

Broadband backscatter from individual Hawaiian mesopelagic boundary community animals with implications for spinner dolphin foraging

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Broadband simulated dolphin echolocation signals were used to measure the *ex situ* backscatter properties of mesopelagic boundary community (MBC) in order to gain a better understanding of the echolocation process of spinner dolphins foraging on the MBC. Subjects were captured by trawling with a 2-m-opening Isaacs-Kidd Midwater Trawl. Backscatter measurements were conducted on the ship in a 2000 L seawater tank with the transducer placed on the bottom pointed upwards. Backscatter measurements were obtained in both the dorsal and lateral aspects for seven myctophids and only in the dorsal aspect for 16 more myctophids, six shrimps, and three squids. The echoes from the myctophids and shrimps usually had two highlights, one from the surface of the animal nearest the transducer and a second probably from the signal propagating through body of the subject and reflecting off the opposite surface of the animal. The squid echoes consisted mainly of a single highlight but sometimes had a low amplitude secondary highlight. The backscatter results were used to estimate the echolocation detection range for spinner dolphins foraging on the mesopelagic boundary community. The results were also compared with multi-frequency volume backscatter of the mesopelagic boundary community sound scattering layer. © 2008 Acoustical Society of America. [DOI: 10.1121/1.2902187]

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I. INTRODUCTION

The mesopelagic boundary community (MBC) found in waters over the slopes of the Hawaiian Islands is a midwater sound-scattering layer. This distinct land-associated community is made up of micronektonic fish, mainly from the myctophid family, shrimp and squid (Reid *et al.*, 1991). The MBC undergoes a diel migration with a vertical component towards the surface and a horizontal migration towards shore after dusk and then a reverse migration to deeper waters after midnight (Benoit-Bird and Au, 2004). The Hawaiian spinner dolphin (*Stenella longirostris*) is one of the high trophic level predators that forage on the micronekton of the MBC (Norris and Dohl, 1980; Benoit-Bird and Au, 2003c; Benoit-Bird, 2004). The spatial and temporal dynamics and behavior of the MBC affect the foraging behavior of spinner dolphins (Benoit-Bird and Au, 2003a) and consequently has been studied extensively by Benoit-Bird using a 200 kHz echosounder (e.g., Benoit-Bird *et al.*, 2001, Benoit-Bird and Au 2003a, 2003b, 2004). The target strength of a number of individual restrained MBC organisms was also measured by Benoit-Bird and Au (2001) using a 200 kHz echosounder. In order to gain insight into role of echolocation by spinner dolphins while foraging, it is important to examine reflec-

tions from these micronekton using broadband simulated dolphin echolocation signals. One of the questions of interest is the strength of the echoes that foraging dolphins may receive. Another question involves the determination of cues in the echoes that may allow dolphins to discriminate between fish, shrimp and squid. Madsen *et al.* (2007) have recently measured the backscatter properties of *Loligo pealeii* using odontocete-like echolocation signal, however their subjects were about five times larger than the MBC species.

Since the earlier studies using a single 200 kHz echosounder, more recent work has involved the multi-frequency Simrad EK-60 system operating at 38 kHz, 70 kHz, 120 kHz, and 200 kHz to study the MBC in Hawaii (Benoit-Bird and Au, 2006; Benoit-Bird, 2006). With the use of multi-frequency echosounders, it becomes important to understand the frequency dependency of the acoustic backscatter process for individual micronekton in order to understand the volume backscattering process of a complex environment with many different types of acoustically reflective entities. It is also important to gain a better understanding of the backscatter process from ship-based surveys with multi-frequency echosounder as we continue to study the interaction of dolphins and small whales with the mesopelagic boundary community.

One of the goals of this study was to determine the broadband target strength of MBC micronekton based on the total energy in the incident and backscattered signals and

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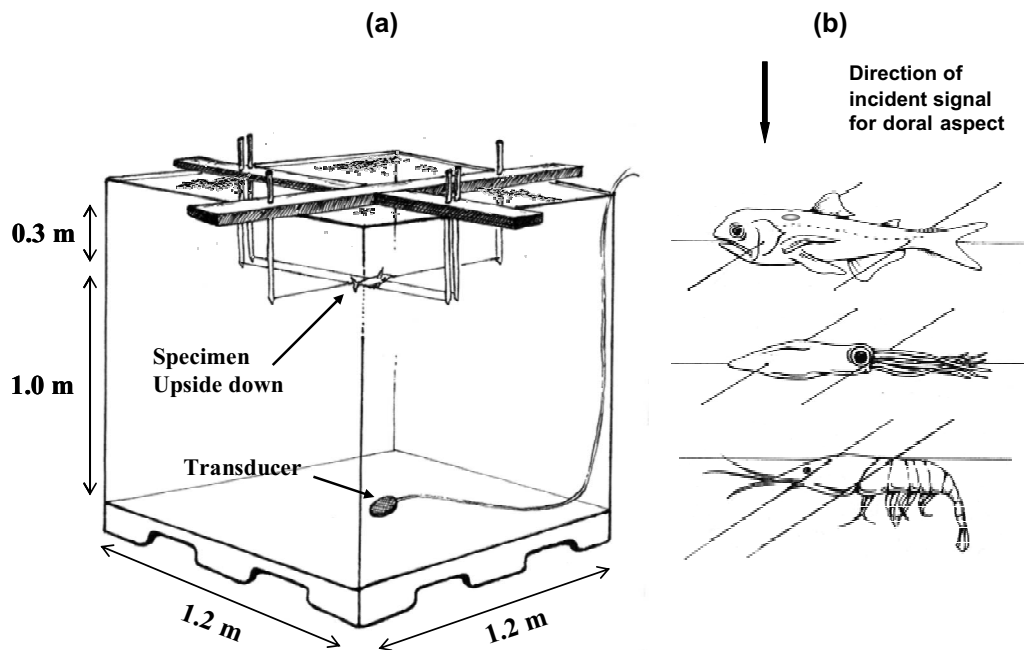


FIG. 1. (a) Schematic of the plastic holding tank in which the backscatter measurements were made. A broadband transducer was mounted on the bottom of the tank pointing upwards and the subjects were attached to monofilament lines and a special support assembly. (b) Pictures of the three classes of micronekton that were measured acoustically.

relate the results to spinner dolphin foraging on the MBC. The second goal was to measure the target strength of individual micronekton using a broadband simulated dolphin echolocation signal to determine the frequency dependency of the target strength. Simulated dolphin echolocation signals have been used extensively since 1980 (Au and Snyder, 1980) for different types of targets used in dolphin echolocation experiments (Au, 1993) and by Au and Benoit-Bird (2003) to measure the spectral structure of backscatter from lutjanid snappers.

The previous study of Benoit-Bird and Au (2001) indicated that the swimbladders of the myctophids used in our study were empty or wax invested. The specimens used in this study were a subset of the earlier study. The shrimps and squids did not contain any gas pockets. Chu and Stanton (1998) found that acoustic reflections from decapod shrimp occurred at the front water-animal interface and a secondary reflection occurred at the back animal-water interface. Therefore, it is expected our backscatter results will also have reflections from the front surface of the animals and from the signal propagating through the animals and reflecting off the back surface and any skeletal structures and also the possibility of the signals propagating along a circumferential path along the skin surface. These multiple echo components or highlights will contribute to deep local minima in the echo spectrum affecting the frequency dependency of the echoes, as was shown by Chu *et al.*, 1992 and Stanton *et al.*, 1996 for decapod shrimp.

