

Target strength measurements of Hawaiian mesopelagic boundary community animals

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(Received 18 December 2000; revised 12 March 2001; accepted 27 April 2001)

A 200-kHz echosounder modified to digitize the envelope of the received echoes directly into a computer was used to measure the *ex situ* target strength (TS) of live animals from the Hawaiian mesopelagic boundary community as a function of animal size, tilt and roll angle, and biological classification. Dorsal aspect TS (in dB//1 m) at 200 kHz was related to the animal's length: myctophid fish TS = 20 log (standard length in cm) - 58.8, $r^2 = 0.91$, squid TS = 18.8 log (mantle length in cm) - 61.7, $r^2 = 0.81$, shrimp TS = 19.4 log (length in cm) - 74.1, $r^2 = 0.83$. Tilting the fish 5° and 10° changed the measured TS by up to 3.0 dB, decreasing TS as the fish was tilted forward and increasing TS as the fish was tilted backwards. In shrimp, forward tilt increased TS while backward tilt decreased TS by up to 3.3 dB. No consistent trend in squid TS change was observed with tilt angle. Roll angles of 5° and 10° increased the TS of all groups by up to 3.0 dB. Myctophid lateral aspect TS was consistently about 6 dB higher than the dorsal TS. Physiological analysis of the fishes' swimbladders revealed that the swimbladder is not the dominant scattering mechanism in the myctophid fishes studied. © 2001 Acoustical Society of America.

[DOI: 10.1121/1.1382620]

PACS numbers: 43.30.Sf, 43.30.Ft, 43.20.Fn [DLB]

I. INTRODUCTION

The mesopelagic boundary community found in the waters over the slopes of the Hawaiian Islands is a distinct, land-associated community of micronektonic fish, shrimp, and squid (Reid *et al.*, 1991). The species composition of the boundary community is different from that of the sound-scattering layer found in the open ocean surrounding the islands (Reid, 1994). Gut-content analyses of a variety of fish including snappers (*Etelis coruscans* and *Etelis carbunculus*) (Haight *et al.*, 1993), tunas (He *et al.*, 1997), billfish (Skillman, 1998) as well as spinner dolphins (*Stenella longirostris*) (Norris and Dohl, 1980) in Hawaii have established that much of their prey is taken from the boundary community. Clearly, the mesopelagic boundary community is an important component of the coastal ecosystem in Hawaii, and other Pacific islands. This layer, however, has not been well studied. Only one study has concentrated specifically on this important zone (Reid, 1994; Reid *et al.*, 1991), with two others looking at it incidentally (Amesbury, 1975; Struhsaker, 1973). All of these studies used trawling as their primary method of sample collection.

Midwater trawling research (Amesbury, 1975; Reid, 1994; Reid *et al.*, 1991; Struhsaker, 1973) has been very valuable in identifying specific species and obtaining some general information about the spatial structure of this boundary community of micronekton. However, trawling techniques alone have severe disadvantages. Trawling studies are relatively localized. Reid's work, for example, consisted of 3 stations around Oahu and another 11 stations around the Maui area. Trawls must be launched from a large ship and are therefore expensive and time consuming. In addition, and

probably most importantly, there is the inherent bias associated with "net avoidance" (Holliday and Pieper, 1995; Medwin and Clay, 1998). In one study a comparison of trawl sampling and acoustic methods found that acoustic sampling estimated biomass seven times greater than trawl estimates (Koslow, 1997). Sampling with nets yields a highly biased assessment of overall biomass and relative composition of marine pelagic communities (Kenchington, 1989). Moreover, trawling cannot assess small-scale spatial and temporal heterogeneity effectively. The combined difficulties of trawling used alone severely hinder any attempt to assess the biomass, diversity, community structure, and trophic organization of marine communities (Koslow, 1997).

The use of acoustic methods to estimate animal abundance in the wild requires information on the acoustic size, target strength, or backscattering cross section, of individual organisms (MacLennan, 1990; Thiebaux *et al.*, 1991) as well as knowledge about other reflective characteristics of individual animals in the community (Love, 1969). Both echo-energy integration and echo-counting techniques require an estimate of the target strength of individual targets (MacLennan, 1990). No target strength measurements are available for myctophid fishes, which comprise more than 50% of the species and individuals of the Hawaiian mesopelagic boundary community (Reid *et al.*, 1991). To understand the dependence of target strength on length and tilt or roll angle, live mesopelagic organisms were tethered in a shipboard seawater tank and ensounded with a 200-kHz signal. The validity and field applicability of tethered single-fish measurements have been established (Foote, 1983). The goal of this work was to obtain reliable estimates of target strength and its variability for use in acoustic surveys of the Hawaiian mesopelagic boundary community.

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TABLE I. Summary of mesopelagic boundary animals measured.

Family	Species	Number measured	Size range (cm)	Mean size (cm)
Fishes				
Myctophidae				
	<i>Benthosema fibulatum</i>	29	2.4–7.9	5.2
	<i>Diaphus adenomus</i>	8	3.7–6.4	5.3
	<i>Diaphus chrysorhynchus</i>	7	3.2–6.4	4.7
	<i>Diaphus trachops</i>	3	3.3–3.9	3.7
	<i>Idiolychnus urolampus</i>	2	3.6–4.7	...
	<i>Myctophum brachygnathos</i>	5	4.4–8.2	6.1
Astronesthidae				
	<i>Astronesthes lucifer</i>	1	5.9	...
Bregmacerotidae				
	<i>Bregmaceros</i> sp.	1	5.0	...
Squids				
Endoploteuthidae				
	<i>Abralia trigonura</i>	5	1.2–4.2	2.5
Chiroteuthidae				
	<i>Chiroteuthis imperator</i>	2	1.8–2.2	...
Cranchiidae				
	<i>Liocranchia reinhardtii</i>	1	3.6	...
Shrimps				
Gnathophausiidae				
	<i>Gnathophausia longispina</i>	2	4.5–7.4	...
Pasiphaeidae				
	<i>Pasiphaea truncata</i>	1	6.8	...
Sergestidae				
	<i>Sergia fulgens</i>	11	2.6–8.3	5.8

II. METHODS

Trawling for micronektonic organisms 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 for 20 to 30 min, reaching a maximum depth of 200 m. The ship was traveling between 3 and 4 kn with wire sent out at 25 m per min. The various live animals from the mesopelagic boundary community that target strength measurements were obtained from are shown in Table I.

