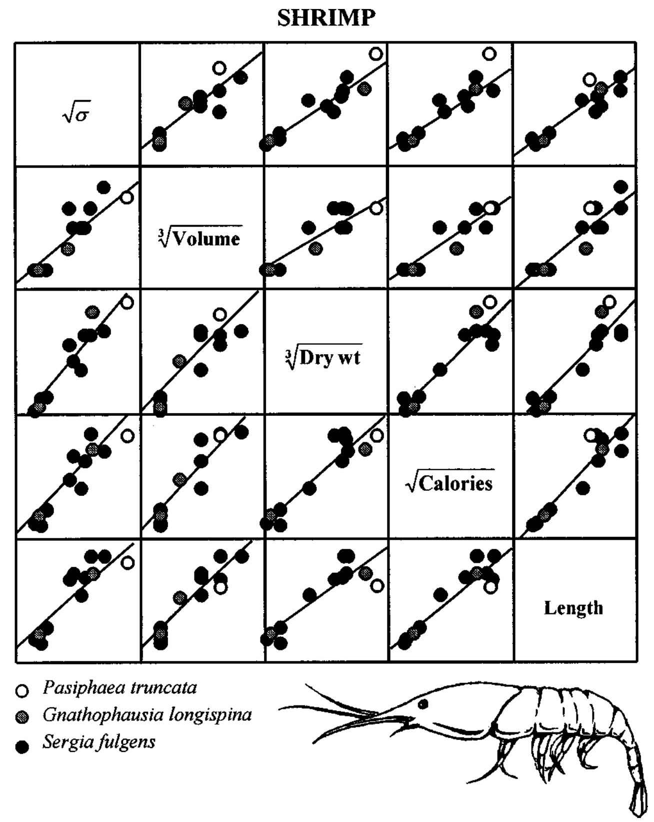

FIG. 3. Matrix of regressions for standardized measures of biomass, shrimp total length, and the square root of dorsal-aspect acoustic cross section of mesopelagic shrimps. All possible combinations are shown with each variable as both the *x* and *y* axis.

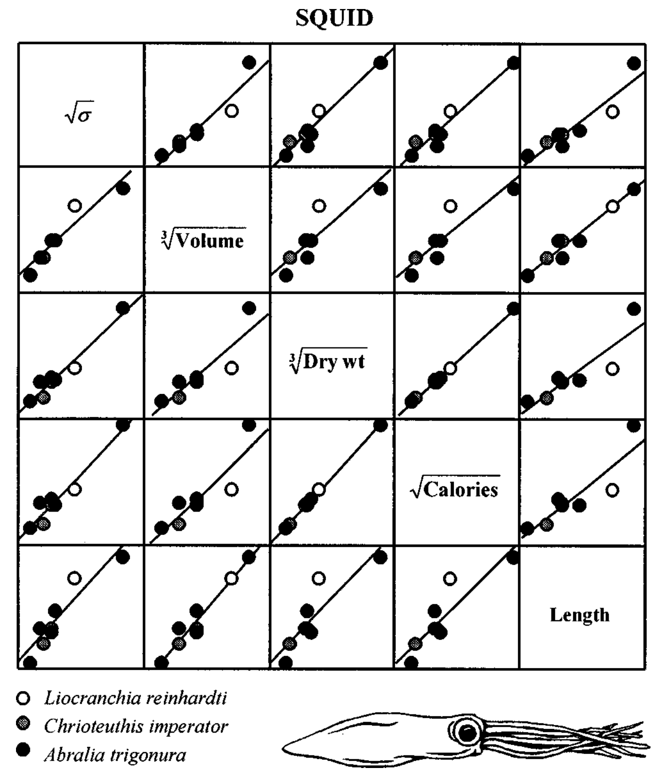

FIG. 4. Matrix of regressions for standardized measures of biomass, squid mantle length, and the square root of dorsal-aspect acoustic cross section of mesopelagic squids. All possible combinations are shown with each variable as both the *x* and *y* axis.

and the square root of σ on the y axis. The graph to the left of the "Volume" box shows the square root of σ on the x axis and the cube root of volume on the y axis. The extreme lower left graph of each matrix shows the square root of σ on the x axis and length on the y axis and so on. These figures show the linear relationship of the paired variables, not their specific values. Acoustic cross section at 200 kHz was a significant predictor of the measures of biomass taken (standardized volume, dry weight, ash-free dry weight, and calories) for all three groups and F tests showed that the slopes of all regressions were significant (Table I).