II. APPROACH

A. Backscatter measurements

The broadband acoustic backscatter measurements were carried out in conjunction with measurements performed by

Benoit-Bird and Au (2001) and much of the details regarding animal collection and preparation can be found in that reference. Micronekton were collected using a 2 m opening Isaccs-Kidd Midwater Trawl during a cruise in July, 2000 aboard the NOAA ship R/V Townsend Cromwell. The trawl was towed obliquely for 20–30 min, reaching a maximum depth of 200 m. Live animals were transferred into an aerated seawater container on deck to await acoustic measurements. Within one-half hour of initial retrieval, a single individual was transferred into a container filled with 1 l of water and tranquilized with bubbling CO₂ using an Alka-Seltzer tablet, introduced 1/4 quarter at a time until the animal was subdued. Air bubbles were removed from the surface of the animal and the monofilament tethers using streaming seawater. Measurements were first performed using a 200 kHz system (Benoit-Bird and Au, 2001). These were followed by the broadband measurements using a broadband transducer that simply flipped in place resting on the 200 kHz transducer. The animals were held 0.3 m from the surface of the water, 1 m above the transducers [Fig. 1(a)]. The subjects were mounted with monofilament lines [Fig. 1(b)] and tied to a wooden frame which rested on the top of a 2000 l freestanding shipboard tank filled with seawater.

A custom-made transducer consisting of a 6.35 cm circular disk of 1–3 composite piezoelectric that had a thickness of 6.35 mm (Material Systems Inc.) was used to project a dolphin-like echolocation signal and receive the corresponding echoes. The transmission and receiving characteristics of the transducer was known from previous calibration using tone bursts and comparison with a standard hydrophone. The transducer in a transmit-receive mode using dolphin-like clicks was also calibrated for amplitude using an indirect procedure incorporating a 0.79-cm-diam solid steel sphere

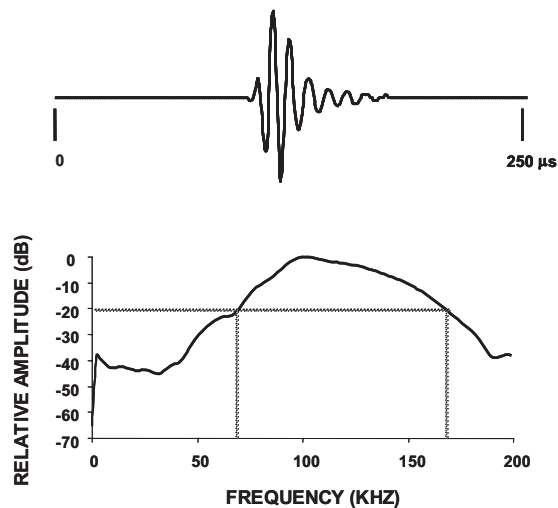


FIG. 2. The waveform and frequency spectrum of the simulated dolphin echolocation signals used in the backscatter measurements.

and a 38.1-mm-diam tungsten carbide reference sphere in a test tank as prescribed by Foote *et al.* (1987). The results from both spheres were consistent (after accounting for differences in diameters) as they should be but the process was done as a check. The incident signal waveform was measured in the same test tank by reflecting the projected signal off an acoustic mirror consisting of a 30.5×30.5-cm-square aluminum plate that was 6.35 mm thick and covered with a close-cell neoprene sheet. The diameter of the closed cells was not known. The plate was suspended by lines tied to a 61.0-cm-long aluminum channel that was attached at its center to a rotor. The plate was rotated so that the incident signal was perpendicular to its surface. This technique has been used for many years (see Au and Snyder, 1980) and the authenticity of the reflected waveform has been verified by using a small B&K 8103 hydrophone to first record the incident signal and later the reflection from the plate, with the same face of the hydrophone directed towards the signal to minimize any hydrophone effects. The incident signal was generated with a Qua-Tech WA-10 board housed in a transportable “lunch-box” personal computer using a 1 MHz sampling rate and fed to a Hafler Transnova amplifier and a step-up transformer which drove the transducer. The waveform and frequency spectrum of the incident signal are shown in Fig. 2. The -20 dB points occurred at 70 and 170 kHz. Echoes were received via a custom-built T/R switch and gated amplifier unit before being digitized.

Twenty echoes were obtained from the dorsal aspect of all animals examined and also the lateral aspect for selected subjects. The echoes were digitized at a sampling rate of 1 MHz with a Rapid System R1200 data acquisition system and 512 points per echo were stored on the hard drive of the computer. Before conducting measurements with animals, echoes with only the frame present were collected in order to ensure that unwanted reverberation would not interfere with the collection of echoes from the subjects.

B. Data analysis

The peripheral auditory system of dolphins can be modeled as an energy detector that integrates the energy in the

acoustic signal (Johnson, 1968; Au *et al.*, 1988). Therefore, target strength most appropriate to a dolphin should be calculated in terms of energy in the broadband incident and reflected signals. Target strength based on energy can be defined as

$$TS_E = 10 \log \left(\frac{\int_0^{T_e} s_e^2(t) dt}{\int_0^{T_i} s_i^2(t) dt} \right) = 10 \log \left(\frac{\int_0^{F_e} |S_e(f)|^2 df}{\int_0^{F_i} |S_i(f)|^2 df} \right), \quad (1)$$

where $s_e(t)$ and $s_i(t)$ are the pressure waveforms of the echo referenced to 1 m from the target and the incident signal at the target, respectively, $S_e(f)$ and $S_i(f)$ are the Fourier transform of the echo and incident waveforms, respectively, T_e and T_i are the durations of the echo and incident signal, respectively, F_e and F_i are the maximum frequencies in the spectrum of the echo and incident signals, respectively, so that $S_e(f) \equiv 0$ for $f > F_e$ and $S_i(f) \equiv 0$ for $f > F_i$, respectively. The expressions inside the right most logarithm of Eq. (1) are the energy flux density of the echo, $E_e(f)$, and the incident signal, $E_i(f)$, in the frequency domain. The frequency dependent target strength of a target can be simply written as

$$TS(f) = 10 \log \left(\frac{|E_e(f)|}{|E_i(f)|} \right). \quad (2)$$

In order to examine the waveform in the time domain and examine the time differences between highlights, the envelope of the cross correlation function was calculated using the equation

$$c(t) = \text{env}[\mathcal{I}^{-1}(S_e(f)S_i(f))], \quad (3)$$

where \mathcal{I}^{-1} is the inverse Fourier transform and the product $S_e(f)S_i(f)$ is the cross-correlation function between the echo and incident waveforms. The envelope was determined using the Hilbert transform procedure (Rihaczek, 1969).

A convenient approach to analyzing multi-highlight echoes is to consider the Fourier transform of such signals. We can express a two-highlight echo and its Fourier transform by the equation

$$\mathcal{I}[s_e(t) + as_e(t - \tau)] = |S_e(f)| \sqrt{1 + a^2 + 2a \cos(2\pi f\tau)}, \quad (4)$$

where \mathcal{I} denotes the Fourier transform of the variables in the bracket, $S_e(f)$ is the Fourier transform of $s_e(t)$, “a” is the reflection coefficient of the secondary reflecting element, and τ is the time delay between the primary and secondary reflection. Equation (4) will have local minima at frequencies where the argument of the cos is equal to odd multiples of π , so that

$$f_{l \min} = \frac{2n + 1}{2\tau}, \quad (5)$$

where $n=0, 1, 2, \dots$. The frequency spacing (Δf) between two consecutive local minima will be $1/\tau$. In a special case of two secondary highlights, both having the same amplitude, $f_{l \min}$ will be the same as in Eq. (2) but τ will be the sum of the two time delays. If the two secondary highlights are not of the same amplitude, a simple analytical solution cannot be found, however, the spectrum of the echo will still follow the basic form as indicated by Eq. (4) with a rippled pattern and

TABLE I. Summary of Mesopelagic boundary animals measured with a simulated dolphin echolocation signal.