Live organisms from the mesopelagic boundary community and other organisms in the same size range were transferred into an aerated seawater container on deck to await study. Within one-half hour of initial retrieval, a single, robust individual was transferred into a container filled with 1 liter of water. To tranquilize the animal for study, bubbling CO₂ was administered via Alka-Seltzer tablets. Tablets were added one-quarter at a time until the animal was subdued. The anesthetized individual was then mounted upside down over an upward-looking transducer on the bottom of the tank. Animals were mounted with monofilament lines as shown in Fig. 1, to a wooden frame that kept the animal motionless. The frame rested on the top of a 2000-L free-standing shipboard tank filled with seawater. Animals were held 0.3 m from the surface of the water, 1 m above the transducer (Fig. 2). Air bubbles were removed from the surface of the animal and the monofilament tethers with streaming seawater. To observe the effect of angle on the measured target strengths, the wooden frame could be rotated 5- and 10 deg about the dorso-ventral and lateral axes of the animal by

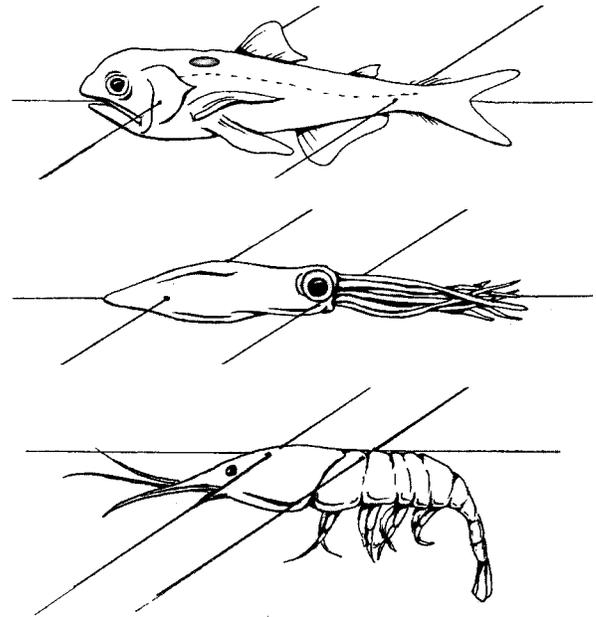


FIG. 1. Illustration of a representative fish, squid, and shrimp showing how they were mounted with six monofilament lines.

raising one side of the frame with a wooden block and re-centering the target animal.

One hundred echoes were obtained from the dorsal aspect of each animal using a Computrol, Tournament Master Echosounder NCC 5300 modified to read directly into a laptop computer. The envelope of the echo was digitized at a sampling rate of 10 kHz with a Rapid System R1200. The echosounder used a 200-kHz outgoing signal with a pulse length of 130 μ s. The acoustic reflection of 20 individuals was also measured 5- and 10-deg from dorsal in both the tilt and roll planes, and 8 individuals were measured from the lateral aspect.

Target strengths of individual animals were calculated using an indirect calibration procedure incorporating reference targets. Calibration of the experimental setup was ac-

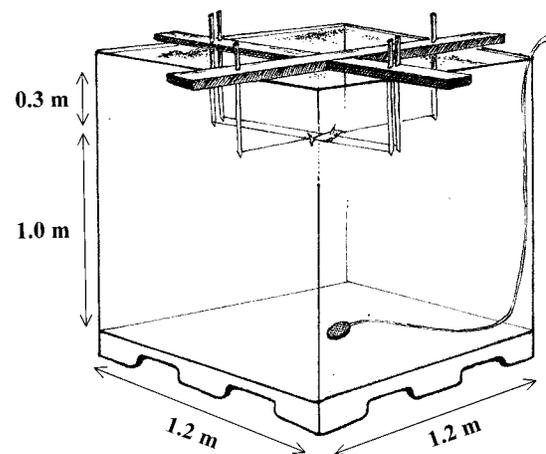


FIG. 2. Experimental setup. A wooden frame that held the subject upside down 0.3 m from the surface of the water and 1 m above an upward-looking transducer rested on a 2000-L seawater tank aboard the ship. The frame could be rotated 5° and 10° about the dorso-ventral and lateral axes of the animal by raising one side of the frame with a wooden block and recentering the target.

TABLE II. Gelatinous mesopelagic organisms caught in the IKMT along with mesopelagic boundary animals. These animals were also measured but none returned an echo above the threshold of the echosounder, -63 dB.

Order Species	Number measured	Size range (cm)	Inclusions
Salps			
Salpida			
<i>Salpa spp.</i>	4	3.8–6.5	gas
Pyrosomes			
Pyrosomidae			
<i>Pyrosomas spp.</i>	3	11.0–16.4	none
Heteropods			
Mesogastropoda			
Family <i>Heteropoda</i> , sp. unknown	2	3.1–4.2	shell
Siphonophores			
Calycophora			
unknown	5	6.2–17.1	gas

completed by substituting a 0.79-cm-diameter solid-steel sphere for the fish and comparing the echo level of the target fish to that of the reference target. A 0.64-cm and 1.11-cm sphere were also measured to confirm the calibration. The target strength of each sphere was measured from the levels of the incident and reflected signal from the sphere measured with a separate, calibrated hydrophone. The target strength of an individual animal from the mesopelagic layer (TS_{mbl}) was determined from the equation

$$TS_{mbl} = 20 \log(V_{envelope}/V_{calibrated}) + TS_{sphere}, \quad (1)$$

where $V_{envelope}$ is the voltage received by the echosounder from the animal, $V_{calibrated}$ is the voltage received from a sphere at the same range, and TS_{sphere} is the known target strength of the sphere.