Total calorie content is arguably the most biologically important measure of biomass used here. The relationships between dorsal-aspect acoustic cross section and calories are shown in Figs. 5, 6, and 7. A comparison of standardized dorsal-aspect acoustic cross section with length, and standardized biomass measures (volume, dry weight, and ash-free dry weight) as independent predictors of total calorie content is shown in Table II. A blocked linear regression shows that for myctophid fish, dorsal-aspect acoustic cross section at 200 kHz is not a significantly different predictor of calorie content than body length or volume. In shrimp, both length and volume are significantly better predictors of calorie content than the dorsal-aspect acoustic cross section. For squid, dorsal-aspect acoustic cross section at 200 kHz is a significantly better predictor of calorie content than either body length or volume. For all three groups of organisms, dry weight and ash-free dry weight are nearly perfect predictors of calorie content ($r^2=0.98$, $r^2=0.97$ overall). Consequently, both are significantly better predictors of calorie content than dorsal-aspect acoustic cross section at 200 kHz in all three groups. Dorsal-aspect acoustic cross section predicts dry weight and ash-free dry weight significantly better than it predicts total calories for shrimp, but it is not significantly different in predicting both weight measures and caloric content in myctophid fishes and squids.

TABLE I. Results of regression analyses between dorsal-aspect acoustic cross section and various measures of biomass, all standardized to be one-dimensional.

Independent	Acoustic cross-section (σ)ˆ1/2							
Dependent	Volumeˆ1/3		Dry weightˆ1/3		Ash-free dry wtˆ1/3		Caloriesˆ1/2	
	r^2	P	r^2	P	r^2	P	r^2	P
Myctophids	0.80	<0.0001	0.83	<0.0001	0.83	<0.0001	0.82	<0.0001
Shrimp	0.67	<0.001	0.89	<0.0001	0.85	<0.0001	0.76	<0.001
Squid	0.89	<0.0001	0.89	<0.0001	0.89	<0.0001	0.89	<0.0001

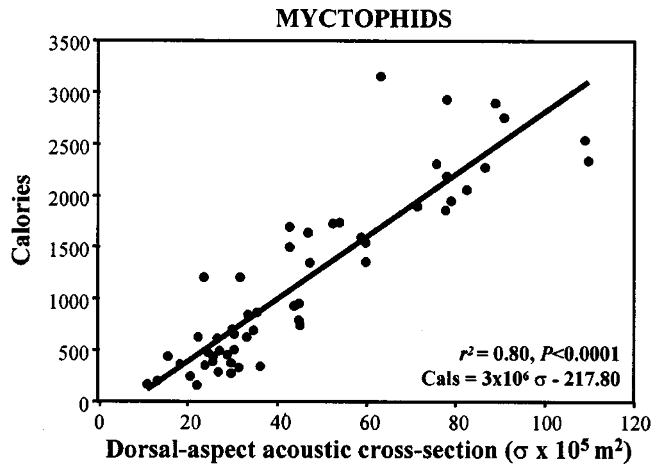

FIG. 5. Regression between dorsal-aspect acoustic cross section and total caloric content for myctophid fishes (includes all specimens).

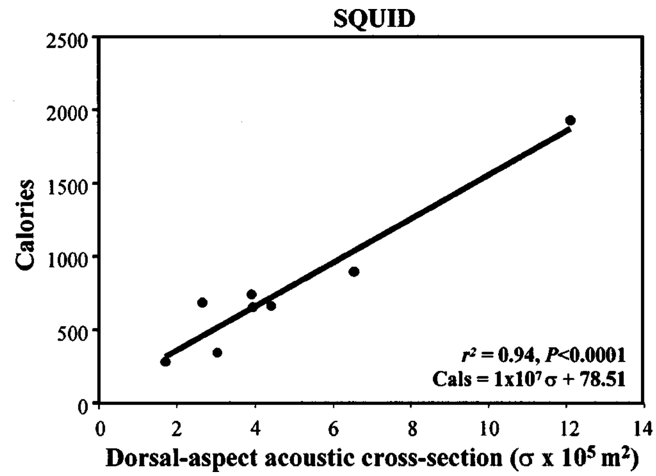

FIG. 7. Regression between dorsal-aspect acoustic cross section and total caloric content for mesopelagic squid (includes all specimens).