Family	Species	Numbers	Size range (cm)	Mean size (cm)
Fishes	Myctophidae			
	<i>Benthosema fibulatum</i>	12	2.9–7.9	5.3
	<i>Diaphus adenomus</i>	4	3.7–6.3	5.3
	<i>Diaphus chrysorhynchus</i>	2	3.8–5.4	5.0
	<i>Diaphus trachops</i>	2	3.3–3.9	3.6
	<i>Myctophum brachygnathos</i>	3	5.2–8.2	7.0
Shrimps	Grathopausidae			
	<i>Grathopausia lonispina</i>	2	4.5–7.4	6.0
	Pasiphaeidae			
	<i>Pasiphaea truncata</i>	1	6.8	6.8
	Sergestidae			
Squids	<i>Sergia fulgens</i>	3	7.1–8.3	7.6
	Endoploteuthidae			
	<i>Abralia trigonura</i>	2	2.2–4.2	3.2
	Cranchiidae			
	<i>Liocranchia reinhardti</i>	1	3.6	3.6

local minima at $f_{l \min}$. A 512 point fast Fourier transform (FFT) was used to compute all spectra.

III. RESULTS

A. Myctophids

Broadband echoes were collected from 23 myctophids, six shrimps and three squids from the dorsal aspect [the direction of the sound source with respect to the subjects in the dorsal aspect is shown in Fig. 1(b)]. A summary of the microneckton for which broadband echoes were collected is shown in Table I. Echoes were also collected from seven myctophids in the lateral aspect [the direction of the signal was perpendicular to the plane of the page shown in Fig. 1(b)]. These lateral aspect echoes were collected from four *Benthosema fibulatum*, two *Diaphus* sp., and one *Myctophum brachygnathos*. For both the dorsal and longitudinal aspects, the subjects were oriented so that the incident signal was nearly perpendicular to the longitudinal axis of the subjects.

The average echo waveform for each species was obtained for the 20 echoes obtained per subject. The average echo waveform was calculated by aligning the peaks of the envelope of each echo. The average spectrum was obtained by averaging the absolute value of the Fourier transform of each echo expressed in dB. The averaged echo waveform, the cross-correlation function between the incident and echo waveforms, and the envelope of the correlation function, and the echo spectrum for a *Benthosema fibulatum*, *Diaphus adenomus*, and *Myctophum brachygnathos* in the dorsal and lateral aspect are shown in Fig. 3. The standard deviation of the spectrum was calculated for the 20 echoes collected per species. In some cases the envelope of the cross-correlation function can be useful in showing the presence and time of occurrence of echo highlights. Interference between the echo from the front surface (surface closest to the transducer) and secondary echoes from other structures including the back

surface of the animal can be seen in the echo waveforms. From a dolphin perspective, the backscatter of myctophids in the lateral aspect would apply to a situation in which the dolphin and the prey are at the same depth. The target strength based on energy for all the myctophid measured in the lateral aspect varied from a high of -51.7 ± 0.2 dB to a low of -59.5 ± 0.8 dB.

Interference between the echo from the front surface (surface closest to the transducer) and secondary echoes from other structures including the back surface of the animals can be seen in the echo waveforms and sometimes in the envelope of the cross-correlation function for the dorsal aspect of the three species represented in Fig. 3. Although the presence of multi-pulse interference effects is more obvious in the echo waveform than in the cross-correlation function, the envelope of the cross-correlation function is useful in obtaining the time separation between multiple echo components. The structures of the echoes for the dorsal and lateral aspects were not very different from one another. This is because the multi-highlights were caused by the same structures but from different aspects, although the thickness of the fish was narrower in the lateral aspect than in the dorsal aspect. The echoes from the *Myctophum brachygnathos* in the lateral aspect had more structure than those of the other two myctophids in Fig. 3 and were slightly longer in duration than its corresponding dorsal reflection. This may have been caused by the longitudinal axis of the fish being slightly off the normal to the direction of the incident signal so that the secondary echoes had slightly longer propagation paths. Unfortunately, we cannot specify the specific parts of the fish anatomy that contributed to specific secondary reflections because the resolution capability of the incident signal was not fine enough.

Target strength calculation based on Eq. (2) was limited to frequencies above 70 kHz. Below 70 kHz, the spectral amplitude of the incident signal dropped below the -20 dB

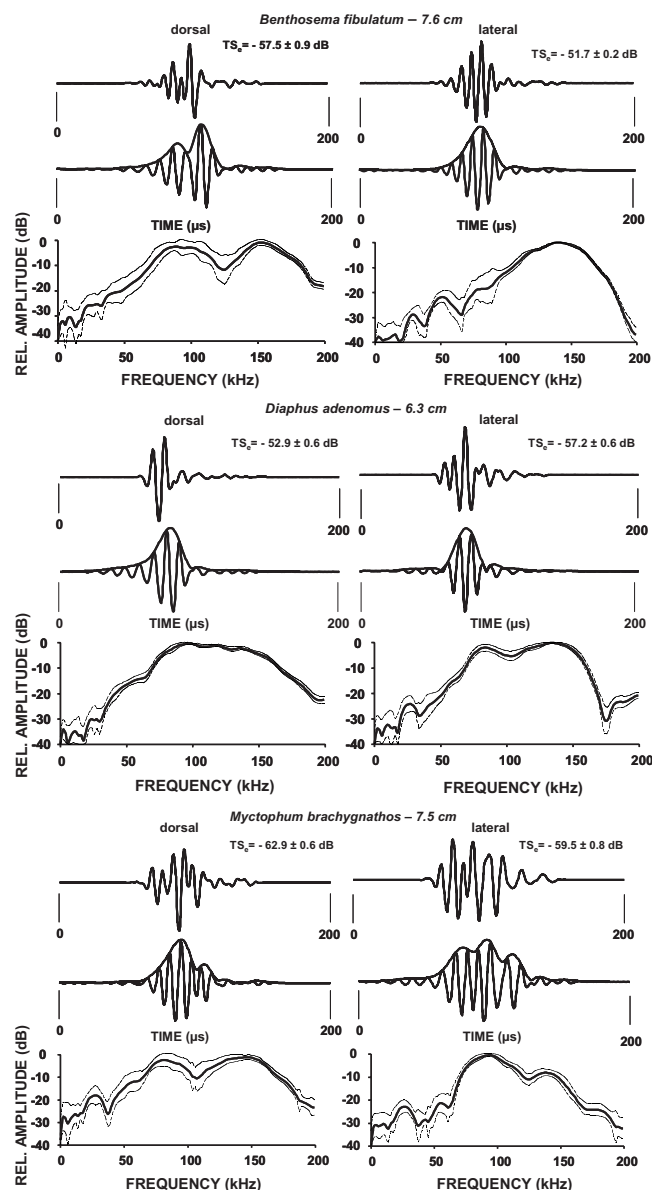


FIG. 3. The averaged echo waveform, the cross-correlation function between the averaged incident signal, and averaged echo waveform, the envelope of the correlation function and the averaged echo spectrum along with its standard deviation over the 20 pings for each orientation are shown for a *Benthosema fibulatum*, *Diaphus adenomus*, *Myctophum brachygnathos* in the dorsal and lateral aspects.