The standard length of fishes (the distance between the snout to the end of the caudal peduncle), the mantle length of the dorsal side of the squids, and the total length of the shrimp species was measured with vernier calipers to the nearest 1 mm. Boundary community organisms were then identified to species and frozen for later analysis. Dorsal aspect target strengths of individuals as a function of the log of their length for practically definable biological classes were analyzed using regressions. F tests were used to test the significance of each regression's slope.

Frozen fish were thawed and dissected under a dissecting microscope to look at the characteristics of their swimbladders. An ocular micrometer was used to measure the maximum length of the major and minor axes of the swimbladder. The state of the swimbladder, inflated or not, was noted and the swimbladder was completely removed. Thin sections were made of the extracted swimbladder to analyze its contents.

III. RESULTS

Echoes from 14 gelatinous animals, shown in Table II, from four major groups were not detectable with the echosounder system. Eleven of the organisms had gas inclusions or shells. The threshold level of the echosounder system was measured to be -63 dB.

Variation among the 100 echoes measured for each individual fish, shrimp, or squid at each aspect was limited to ± 2.6 dB and was distributed normally about the mean. The dorsal aspect target strength at 200 kHz of mesopelagic fish ($n=56$) was a function of the log of the fish's standard length [Fig. 3(A)]. All measurements are within the range of geometric scattering. This relationship can be expressed as

$$TS = 20 \log(\text{standard length in cm}) - 58.8. \quad (2)$$

in dB *re* 1 m. The r^2 of this relationship was 0.83. An F test revealed that the slope of the regression was significantly different from zero ($P < 0.05$). If only myctophid fish are considered by removing the bregmaceroid and astronesthid, the relationship remains the same; however, the r^2 for this relationship was 0.91 and was significant at $P < 0.01$. One myctophid fish species was abundant enough to be considered independently. The regression for *Benthosema fibulatum* can be represented by the same equation; however, the r^2 increased to 0.94. An F test revealed the slope of the regression was significantly different from zero at $P < 0.01$. Myctophid fish from the genus *Diaphus*, represented by three species, *D. adenomus*, *D. chrysorhynchus*, and *D. trachops*, had the same relationship as well. The r^2 for *Diaphus* was 0.91 and the slope was significant at the $P < 0.05$ level.

The dorsal aspect target strength of eight individuals from three squid species, *Abralia trigonura*, *Chrioteuthis imperator*, and *Liocranchia reinhardtii*, was correlated with the log of the squid's mantle length [Fig. 3(B)]. The best-fit regression for these measurements, which are within the range of geometric scattering, can be expressed as

$$TS = 18.8 \log(\text{mantle length in cm}) - 61.7, \quad (3)$$

in dB *re* 1 m. The data had an $r^2 = 0.81$ and an F test revealed that the slope of the regression was significant ($P < 0.05$).

The dorsal aspect target strength of 12 individuals of three species of mesopelagic shrimps, *Gnathophausia longispina*, *Pasiphaea truncata*, and *Sergia fulgens* was correlated with the log of the shrimp's total length [Fig. 3(C)]. The best-fit regression line can be expressed by the equation

$$TS = 19.4 \log(\text{length in cm}) - 74.1, \quad (4)$$

in dB *re* 1 m. The data were within the range of geometric scattering and had an $r^2 = 0.83$ and the slope was significant at the $P < 0.05$ level. The echoes from two shrimps, 2.6- and 3.2-cm long, were not detectable.

The effect of tilt angle and roll angle on the target strength of 13 myctophids is shown in Fig. 4(A). Target strengths of fish tilted 5° head down were, on average, 1.6 dB lower than the dorsal aspect target strength of the same individual. Tilting the fish head down by 10° decreased the target strength by an average of 2.3 dB relative to dorsal aspect target strengths. Tilting the fish's head up 5° increased the target strength relative to the dorsal target strength by an average of 0.9 dB. Tilting the fish head up by 10° increased the target strength relative to the dorsal aspect target strength by an average of 1.7 dB. When the fish was angled 5° to one side, the target strength increased an average of 1.0 dB. A roll angle of 10° caused an increase of an average of 1.8 dB.