Energy density (calories per gram of ash-free dry weight), an important measure of food quality that allows comparison between animal groups, is summarized in Table III for the midwater animals measured. The distribution of energy density values for myctophids was skewed towards lower values. The distribution of shrimp energy density was bimodal, with modes above and below the mean energy density. The distribution of squid energy density approximated a normal distribution.

The correlation between caloric content and dorsal-aspect acoustic cross section at 200 kHz, despite large differences caloric density, suggests that energy density and acoustic scattering may be related. To examine this relationship, the energy density of animals with target strengths higher than the average for the taxonomic group to which they belong was compared with the energy density of animals with lower than average target strengths. Average was defined as the target strength predicted by the regression of length versus target strength at 200 kHz for an animal belonging to that taxonomic group (Benoit-Bird and Au, 2001). The individuals in the two groups were spread randomly throughout the size range measured. A two-tailed *t* test without assuming equal variances revealed that animals with lower than average target strength at 200 kHz had significantly higher energy density than animals with higher than average target strength at 200 kHz (Table IV).

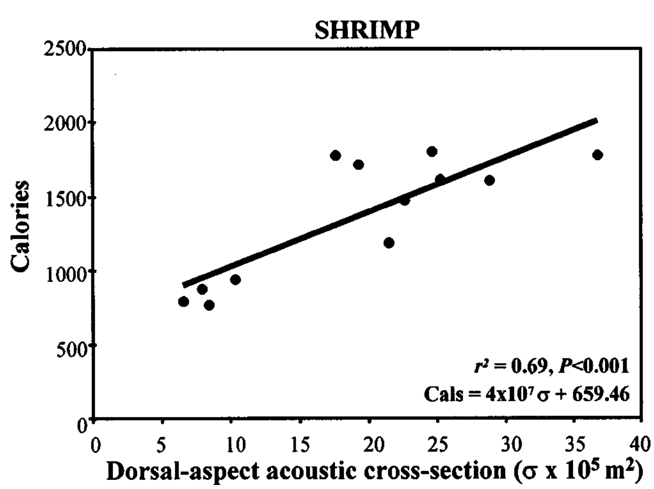

FIG. 6. Regression between dorsal-aspect acoustic cross section and total caloric content for mesopelagic shrimp (includes all specimens).

IV. DISCUSSION AND CONCLUSIONS

The strong relationship between acoustic scattering strength and biomass measures should perhaps not be surprising. Much has been written in the acoustic literature on the relationship between animal length and scattering strength (see, for example, Love, 1970). In the biological literature, animal length is routinely related to biomass measures (see, for example, Sarvala *et al.*, 1999). Both of the relationships are strong and show the same directional trend. Consequently, the relationship between acoustic scattering and biomass should also be strong.

Acoustic scattering strength was an equally good predictor of standardized measures of volume, dry weight, ash-free dry weight, and total caloric value for myctophid fish and squid. For shrimps, acoustic scattering predicted standardized dry weight and ash-free dry weight equally well, and standardized volume and calories equally well, but the weight measures were predicted significantly better than the volume or caloric content. The small sample size for both the shrimp and squid makes it difficult to interpret the meaning of this difference. Perhaps the chitinous exoskeleton of the shrimp, which made the percent of ash higher than in the other two groups, is responsible for the poorer fit of the caloric data in this group. Also, the low scattering strength of the shrimp compared with the fishes and squids means that the range of values of acoustic scattering is small compared with the range of values for fish and squid. This would make an existing relationship more difficult to detect, particularly with a small sample size. For myctophid fishes however, the predictive relationships were especially strong for caloric content, the appropriate measure of biomass for the purposes of a field study. Predictions based on dorsal-aspect acoustic backscattering, for myctophid fish and midwater squid, are at least as good as those based on length or volume, which are standard biological predictors of biomass. These data suggest

TABLE II. Results of regression analyses between one-dimensional biological and acoustic measures of individual animals and caloric content.

Independent					Dry weightˆ1/3					
Dependent	Length		Volumeˆ1/3		Caloriesˆ1/2		Ash-free dry wtˆ1/3		(σ)ˆ1/2	
	r^2	P	r^2	P	r^2	P	r^2	P	r^2	P
Myctophids	0.80	<0.0001	0.81	<0.0001	0.97	<0.0001	0.96	<0.0001	0.82	<0.0001
Shrimp	0.88	<0.0001	0.79	<0.0001	0.90	<0.0001	0.87	<0.0001	0.76	<0.001
Squid	0.84	<0.0001	0.79	<0.0001	0.99	<0.0001	0.99	<0.0001	0.89	<0.0001

that the use of acoustics for studying biomass is warranted and merits further work to validate the generality of the relationship.