point and the target strengths fluctuated considerably with frequency within a ping and between pings. This type of behavior was probably caused by having a progressively smaller value in the denominator of an equation and by quantization errors inherent in the 12 bit digitization process. The fluctuation problem did not exist for frequencies above 170 kHz, however, target strength results above 170 kHz were denoted by a dashed curve to suggest that the results may not be as reliable as those between 70 and 170 kHz. The averaged target strengths as a function of frequency for the same subjects shown in Fig. 3 are shown in Fig. 4 for both the dorsal and lateral aspects. The thick solid curve is the averaged target strength and the thin curves represent the \pm one standard deviation values over the 20 echoes collected

per subject. The presence of a weak cosine ripple structure in both the echo and the target strength spectra was most obvious for the *Diaphus adenomus* in the lateral aspect, having two distinct local minima, and for the *Myctophum brachygnathos* in both aspects. Less developed cosine ripple structure can also be seen in the spectra for the *Myctophum brachygnathos* in both aspects and for the *Diaphus adenomus* in the dorsal aspect. The target strength spectra from all of the subjects shown in Fig. 4 had relatively deep local minima between -70 and -80 dB except for *Diaphus adenomus* in the dorsal aspect. Unfortunately, the bandwidth of the incident signal was not wide enough so that more than one ripple could be seen except for *Diaphus adenomus* in the lateral aspect. Nevertheless, the presence of the local minima and ripples are clear indicators of the presence of multiple highlight components in the waveform of the echoes.

The presence of multiple reflective components in an echo will also tend to increase the length of the echo compared with the incident signal. The greater the number of reflective components in the echo, the longer the echo will be. The larger the sum of all the echo delay will also make the frequency spacing between local minimas shorter. The echo from the lateral aspect of both the *Diaphus adenomus* and *Myctophum brachygnathos* are longer in duration than for the dorsal aspect. The sum of the highlight delays was large enough to make the frequency spacing between two consecutive local minima small enough so that both minima could be seen in the target strength spectra.

The frequency at which the local minima occurred in the target strength as a function of length is shown in Fig. 5 for the 18 *Benthosema fibulatum* that were insonified in the dorsal aspect. The data fell into two distinct groups: (1) length smaller than 5.75 cm and minima frequencies less than 107 kHz, and (2) length greater than 7.25 cm and minima frequencies clustered about 60 kHz. The linear regression line has a negative correlation between the frequency of the local minima and fish length ($R^2=0.772$). Unfortunately, we did not capture any specimen with lengths between the two clusters. Within both clusters, there is hardly any trends of $f_{l \min}$ with frequency, probably because the length differences were small. It is only when all the data are considered together that a negative correlation with minima frequency was found. Nevertheless, the regression line suggests a general tend of decreasing local minima frequency with length and since height should increase with length, longer delays between multiple echo components and lower local minima frequencies should occur. However, the possibility exists that the decrease in $f_{l \min}$ may not be best represented by a linear regression curve. The length variable was used because we unfortunately did not measure the height or thickness of the subjects. However, we were able to obtain ten *Benthosema fibulatum*, preserved in formaldehyde and measured the length, height, and thickness of the samples. The height measurements are shown as a function of length in Fig. 6. The longest *Benthosema* was 4.3 cm and the linear regression line fitting the data had a R^2 value of 0.88. Therefore, the height of myctophids with length smaller than 4.3 cm was directly proportional to height.

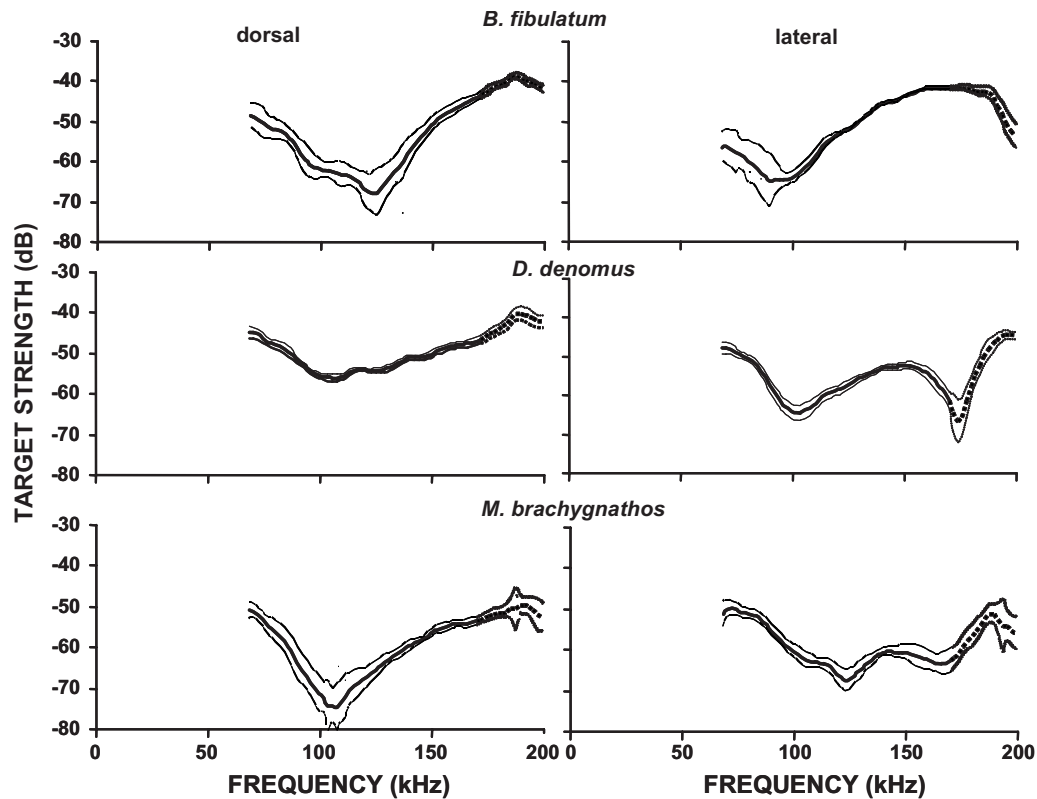


FIG. 4. The mean and standard deviation of the target strength spectra taken over 20 pings for the subjects of Fig. 3 in both the dorsal and lateral aspects.

B. Shrimps and squids

The averaged echo waveform, the cross-correlation function between the averaged incident signal and averaged echo waveform, the envelope of the correlation function and the averaged echo spectrum for three shrimps, *Sergia fulgen*, *P. truncata*, and *Gnathophausia longispina*, are depicted in Fig. 7 and for two squids, *Liocranchia reinhardti* and *Abraia trigonura* in Fig. 8. All echoes from the shrimp and squid were collected with the animals in the dorsal aspect. The effects of multipath interference can be seen in the waveform and the cross-correlation function of both echoes by an abrupt change in the shape of the curves consisting of a sharp

drop off in the amplitude when compared with the incident signal. The echo waveforms are less complex in shape than those of the myctophids, with fewer echo components. As with the other micronekton, the effects of multipath interference can be seen in the waveform and the cross-correlation function of both echoes.