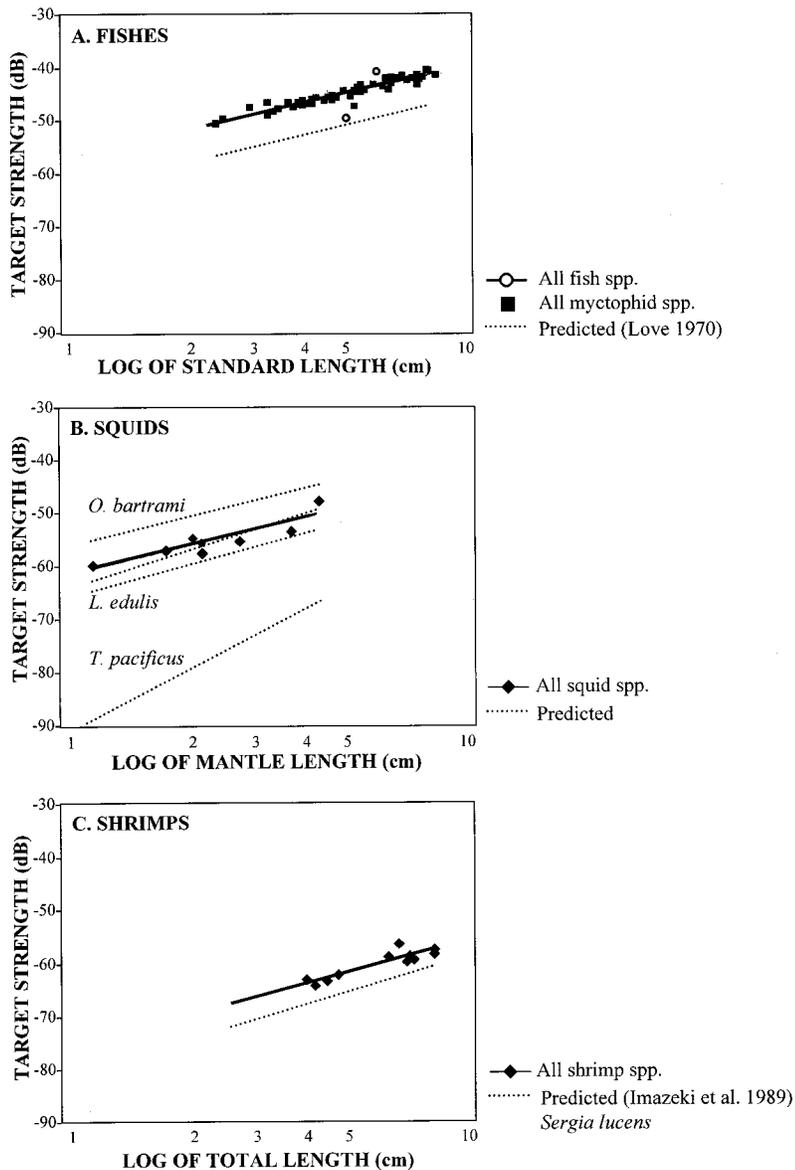


FIG. 3. (A) Dorsal aspect target strengths at 200 kHz of 56 individuals of various mesopelagic fish species plotted against the log of the fish's standard length in cm. The predictions of Love (1970) for dorsal aspect target strength values for fish equal in size to the measured individuals are represented by the dashed line. All mesopelagic fish are represented by empty circles, the best-fit logarithmic curve for all fish, $TS = 20 \log(\text{standard length}) - 58.8$, had an r^2 of 0.83. Only myctophid species are represented by a square ($n = 54$), including only this data, the curve had an r^2 of 0.91. (B) Dorsal aspect target strengths at 200 kHz of eight individuals representing three mesopelagic squid species plotted against the log of the squid's mantle length in cm. The measured dorsal target strengths are represented by the filled diamonds. The best-fit logarithmic curve, $TS = 18.8 * \log(\text{mantle length}) - 61.7$, had an $r^2 = 0.81$ and a significant slope ($P < 0.05$). The predictions of dorsal aspect target strength at 200 kHz for individuals of the same size as the measured individuals are represented by the dashed lines: flying squid, *Ommastrephes bartrami* (Arnaya et al., 1989; Kajiwaru et al., 1990), *Loligo edulis* (Lee et al., 1991), and *Todarodes pacificus* (Arnaya et al., 1989). (C) Dorsal aspect target strengths at 200 kHz of 12 individuals representing three mesopelagic shrimp species plotted against the log of the shrimp's length in cm. The best-fit logarithmic curve, $TS = 19.4 * \log(\text{length}) - 74.1$, had an $r^2 = 0.83$ and had a significant slope ($P < 0.05$). The dashed line represents the dorsal target strength at 200 kHz of *Sergia lucens* (Imazeki et al., 1989), a species closely related to *Sergia fulgens*, the most abundant species in this sample.

The lateral (side aspect) target strength at 200 kHz of eight mesopelagic fishes, one astronesthid, and seven myctophids is given in Table III. The lateral target strength of the astronesthid was 0.8 dB lower than its dorsal target strength. The lateral target strengths of the myctophids were an average of 6.0 dB higher than their dorsal target strengths.

The effect of tilt and roll angle on the target strength of four squids showed that tilting the squid head down 5° increased the target strength relative to the dorsal aspect target strength an average of 0.6 dB [Fig. 4(B)]. Tilting the squid's head down 10° increased its target strength by an average of 0.7 dB, while tilting the squid head back 5° increased its target strength relative to its dorsal target strength by an average of 0.6 dB. Tilting the squid back 10° increased its target strength by 0.9 dB, on average. Changing the squid's angle by rolling it 5° to one side increased its target strength by an average of 0.7 dB relative to its dorsal aspect target strength, while rolling the squid 10° to one side increased the target strength by 0.6 dB.

The effects of tilt and roll angle on the target strengths

of three shrimps are shown in Fig. 4(C). Tilting the shrimps forward, head down, by 5° increased their target strength relative to their dorsal target strength by an average of 1.6 dB. Tilting the shrimps forward by 10° increased their target strength relative to their dorsal target strength by an average of 2.6 dB. Tilting the shrimps backward by 5° and 10° decreased their target strengths relative to dorsal by an average of 2.0- and 3.3-dB, respectively. Rolling the shrimp 5° to one side increased its target strength relative to dorsal by an average of 0.7 dB. The target strengths of shrimps rolled 10° to one side also increased their target strength by an average of 0.7 dB.

The relationship between the standard length of fish and the maximum length of the major and minor axes of the fish's swimbladder was not regressive (Fig. 5). The r^2 for fish standard length against the length of the swimbladder's major axis was 0.02. For the swimbladder's minor axis, the r^2 was 0.01. F tests show that neither line has a significant slope ($P \gg 0.05$). There is also no relationship between the log length of the major or minor axes of the swimbladder and