Mesopelagic boundary animals from all three taxa with higher than average target strengths have lower energy densities than those with lower than average target strengths at 200 kHz. Although proximate analysis was not conducted on the animals in this study, other studies have shown a positive correlation between lipid content and caloric density (Donnelly *et al.*, 1993; Donnelly *et al.*, 1990; Ikeda, 1996; Stickney and Torres, 1989). This suggests that an increase in the proportion of lipid may be responsible for reducing the scattering strength of individuals from the boundary layer with high caloric density. This is likely because the density of marine lipids, while variable, is closer to the density of water than other body components (Donnelly *et al.*, 1990; Neighbors and Nafpaktitis, 1982; Ohshima *et al.*, 1987; Stickney and Torres, 1989), potentially making the impedance match closer, reducing the target strength. This relationship likely will not be extendable to taxa that have air-filled cavities. The presence of an air-filled cavity can increase the acoustic cross section of similarly sized animals by orders of magnitude (Medwin and Clay, 1997). The myctophid fish measured often had wax-invested or fully deflated swimbladders that did not significantly affect their backscattering strength (Benoit-Bird and Au, 2001). The shrimp and squid also lacked air-filled cavities.

This study may be the first to compare paired measures of acoustic backscatter cross section and measures of biomass. Interestingly, the strong linear relationships between one-dimensional versions of all the variables measured—length, volume, dry weight, ash-free dry weight, calories, and dorsal-aspect acoustic cross section at 200 kHz—make it possible to estimate any one of these variables from the others, within a taxonomic group. Biologists conducting biomass analyses have long reported data derived from length–weight curves, weight–calorie curves, and length–calorie curves (Cummins and Wuycheck, 1977). Acousticians doing fisheries work have applied these curves, primarily those relating length and weight, to their data to estimate biomass (Bethke *et al.*, 1994). However, the results from this study provide additional capabilities. First, these data show that in these midwater animals, acoustic scattering measurements can be used as a direct index of biomass in monospecific aggregations or when the proportion of each group within the survey area is known. Such estimation is commonly done (Liao *et al.*, 1999) but the relationship of scattering to biomass has not been directly validated. Second, the relationship between dorsal-aspect acoustic cross section and caloric content of Hawaiian mesopelagic animals is linear and additive (Foote, 1983). Consequently, in the Hawaiian mesopelagic boundary layer where the size range of animals present is very narrow, it is possible to directly convert acoustic energy to organic resource units without having knowledge of the size distribution of the population being studied. However, it is necessary to know the proportion of each biological group (myctophid fish, shrimp, and squid) because myctophid fish have higher scattering values than equivalently sized squid and shrimp (Benoit-Bird and Au, 2001), while equivalently sized animals have similar caloric values.

Our results suggest that acoustic scattering can provide a useful measure of biomass for these midwater species and can be converted to biologically relevant units without intermediate steps. However, we have no evidence that such estimates can be extrapolated to other species in other areas. The process of directly measuring energy density is very time consuming, but the measurement of dry weight is relatively simple. Individual animals need not be homogenized before drying if calorimetric analysis is not to be conducted. The only equipment necessary is a freeze-dryer (also known as a lyophilizer) and an accurate balance appropriate to the size of the sample. Biovolume is an even simpler measurement to take, requiring only a graduated cylinder and water. We suggest that measures of biomass should become a routine part of studies measuring acoustic scattering under controlled conditions. These types of paired measurements would prove useful for field studies and models of ecosystems. Such measurement of biomass has been relegated by most acousticians to biologists. However, measuring acoustic backscatter may be much more difficult for biologists than measuring biomass is for acousticians. It is crucial that acousticians participate in obtaining the important paired measurements of acoustic backscattering and biomass for other species.

TABLE III. Summary of energy density, calories per gram of ash-free dry weight, for the midwater animals measured.

	n	Minimum	Maximum	Mean	Std. deviation
Myctophids	54	3721	9071	5309	909
Shrimp	12	3823	5785	4836	569
Squid	8	4492	4949	4712	153

TABLE IV. Two-tailed t test for equality of energy density means for mesopelagic animals that have lower than average target strength and those that have higher than average target strength.

T	df	P (2-tailed)	Mean difference	Std. error difference
2.0	70.2	<0.05	373.4	187.0

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