The target strength spectra for the three shrimps and two squids are shown in Fig. 9. The effect of multi-path interference is clearly seen by the presence of a local minima in the frequency spectra. Both spectra suggest that a rippled pattern would be present if the frequency range of the incident signal extended beyond 200 kHz. The target strength spectra for the squids had the largest variations throughout the entire frequency range (68–200 kHz) on a ping to ping basis, suggesting that the echo formation process was more sensitive to slight changes in aspect angle caused by the movement of the ship than for the other micronekton.

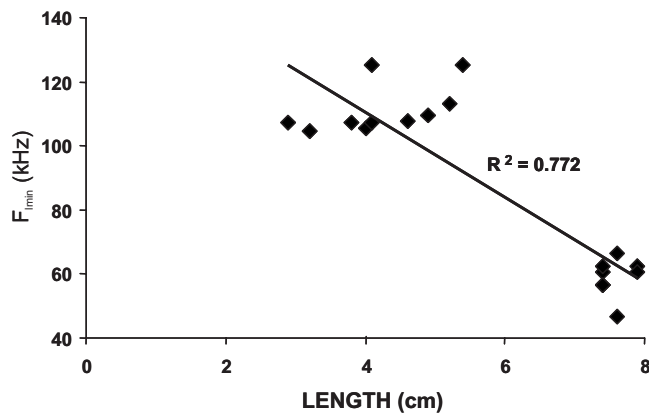


FIG. 5. The local minima frequency (associated with $n=0$) in the target strength and echo spectra plotted as a function of length echoes from the dorsal aspect for all the *Benthosema fibulatum*. The averaged echo waveforms and spectra were taken over the 20 echoes recorded per orientation for each animal.

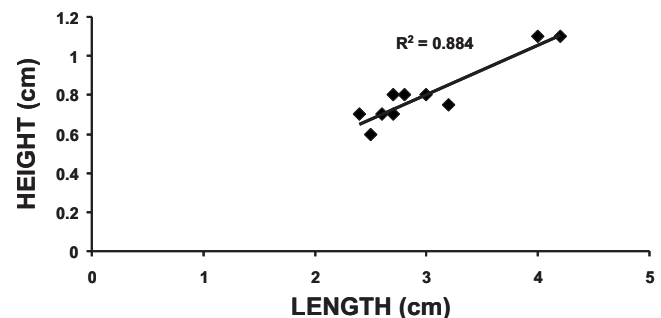


FIG. 6. Results of height versus length for *Benthosema fibulatum* preserved in formaldehyde.

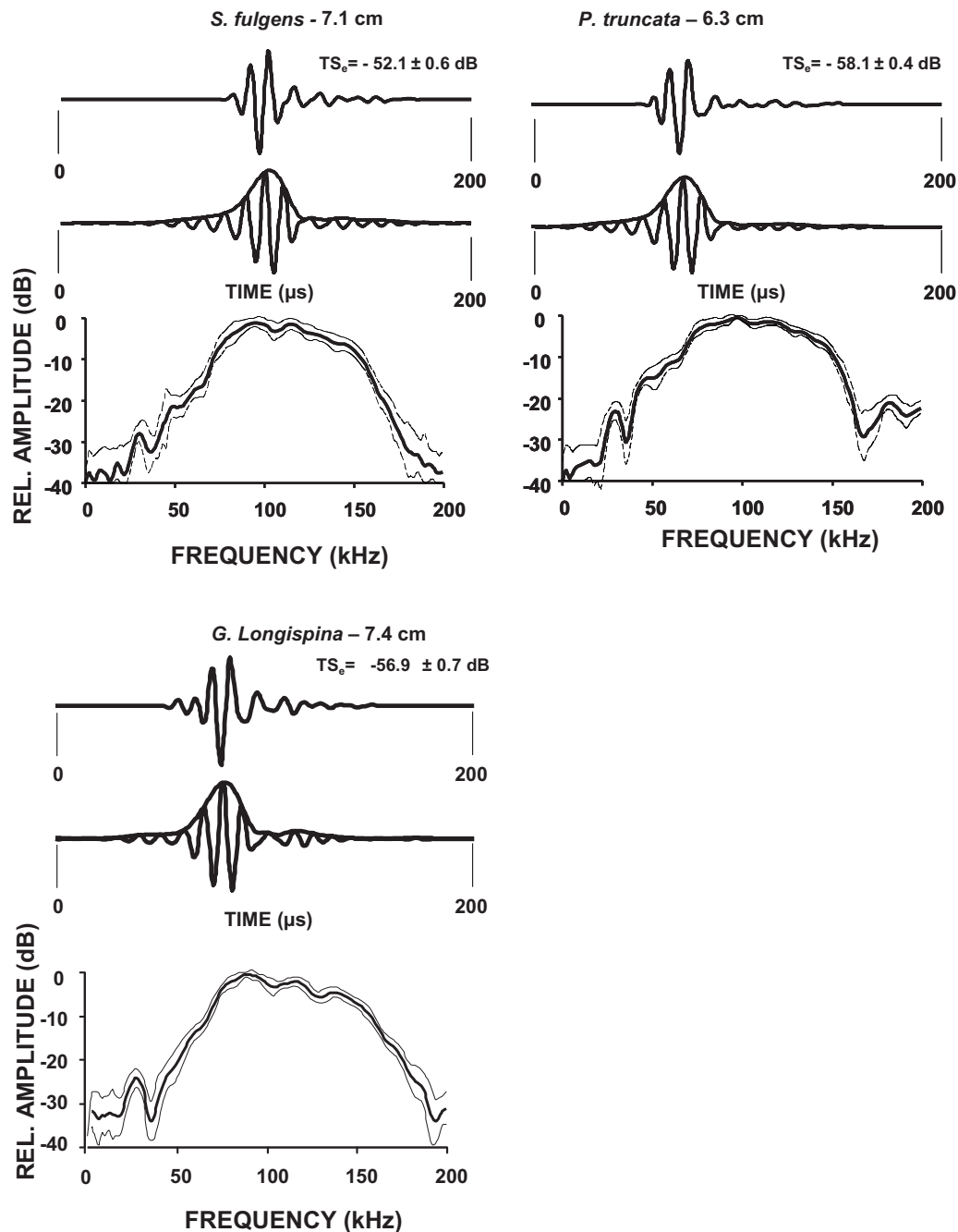


FIG. 7. The echo waveform, cross-correlation function, the envelope of the cross-correlation function, and the echo spectra for three species of shrimps, *Sergia fulgens* and *Pasiphaea truncata* and *Gnathophausia longispina*. The length of the specimen is denoted below the species name. The averaged echo waveforms and spectra were taken over the 20 echoes recorded per orientation for each animal.

IV. DISCUSSION AND CONCLUSIONS

The spectra of all of the target strength results were dominated by the presence of minima and associated ripple-like variations in the echo and target strength spectra. The results are relatively consistent with the broadband acoustic backscatter work of [Chu *et al.* \(1992\)](#), [Stanton *et al.* \(1996\)](#), and [Chu and Stanton \(1998\)](#). Their studies involved zooplankton from several groups including decapod shrimps, euphausiids, hard shelled gastropods, and gas bearing siphonophores. Because of the small size of the organisms, higher frequency modulated signals from 400 to 800 kHz were used. The broadband dolphin-like signal used in this study had a usable band between 70 and 200 kHz, slightly larger

than the octave band used by [Chu and Stanton \(1998\)](#). The shrimp-like krill, euphausiid and decapod shrimp are similar to the shrimp species used in this study. We could not find any references of broadband acoustic studies with myctophids, the main subject of our study.