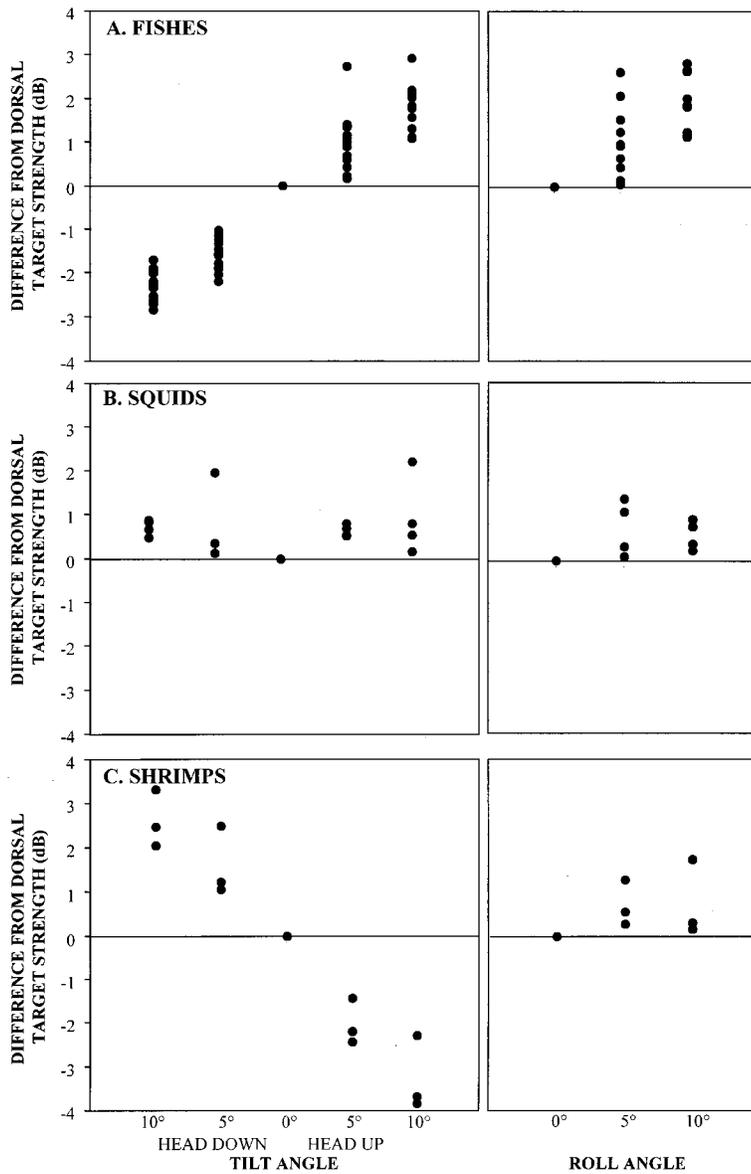


FIG. 4. (A) The effect of tilt angle (left) and roll angle (right) on the 200-kHz target strength of 13 myctophid fish. The y axis shows the difference of the measured target strength from the dorsal aspect target strength of the same individual. (B) The effect of tilt angle (left) and roll angle (right) on the target strengths of four squids. The y axis shows the difference of the measured target strength from the dorsal aspect target strength of the same individual. (C) The effect of tilt angle (left) and roll angle (right) on the target strengths of three shrimps. The y axis shows the difference of the measured target strength from the dorsal aspect target strength of the same individual.

target strength. The r^2 for each comparison was less than 0.1 with $P \geq 0.05$. Of the 38 swimbladders examined, 11 were completely empty, 1 was filled only with gas, 16 were filled only with a solid wax, and 10 had a solid wax core surrounded by a thin layer (1 mm or less) of gas. The empty

TABLE III. Lateral target strengths at 200 kHz for 8 mesopelagic fishes, 1 astronesthid and 7 myctophids. The lateral target strength of the astronesthid was 0.81 dB lower than its dorsal target strength. The lateral target strengths of the myctophids were an average of 6.0 dB higher than their dorsal target strengths.

Species	Dorsal TS (dB)	Lateral TS (dB)	TS diff (dB)
<i>Astronesthes lucifer</i>	-41.6	-42.4	-0.8
<i>Benthoosema fibulatum</i>	-51.2	-44.6	6.6
<i>Benthoosema fibulatum</i>	-43.3	-35.4	7.9
<i>Benthoosema fibulatum</i>	-41.8	-34.9	6.9
<i>Benthoosema fibulatum</i>	-41.4	-35.3	6.1
<i>Diaphus adenomus</i>	-44.2	-39.1	5.2
<i>Diaphus chrysohynchus</i>	-43.2	-38.6	4.6
<i>Myctophum brachygnathos</i>	-42.2	-37.3	4.9

swimbladders looked like two thin layers of tissue completely adhered to each other; there appeared to be no gas content in these swimbladders. Only one species, *Diaphus adenomus*, was observed with all swimbladders in the same state (empty). All other species had at least one individual with an empty swimbladder and at least one with solid wax in its swimbladder. The lack of relationships between fish length or target strength and swimbladder length did not change if animals were broken down by species or by swimbladder content. The lengths of the two axes of the same swimbladder were significantly correlated with an r^2 of 0.49 and $P < 0.01$. It is important to note that, unlike many other species of fish whose swimbladder's length is often more than 70% of the length of the fish (Saenger, 1989), the maximum length of the swimbladder in these myctophid fishes was, on average, 5% of the length of the fish. The small sizes of these swimbladders, represented by the filled oval within the fish in Fig. 1, all less than 12 mm in maximum length, precluded any measures of the position of the swimbladder relative to the fish.

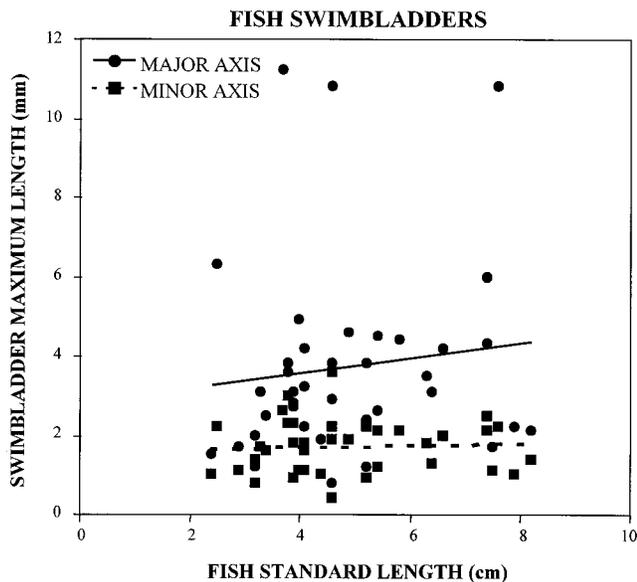


FIG. 5. The standard length of myctophid fish against the maximum length of the major and minor axes of their swimbladders. No regressive relationship was found for either measurement. The r^2 for fish length against the major axis was 0.02 with a $P \geq 0.05$. The r^2 for fish length against the minor axis was 0.01 with a $P \geq 0.05$.