We can gain a general appreciation of the role of echolocation by spinner dolphins while foraging on the MBC by relating results obtained here with our knowledge of the echolocation signals used by spinner dolphins and the echolocation detection capability of bottlenose dolphin in waters inhabited by snapping shrimp. The echolocation signals emitted by spinner dolphins ([Schotten *et al.*, 2003](#)) are relatively similar in spectra and source energy flux density to

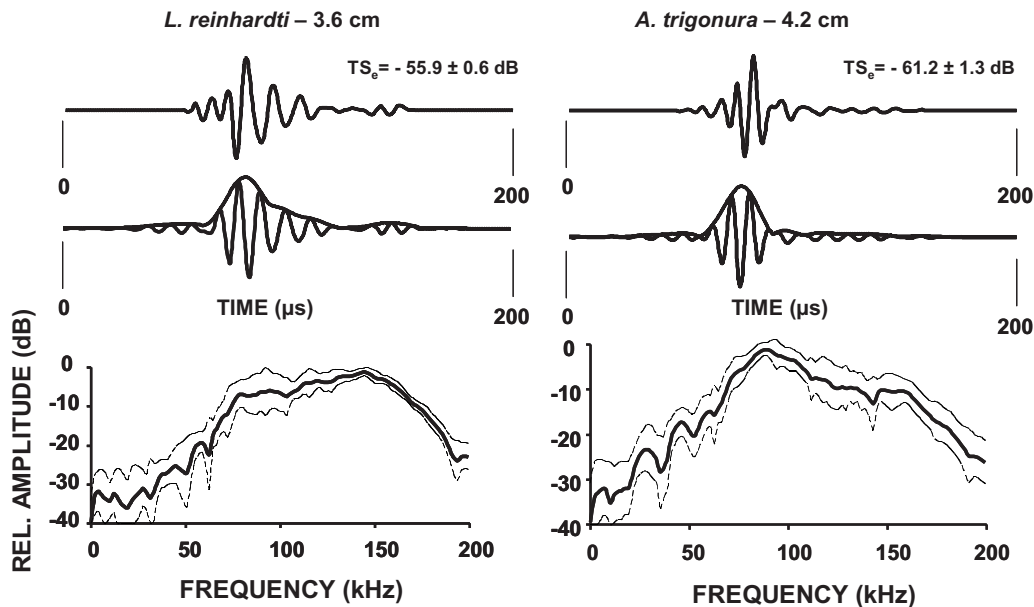


FIG. 8. The echo waveform, cross-correlation function, the envelope of the cross-correlation function and the target strength for two species of squid, *Liocranchia reinhardtii* and *Abralia trigonura*. The length of the specimen is denoted below the species name. The averaged echo waveforms and spectra were taken over the 20 echoes recorded per orientation for each animal.

those used by bottlenose dolphins (Au, 1993). The target strength based on energy (-51.7 to -59.5 dB) of myctophids in the lateral aspects can be used to estimate the echolocation detection ranges of spinner dolphins swimming at about the same depth as a single fish. The target detection threshold of a bottlenose dolphin for a 2.54-cm-diam solid stainless steel sphere with a target strength of -41.0 dB was 73 m in waters inhabited by snapping shrimp (Au, 1993). The inshore waters around the Hawaiian Islands where spinner dolphins forage are also inhabited by snapping shrimp (Lammers *et al.*, 2008). If we assume that the snapping shrimp noise levels are about the same as for the waters of Kaneohe Bay, Oahu, Hawaii, where the bottle experiment was conducted and that the echolocation detection capability of bottlenose and spinner dolphins are roughly equivalent, then we can estimate range at which myctophids may be detected. Following the approach of Au *et al.* (2007) the echo energy flux density in dB that a dolphin will receive can be expressed by the equation

$$EE = SE - 2TL + TS, \quad (6)$$

where SE is the source energy flux density, TL is the one way transmission loss and TS is the target strength based on energy. If we assume that the source energy flux density and received echo energy flux density are the same for the bottlenose and spinner dolphins, we will have the following equation to satisfy:

$$-2TL_B + TS_B = -2TL_S + TS_S, \quad (7)$$

where the subscript B and S refer to the bottlenose and spinner dolphins, respectively. Assuming spherical spreading, we have

$$40 \log(r_S) + 2\alpha r_S = 40 \log(r_B) + 2\alpha r_B + TS_S - TS_B, \quad (8)$$

where $r_B = 73$ m, $TS_B = -41$ dB, $TS_S = -52$ to -60 dB, and the absorption loss at 120 kHz is approximately

0.044 dB/m. Inserting the values appropriate to the bottlenose and spinner dolphin situations, the detection range of MBC organisms can be estimated. However Eq. (8) belongs to a class of transcendental equation that does not have a closed-form solution so it must be solved numerically. Inserting the appropriate values into Eq. (8), we obtained a maximum detection range for a single myctophid to be between 30 and 45 m. The MBC contains patches that can be quite dense over spatial scales of tens of meters (Benoit-Bird and Au, 2003c) with the orientation of the swimming myctophids dynamically varying with respect to a dolphin so that the use of a broadside target strength values should be appropriate. The detection range of an ensemble within the two-way beam of echolocating dolphins will increase over that of a single myctophid if their echoes are within the short integration time of the dolphin (264 μ s, Au, 1993) or about 40 cm. Given the animal densities reported from field studies (2001, 2006), micronekton in these layers can be spaced 1 every 8.5 cm. With the averaged sized individual being about 7 cm, the resulting spacing between animals in the scattering layer would be less than 2 cm, well within the integration time of the dolphin. Only at densities below about 10 animals/m³ would an animal of this size be detected individually by the dolphin. If for example four additional myctophids at the normal aspect are within the beam, the target strength will increase by 6 dB and the maximum detection range would increase to about 57 m. This rough calculation suggests that spinner dolphins may be able to detect patches in the MBC at sufficient range to influence their foraging behavior.

The detection of patches in the MBC will probably depend on the presence of myctophids rather than either squids or shrimps. Benoit-Bird and Au (2001) had slightly more squid and shrimp specimens and obtained results that clearly showed the target strength of myctophids at 200 kHz was

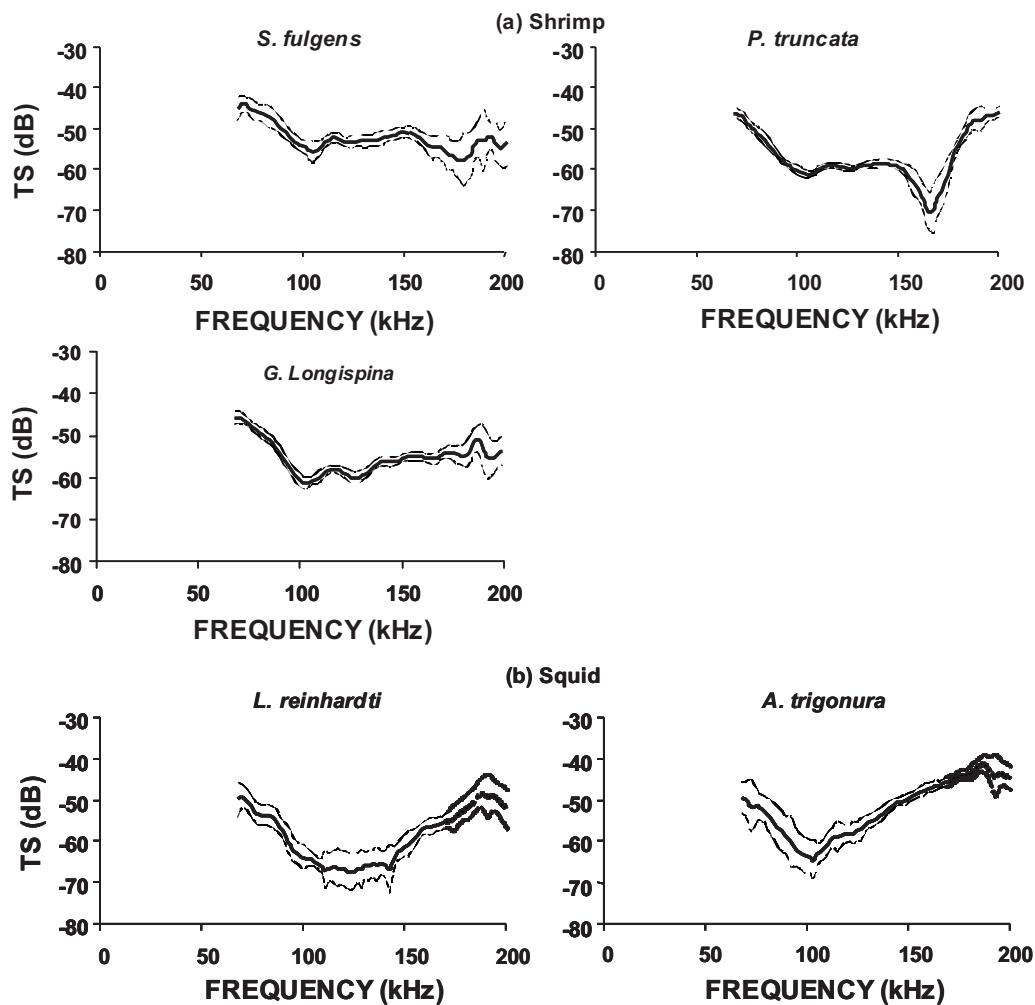


FIG. 9. The target strength spectra calculated from the dorsal aspect echoes for the shrimp species of Fig. 7 and the squid species of Fig. 8.

about 5 dB higher than squid and about 15 dB higher than shrimp of equivalent length. The three squids captured in this study were relatively small (2.2, 3.6, and 4.4 cm length) with the target strengths between -56 and -61 dB. The five shrimps were larger than the squids with lengths between 4.5 and 8.3 cm and target strength between -52 and -58 dB.

In order to consider whether or not an echolocating spinner dolphin can discriminate between myctophids, squids, and shrimps based on their echoes, the two-way 3 dB beamwidth of about 10° for the bottlenose dolphin (Au, 1992) must be taken into account. If we assume that the spinner dolphin would have approximately the same two-way beamwidth, then in most situations, a spinner dolphin echolocating on the MBC would have more than one micronekton within its beam. The example provided by Benoit-Bird and Au (2003c) of broadband backscatter from the MBC obtained with a planar transducer having a two-way beamwidth of 8° showed a series of echoes highlights within a $200 \mu\text{s}$ window, making it difficult to separate echoes from different organisms. Madsen *et al.* (2005) suggest that beaked whales can discriminate prey type in a relatively dense prey field. However, the prey field of the beaked whale is not nearly as dense as the MBC. The example in Madsen *et al.* (2005) shows a single echo from a prey in a 5 m range space. The example provided by Benoit-Bird and Au (2003a) had eight

echoes, one following immediately after another in less than a meter range space. This would make discrimination of different species highly unlikely. Besides, the echo spectra for the different micronekton examined were complex and without any specific features useful for species identification. A species may be recognized from information on its swimming behavior collected over several echolocation transmissions, however, this process will be complicated by the presence of several micronekton within the beam. Furthermore, dolphin echolocation signals are Doppler tolerant so that negligible Doppler information can be obtained from a single echo (Au, 1993).

Although all animal groups in our study, myctophid, shrimp and squid, exhibited relatively similar patterns of variation with frequency, the presence of a skeletal structure in the myctophid made the backscatter process slightly more complicated than for shrimp and squid. In all three groups of animals, the presence of the minima were directly associated with the presence of multi echo components, the first being a reflection of the incident acoustic signal at the front surface, the surface nearest to the transducer, and the second being a reflection of the signal that penetrated into the body of the organisms and then reflected either off the skeletal structure or the back surface of the specimen. The minima in the spectra are not as deep as would be suggested by Eq. (4). In Eq.

(4), the assumption of perfect reflection off flat surfaces that are perpendicular to the direction of the incident signal was made. In our case, the reflective surfaces were not flat but curved. Furthermore, the front surface of the myctophids in the dorsal aspect had a slight concave shape while the back surface had a convex shape. Therefore, the secondary highlights may have been correlated with the primary highlight off the front surface. The correlation was probably far from perfect, however, affecting the spectral interference between the highlights.

The frequency of the first local minima between 60 and 200 kHz had a strong negative correlation with the length of *Benthosema fibulatum*. This characteristic is consistent with the notion that the height is directly proportional to the length of the fish, at least for fish smaller than 6 cm. As the height of the fish increase, the delay time between echo components should increase, causing the frequency of the local minima to decrease as our data showed in Fig. 5.

Recent measurements at 38, 70, 120, and 200 kHz of the volume backscatter of the mesopelagic boundary community by Benoit-Bird (2006) in the waters of Oahu, Hawaii indicated that the volume scattering decreased with frequency whereas our target strength results exhibited a local minima between 100 and 150 kHz. The frequency dependency of individual micronektons of the MBC may not be directly related to volume scattering from an ensemble of the same organisms suggesting that the volume scattering process is very complex and not well understood. It should also be noted that Benoit-Bird (2008) did not use the same pulse length at the four frequencies so that the same volume of water was not examined. The 70, 120, and 200 kHz versions of the Simrad EK-60 have conical beams of approximately the same width so that the volume of water examined at any depth will be a truncated cone with its height being determined by the pulse length (Urlick, 1983). The pulse lengths were 256 μ s at 38 kHz, 128 μ s at 70 and 64 μ s at 120 and 200 kHz making the height of the examined region four times greater at 38 kHz and two times greater at 70 kHz than at 120 and 200 kHz. The effects of examining different volumes are not known.

Backscatter from a mesopelagic layer can be rather complex if the density of organism is high and a number of organisms are within the beam of the echosounder. In such a case, there will be a large amount of constructive and destructive interference, making the backscatter process so complicated that any analogy with a simple frequency response from individual organisms seems irrelevant. To illustrate this, we created a simulated echo using the dorsal aspect echo from the *B. fibulatum* in Fig. 3 by adding seven versions of the echo but with arbitrary delays between each echo and obtained the echo waveform shown in Fig. 10. Below the waveform are the echo and target strength spectra. There are obvious differences in the spectra shown in Fig. 10 and Fig. 3. The results of our simulation suggest that the spectral integrity of echoes from individual animals will not be preserved when echoes contain backscatter from several identical animals.