IV. DISCUSSION

The gelatinous animals captured in the same trawls as the mesopelagic boundary community animals did not return echoes high enough to be detected by the echosounder system. Many of these animals had intact gas inclusions or shells that might have been predicted to serve as strong targets. However, Stanton and his colleagues (1998) found that siphonophores with gas enclosures had a target strength near -70 dB, at 200 kHz. They also found that shelled pelagic gastropods, morphologically similar to the heteropods examined here, had target strengths less than -70 dB at 200 kHz. The target strength of a gelatinous animal lacking either a shell or gas inclusion, *Aurelius aurelia*, equivalent in size to the animals observed in this study would have a target strength of about -75 dB (Mutlu, 1996). The lowest target strength the echosounder system can measure was measured to be -63 dB, well above the various target strength measures for gelatinous animals. Wiebe *et al.* (1990) found that it took more than a thousand pelagic gastropods per cubic meter to create a scattering strength of -43 dB, in the range of the target strength of one mesopelagic boundary community animal. While densities of gelatinous animals with inclusions might occur in Hawaii, the change in echo-energy estimates of density in the field would be very small relative to the high densities of the boundary community that have been observed (Benoit-Bird *et al.*, 2001).

The dorsal aspect target strength of myctophid fish was strongly dependent on the log of their standard length. The slope and y intercept of the regression were not affected by including only the most abundant species or genus. There appears to be little effect of taxonomy on target strength within the myctophids represented in this sample. The y intercept of the regression line for myctophids was 5.2 dB *re* 1 m higher than the generalized regression for fish presented

by Love (1970) corrected to be referenced to 1 m. It is unclear why the observed target strengths of the myctophids in this study were consistently so high. The pulse length used was not short enough to resolve parts of an individual fish except perhaps of our largest specimens. The use of only the envelope of the echo limits the possibility that highlights from the echo could be resolved even on the largest specimens because of their relatively small size, further eliminating the possibility that target strength based on a highlight could be obtained. If target strength based on a highlight was measured, we would expect the largest individuals to be outliers on the graph, which is not the case. The values measured for the myctophids in this study are within the range of values presented by Love (1970) for fish in the same size range. It is probable that morphological differences between the species used in previous work and the myctophids used here, as well as differences between individual fish, the relatively small sample sizes, and the different methodologies used, could explain the variation.

Other researchers have found that the swimbladders of fish from the myctophid genus that are represented in this study are often uninflated, wax invested, or apparently non-functional (Brooks, 1977; Neighbors, 1992; Neighbors and Nafpaktitis, 1982; Saenger, 1989). The fish of the species investigated here also were rarely filled with only gas. Most were empty or wax invested. Depth of capture was apparently not the cause of the observation of empty swimbladders, as two of the fish with empty swimbladders, two with a mixture of solid wax and gas in their swimbladders, and one with only solid wax in its swimbladder were caught at the surface with a dipnet. This reduction or loss of a gas-filled bladder, shown to be the largest component of backscattering from swimbladdered fish (Foote, 1980), raises the question: what is the dominant scattering mechanism of these fish? Our data show no relationship between a fish's length or target strength and the size of its swimbladder or its content. Clearly, the swimbladder is not causing the echoes observed here. Perhaps as in other fish observed, the head region, primarily the skull, is an important source of scattering (Reeder *et al.*, Sun *et al.*, 1985).

The target strength of mesopelagic squids was positively correlated with their mantle length. The target strengths of the squids in this study were similar to the 200-kHz target strengths of the flying squid, *Ommastrephes bartrami*, of the same size. The target strengths measured in this study were 3.9 dB less than those measured by Kajiwara *et al.* (1990) for flying squid and 3.1 dB higher than those of Arnaya *et al.* (1989) for the flying squid. The target strengths for the mesopelagic squids in this study were also only 4 dB higher than the target strengths measured by Arnaya *et al.* (1989) for equally sized *Loligo edulis*. Target strengths have been reported for *Todarodes pacificus* which were about 30 dB less than those observed for the mesopelagic squids in this study (Lee *et al.*, 1991). The slope of the regression of length versus target strength for mesopelagic squids was somewhat less than those of the other squids, suggesting that target strength is less dependent on mantle length in this sample. This difference might be attributable to differences in morphology and scattering characteristics between the three spe-

cies of squids in this sample, as well as the relatively small sample size.

The dorsal target strength at 200 kHz of the three mesopelagic shrimp species was significantly correlated with the total length of the shrimp. Eleven of the 14 shrimps in this sample were *Sergia fulgens*. The target strengths of the shrimps in this sample were 4.1 dB higher than those found for *Sergia lucens* (Imazeki *et al.*, 1989), a species closely related to *Sergia fulgens*. The difference in target strength between the two samples is likely a result of the multispecies composition of this sample, differences between *S. fulgens* and *S. lucens*, and differences in methodology and equipment.

Tilting myctophid fish by 5° and 10° changed the measured target strengths by up to 3 dB. The target strength decreased as the fish was tilted forward, head down. The farther the fish was tilted forward, the more the target strength decreased relative to dorsal target strength. Target strength increased as the fish was tilted backward, increasing more with increased tilt angle. This agrees with the pattern observed for target strength changes as a function of tilt angle in many species of fish (Kubecka, 1994; MacLennan and Simmonds, 1992). The opposite pattern has been observed in other fish species (Do and Surti, 1990). Maximum target strength is generally observed when the primary source of scattering is oriented perpendicular to the acoustic beam (Kubecka, 1994). Thus, the orientation of the primary source of scattering relative to the axis of the fish determines the tilt angle that will produce the maximum scattering strength. The source of scattering in myctophid fish appears to be tilted forward (about 10° down) relative to the axis of the fish.