It is important to understand the relationship between backscatter measured by an echo-sounder and that which an

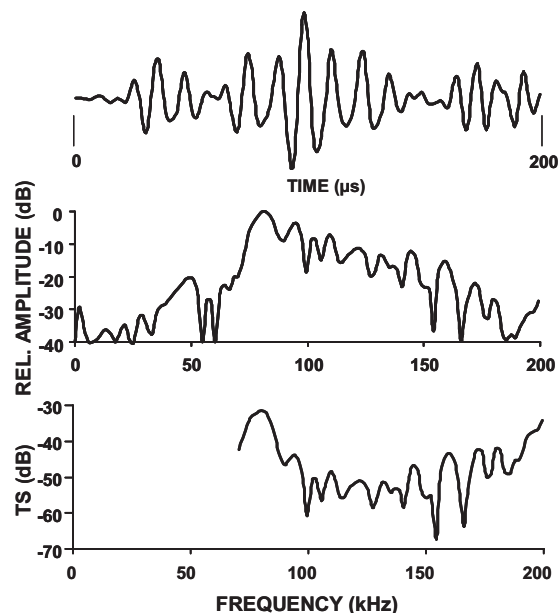


FIG. 10. Waveform for a simulated *Benthosema fibulatum* echo consisting of seven versions of the dorsal aspect echo waveform shown in Fig. 3, summed together with an arbitrary delay for each replica. The echo and target strength spectra are shown below the echo waveform.

echolocating spinner dolphin receives. Clearly, the backscatter process from either an echosounder or dolphin perspective is very complicated and deserves more attention. The complexity of the backscatter process results from the high density of mixed species and inhomogeneity that seems inherent in the mesopelagic layer. Zooplankton may contribute to some of the volume backscatter obtained by an echosounder since the micronekton of the mesopelagic boundary migrate horizontally over 2 km towards shore to forage on zooplankton at night. It stands to reason that zooplankton density should be several orders of magnitude higher than the density of micronekton, otherwise the long horizontal migration would not result in sufficient energetic gain. The contribution of a large zooplankton population on the volume backscatter cannot be overlooked.

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- Au, W. W. L. (1993). *The Sonar of Dolphins* (Springer-Verlag, New York).
- Au, W. W. L. (1992). "Application of the reverberation-limited form of the sonar equation to dolphin echolocation," *J. Acoust. Soc. Am.* **92**, 1822–1826.
- Au, W. W. L., and Snyder, K. J. (1980). "Long-range target detection in open waters by an echolocating atlantic bottlenose dolphin (*Tursiops truncatus*)," *J. Acoust. Soc. Am.* **68**, 1077–1084.
- Au, W. W. L., Moore, P. W. B., and Pawloski, D. A. (1988). "Detection of complex echoes in noise by an echolocating dolphin," *J. Acoust. Soc. Am.* **83**, 662–668.
- Au, W. W. L., and Benoit-Bird, K. J. (2003). "Acoustic backscattering by Hawaiian Lutjanid snappers II: Broadband temporal and spectral structure," *J. Acoust. Soc. Am.* **114**, 2767–2774.
- Au, W. W. L., Benoit-Bird, K. J., and Kastelein, R. A. (2007). "Modeling the detection range of fish by echolocating bottlenose dolphins and harbor porpoises," *J. Acoust. Soc. Am.* **121**, 3954–3962.
- Benoit-Bird, K. J., and Au, W. W. L. (2001). "Target strength measurements of hawaiian mesopelagic boundary community animals," *J. Acoust. Soc. Am.* **110**, 812–819.
- Benoit-Bird, K. J., Au, W. W. L., Brainard, R. E., Lammers, M. O. (2001). "Diel horizontal migration of the Hawaiian mesopelagic boundary community observed acoustically," *Mar. Ecol.: Prog. Ser.* **217**, 1–14.
- 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.* **217**, 1–14.
- Benoit-Bird, K. J., and Au, W. W. L. (2003a). "Prey dynamics affect foraging by a pelagic predator (*Stenella longirostris*) over a range of spatial and temporal scales," *Behav. Ecol. Sociobiol.* **53**, 364–373.
- Benoit-Bird, K. J., and Au, W. W. L. (2003b). "Spatial dynamics of the Hawaiian mesopelagic boundary community," *ICES J. Mar. Sci.* **60**, 899–913.
- Benoit-Bird, K., and Au, W. W. L. (2003c). "Target strength and density structure of Hawaiian mesopelagic boundary community patches," *J. Acoust. Soc. Am.* **114**, 1888–1897.
- Benoit-Bird, K. J., and Au, W. W. L. (2004). "Fine-scale diel migration dynamics of an island-associated sound-scattering layer," *Deep-Sea Res., Part I* **59**, 707–719.
- Benoit-Bird, K. J. (2004). "Prey value and energy needs: Foraging predictions for wild spinner dolphins," *Mar. Biol. (Berlin)* **145**, 435–444.
- Benoit-Bird, K. J., and Au, W. W. L. (2006). "Extreme diel horizontal migrations by a tropical nearshore resident micronekton community," *Mar. Ecol.: Prog. Ser.* **319**, 1–14.
- Benoit-Bird, K. J. (2006). "Effects of scattering layer composition, animal size, and numerical density on the frequency response of volume backscatter," *J. Acoust. Soc. Am.* **120**, 3001.
- Chu, D., Stanton, T. K., and Wiebe, P. H. (1992). "Frequency dependence of sound backscattering from live individual zooplankton," *ICES J. Mar. Sci.* **49**, 97–106.
- Chu, D., and Stanton, T. K. (1998). "Application of pulse compression techniques to broadband acoustic scattering by live individual zooplankton," *J. Acoust. Soc. Am.* **104**, 39–55.
- Foot, K. G., Vestnes, G., MacLennan, D. N., and Simmonds, E. J. (1987). "Calibration of acoustic instruments for fish density information: A practical guide," in *International Council for the Exploration of the Sea Cooperative Research Report No. 144*.
- Johnson, C. S. (1968). "Relation between absolute threshold and duration of tone pulse in the Bottlenosed porpoise," *J. Acoust. Soc. Am.* **43**, 757–763.
- Lammers, M. O., Brainard, R. E., Au, W. W. L., Mooney, T. A., and Wong, K. (2008). "An ecological acoustic recorder (EAR) for long-term monitoring of biological and anthropogenic sounds on coral reefs and in nearby waters," *J. Acoust. Soc. Am.* **123**, 1720–1728.
- Madsen, P. T., Wilson, M., Johnson, M., Hanlon, R. T., Bocconcelli, A., Aguilar de Soto, N., and Tyack, P. L. (2007). "Clicking for calamari: Toothed whales can echolocate squid *Loligo pealeii*," *Aquat. Biol.* **1**, 141–150.
- Madsen, P. T., Johnson, M., Aguilar de Soto, N., Ximmer, W. M., and Tyack, P. (2005). "Biosonar performance of foraging beaked whales (*Mesoplodon densirostris*)," *J. Exp. Biol.* **208**, 181–194.
- Norris, K. S., and Dohl, T. P. (1980). "Behavior of the Hawaiian spinner dolphin, *Stenella longirostris*," *Fish. Bull.* **77**, 821–849.
- 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.
- Rihaczek, A. W. (1969). *Principles of High-Resolution Radar* (McGraw-Hill, New York).
- Stanton, T. K., Chu, D., and Wiebe, P. H. (1996). "Acoustic scattering characteristics of several zooplankton group," *ICES J. Mar. Sci.* **53**, 289–295.
- Schotten, M., Au, W. W. L., Lammers, M. O., and Aubauer, R. (2003). "Echolocation recordings and localizations of wild spinner dolphins (*Stenella longirostris*) and pantropical spotted dolphins (*Stenella attenuata*) using a four hydrophone array," in *Echolocation in bats and dolphins*, edited by J. Thomas, C. Moss, and M. Vater (University of Chicago Press, Chicago), pp. 393–409.
- Urick, R. J. (1983). *Principles of Underwater Sound*, McGraw-Hill, New York.