The pattern of target strength changes observed for myctophids was reversed for shrimps; forward tilt increased target strength while backward tilt decreased it. The magnitude of the change could reach 3.3 dB. This fits the direction of change predicted by the bent cylinder model of Clay (1992) when defining dorsal aspect the way we have here, as parallel to the carapace.

No consistent pattern in target strength was observed with changing tilt angle for squids. The greatest change was 2.2 dB. This is consistent with the observations of Lee *et al.* (1991) and Arnaya and Sano (1990), who found that the species of squids they measured were omnidirectional with respect to acoustic scattering strength. The scattering process associated with squid is still poorly understood and, unfortunately, these data are not helpful at obtaining a deeper understanding of the process.

Roll angles of 5° and 10° increased the target strength of myctophid fish relative to their dorsal aspect target strength. The greater angle had a greater effect on the target strength, causing a maximum change in target strength of 3 dB. Lateral target strength of myctophids was consistently approximately 6 dB higher than the dorsal target strength for the same individual. The single astronesthid measured had a lateral target strength lower than its dorsal target strength, by less than 1 dB. Rolling shrimps 5- and 10-deg showed a similar pattern in target strength change as myctophids, an increase in target strength with increasing roll angle. The

maximum effect of roll angle on shrimp target strength was 1.7 dB. Again, no pattern was evident for squids where the maximum change in target strength due to roll angle for an individual was 1.3 dB. There was large variability in the effect of tilt or roll on target strength changes and not every individual conformed to these generalities.

Tilt and roll angles have been shown to have a profound impact on acoustic field measures of animal abundance (Huse and Ona, 1996; Mukai and Iida, 1995). These observations, however, were made on single species aggregations. The use of information on the effect of tilt and roll angle on target strength in the field is most effective when studying not only single species aggregations, but also animals from the same size class. The mesopelagic boundary community is diverse and is found in assemblages composed of many size classes and not only a variety of species, but also species from more than one biological group. The differences in target strength as a function of tilt angle observed in animals from the Hawaiian mesopelagic boundary community were relatively small, less than 3.5 dB. In the field, these differences would be overshadowed by the differences caused by species and size class variability. Consequently, these measurements of tilt angle provide valuable information for error estimation in the field, particularly on this vertically migrating community. As the community rises early in the evening, the target strength of fish will be lower than their target strength as they swim downwards later in the evening. The opposite will be true for the shrimps. These differences may cause the echo-energy integration estimates of density or biomass to appear different between two times at the opposite ends of the migration when the real densities are equivalent. They could also cause field estimates of the size of individuals creating echoes to be under- or overestimated, depending on the animal group being measured and the time observed as even at rest, myctophids, for example, are often observed at a significant tilt (Barham, 1971). However, tilt angle data cannot be directly applied to abundance estimates or used for identification of animal behavior without more information on community composition than can be obtained from single-frequency acoustics alone.

The information obtained in this study will support quantitative estimates of abundance in future acoustic field studies of the Hawaiian mesopelagic boundary community. These data will also allow estimation of the levels of variation and uncertainty in field data and may permit major compositional differences in the boundary community to be observed with acoustics, particularly since the fishes and squids have such different target strength-length relationship than the shrimps.

ACKNOWLEDGMENTS

The National Marine Fisheries Service's Honolulu Laboratory generously provided ship time aboard the TOWNSEND CROMWELL and Chief Scientist Robert Humphreys kindly worked with us to maximize accomplishment of both his and our cruise objectives. The officers and crew of the TOWNSEND CROMWELL provided excellent scientific support, especially Phil White. NMFS also supplied the free-standing tank. Bruce Mundy provided assistance in the field

and fish species identification while Curt Fiedler assisted in identifying the shrimp species. Chris Bird provided assistance constructing the mounting frame and conducting field work. Mark Latham of Computrol provided invaluable assistance in modifying the echosounder. Timothy Stanton, Andone Lavery, Paul Nachtigall, and two anonymous reviewers made helpful comments on earlier drafts of this manuscript. This is HIMB Contribution No. 1110.

- Amesbury, S. S. (1975). "The vertical structure of the midwater fish community off leeward Oahu, Hawaii," Ph.D. dissertation (University of Hawaii).
- Arnaya, I. N., and Sano, N. (1990). "Studies on acoustic target strength of squid. V. Effect of swimming on target strength of squid," Bull. Fac. Fish., Hokkaido Univ. **41**, 18–31.
- Arnaya, I. N., Sano, N., and Iida, K. (1989). "Studies on acoustic target strength of squid. III. Measurement of the mean target strength of small live squid," Bull. Fac. Fish., Hokkaido Univ. **40**, 110.
- Barham, E. G. (1971). "Deep sea fishes: Lethargy and vertical orientation," in *Biological Sound Scattering in the Ocean*, edited by G. B. Farquar (U.S. Government Printing Office, W100–118).
- Benoit-Bird, K. J., Au, W. W. L., Brainard, R. E., and Lammers, M. O. (2001). "Diel horizontal migration of the Hawaiian mesopelagic boundary community observed acoustically," Mar. Ecol.: Prog. Ser. (in press).
- Brooks, A. H. (1977). "A study of the swimbladders of selected mesopelagic fish species," in *Oceanic Sound Scattering Prediction*, edited by N. R. Andersen and B. J. Zahuranec (Plenum, New York), pp. 565–590.
- Clay, C. S. (1992). "Composite ray-mode approximations for backscattered sound from gas-filled cylinders and swimbladders," J. Acoust. Soc. Am. **94**, 2173–2180.
- Do, M. A., and Surti, A. M. (1990). "Estimation of dorsal aspect target strength of deep-water fish using a simple model of swimbladder backscattering," J. Acoust. Soc. Am. **87**, 1588–1596.
- Foote, K. G. (1980). "Importance of the swimbladder in acoustic scattering by fish: A comparison of gadoid and mackerel target strengths," J. Acoust. Soc. Am. **67**, 2084–2089.
- Foote, K. G. (1983). "Linearity of fisheries acoustics with addition theorem," J. Acoust. Soc. Am. **73**, 1932–1940.
- Haight, W. R., Parrish, J. D., and Hayes, T. A. (1993). "Feeding ecology of deepwater lutjanid snappers at Penguin Bank, Hawaii," Proc. Am. Fish. Soc. **122**, 328–347.
- He, X., Bigelow, K. A., and Boggs, C. H. (1997). "Cluster analysis of longline sets and fishing strategies within the Hawaii-based fishery," Fish. Res. **31**, 147–158.
- Holliday, D. V., and Pieper, R. E. (1995). "Bioacoustical oceanography at high frequencies," ICES J. Mar. Sci. **52**, 279–296.
- Huse, I., and Ona, E. (1996). "Tilt angle distribution and swimming speed of overwintering Norwegian spring spawning herring," ICES J. Mar. Sci. **53**, 863–873.
- Imazeki, A., Yonemoto, H., Saotome, Y., Isouchi, T., and Hamada, Y. (1989). "Multifrequency measurements of target strength of the sergestid shrimp *Sergia lucens*," J. Tokyo Univ. Fish. **76**, 37–44.
- Kajiwara, Y., Iizuka, K., and Kamei, Y. (1990). "Measurement of target strength for the flying squid (*Ommastrephes bartrami*)," Bull. Fac. Fish., Hokkaido Univ. **41**, 205–212.
- Kenchington, T. J. (1989). "Estimation of catchability coefficients," Mar. Biol. (Berlin) **101**, 24–35.
- Koslow, J. A. (1997). "Seamounts and the ecology of deep-sea fisheries," Am. Sci. **85**, 168–176.
- Kubecka, J. (1994). "Simple model on the relationship between fish acoustical target strength and aspect for high-frequency sonar in shallow waters," J. Appl. Ichthyol. **10**, 75–81.
- Lee, K.-T., Shih, W.-H., Liao, C.-H., and Wang, J.-P. (1991). "Studies on the hydroacoustic scattering properties of individual squid, *Loligo edulis*," J. Fish. Soc. Taiwan **18**, 215–225.
- Love, R. H. (1969). "Maximum side-aspect target strength of an individual fish," J. Acoust. Soc. Am. **46**, 746–752.
- Love, R. H. (1970). "Dorsal-aspect target strength of an individual fish," J. Acoust. Soc. Am. **49**, 816–823.
- MacLennan, D. N. (1990). "Acoustical measurement of fish abundance," J. Acoust. Soc. Am. **87**, 1–15.
- MacLennan, D. N., and Simmonds, E. J. (1992). *Fisheries Acoustics* (Chapman and Hall, New York).
- Medwin, H., and Clay, C. (1998). *Fundamentals of Acoustical Oceanography* (Academic, San Diego).
- Mukai, T., and Iida, K. (1995). "Diurnal variation of encaged fish echoes, and estimation of fish tilt angle distribution," Fish. Sci. **61**, 647–652.
- Mutlu, E. (1996). "Target strength of the common jellyfish (*Aurelia aurita*): A preliminary experimental study with a dual-beam acoustic system," ICES J. Mar. Sci. **53**, 309–311.
- Neighbors, M. A. (1992). "Occurrence of inflated swimbladders in five species of lanternfishes (family Myctophidae) from waters off southern California," Mar. Biol. (Berlin) **114**, 355–363.
- Neighbors, M. A., and Nafpaktitis, B. G. (1982). "Lipid compositions, water contents, swimbladder morphologies and buoyancies of nineteen species of midwater fishes (18 myctophids and 1 neoscopelid)," Mar. Biol. (Berlin) **66**, 207–215.
- Norris, K. S., and Dohl, T. P. (1980). "Behavior of the Hawaiian spinner dolphin, *Stenella longirostris*," Fish. Bull. **77**, 821–849.
- Reeder, D. B., Stanton, T. K., Chu, D., and Jech, M. (2000). "Broadband acoustic backscattering by Alewife fish: Experiment and analysis," J. Acoust. Soc. Am. **108**, 2457.
- Reid, S. B. (1994). "Spatial structure of the mesopelagic fish community in the Hawaiian boundary region," Ph.D. dissertation (University of Hawaii).
- Reid, S. B., Hirota, J., Young, R. E., and Hallacher, L. E. (1991). "Mesopelagic-boundary community in Hawaii: Micronekton at the interface between neritic and oceanic ecosystems," Mar. Biol. (Berlin) **109**, 427–440.
- Saenger, R. A. (1989). "Bivariate normal swimbladder size allometry models and allometric exponents for 38 mesopelagic swimbladdered fish species commonly found in north Sargasso Sea," Can. J. Fish. Aquat. Sci. **46**, 1986–2002.
- Skillman, R. A. (1998). "Central Pacific swordfish, *Xiphias gladius*, fishery development, biology, and research," NOAA Technical Report 142.
- Stanton, T. K., Chu, D., Wiebe, P. H., Martin, L. V., and Eastwood, R. L. (1998). "Sound scattering by several zooplankton groups. I. Experimental determination of dominant scattering mechanisms," J. Acoust. Soc. Am. **103**, 225–235.
- Struhsaker, P. (1973). "A contribution to the systematics and ecology of Hawaiian bathyal fishes," Ph.D. dissertation (University of Hawaii).
- Sun, Y., Nash, R. D. M., and Clay, C. S. (1985). "Acoustic measurements of the anatomy of fish at 220 kHz," J. Acoust. Soc. Am. **78**, 1772–1776.
- Thiebaut, M. L., Boudreau, P. R., and Dickie, L. M. (1991). "An analytical model of acoustic fish reflection for estimation of maximum dorsal aspect target strength," Can. J. Fish. Aquat. Sci. **48**, 1772–1782.
- Wiebe, P. H., Greene, C. H., Stanton, T. K., and Burczynski, J. (1990). "Sound scattering by live zooplankton and micronekton: Empirical studies with a dual-beam acoustical system," J. Acoust. Soc. Am. **88**, 2346–2360.