

# Acoustic basis for fish prey discrimination by echolocating dolphins and porpoises

Whitlow W. L. Au

Marine Mammal Research Program, Hawaii Institute of Marine Biology, University of Hawaii, P.O. Box 1106, Kailua, Hawaii 96734

Brian K. Branstetter

U.S. Navy Marine Mammal Program, Space and Naval Warfare Systems Center, San Diego, Code 71510, 53560 Hull Street, San Diego, California 92152

Kelly J. Benoit-Bird

College of Oceanic and Atmospheric Sciences, Oregon State University, Corvallis, Oregon 97331

Ronald A. Kastelein

SEAMARCO, Julianalaan 46, 3843 CC Harderwijk, The Netherlands

(Received 24 December 2008; revised 1 April 2009; accepted 9 May 2009)

The biosonar system of dolphins and porpoises has been studied for about 5 decades and much has been learned [Au, W. W. L. (1993). *The Sonar of Dolphins* (Springer, New York)]. Most experiments have involved human-made targets; little is known about odontocetes' echolocation of prey. To address this issue, acoustic backscatter from Atlantic cod (*Gadus morhua*), gray mullet (*Chelon labrosus*), pollack, (*Pollachius pollachius*), and sea bass (*Dicentrarchus labrax*) was measured using simulated biosonar signals of the Atlantic bottlenose dolphin and harbor porpoise. The fish specimens were rotated so that the effects of the fish orientation on the echoes could be determined. Echoes had the highest amplitude and simplest structure when the incident angle was perpendicular to the longitudinal axis of the fish. The complexity of the echoes increased as the aspect angle of the fish moved away from the normal aspect. The echoes in both the time and frequency domains were easily distinguishable among the four species of fish and were generally consistent within species. A cochlear model consisting of a bank of band-passed filters was also used to analyze the echoes. The overall results suggest that there are sufficient acoustic cues available to discriminate between the four species of fish based on the echoes received, independent of aspect angle.

© 2009 Acoustical Society of America. [DOI: 10.1121/1.3147497]

PACS number(s): 43.80.Ka, 43.80.Lb, 43.80.Jz [JAS]

Pages: 460–467

## I. INTRODUCTION

Echolocation experiments with captive dolphins began about 5 decades ago with Scheville and Lawrence (1956) and Kellogg (1958) attempting to obtain evidence that bottlenose dolphins (*Tursiops truncatus*) echolocated. Norris *et al.* (1961) provided unequivocal evidence to demonstrate echolocation in dolphins by using suction cup blindfold to cover a dolphin's eyes while the animal was required to swim and avoid obstacles and retrieve fish rewards that were thrown into the animal's tank. Busnel and Dzedzic (1967) also trained a blindfolded harbor porpoise (*Phocoena phocoena*) to swim through a maze of vertically hanging wire. Following these initial studies, various types of echolocation experiments have been performed to study the biosonar process and determine the capabilities of odontocetes to detect, discriminate, localize, and recognize targets.

The biosonar capabilities of dolphins to perform complex target discrimination tasks have been conducted mainly with objects that are foreign to these animals but familiar to humans. Review articles on the target discrimination experiments have been written by Nachtigall (1980), Au (1993), and Au and Hastings (2008). Some of these experiments included material and wall thickness discrimination of metallic

plates (Evans and Powell, 1967), material composition of cylinders at arbitrary aspects (Au and Turl, 1991), material composition discrimination of spheres (Aubaurer *et al.*, 2000), shape discrimination of planar targets (Barta, 1969), shape discrimination between spheres and cylinders (Au *et al.*, 1980), shape matching of polyvinyl chloride (PVC) objects across vision and echolocation (Pack *et al.*, 2002), and wall thickness of metallic cylinders (Au and Pawloski, 1992). These and other experiments have clearly shown that dolphins possess a very sophisticated biosonar system that has certain capabilities beyond the most modern and sophisticated technological sonar. From these experiments, we have gained much knowledge about the target discrimination and recognition capabilities of the dolphin biosonar system, yet these experiments provide little insight on the issues involving dolphins and porpoises foraging for prey in the wild.

The question of how far an echolocating dolphin can detect fish prey has only been addressed recently by Au *et al.* (2004) who calculated the biosonar detection ranges of killer whales foraging for Chinook salmon, by Madsen *et al.* (2004) who estimated the detection ranges of false killer whales and Risso's dolphin foraging for unspecified species of fish, and by Au *et al.* (2007) who calculated the biosonar

detection ranges of bottlenose dolphins and harbor porpoises foraging for Atlantic cod, mullet, sea bass, and pollack. However, we still need to address the issue of acoustic cues from echoes that would allow a dolphin to discriminate and recognize different species of fish allowing for selective foraging. The focus of this paper is to determine what acoustic cues are present in the echoes of fish prey would allow dolphins and porpoises to discriminate and recognize different species of fish. While it is extremely difficult to address the issue of selective foraging by echolocating dolphins and porpoise because of the difficulties in making good, regular, and consistent observations of underwater foraging behavior in the wild, a clear case of selective foraging exists for fish eating killer whales in the waters of British Columbia (Ford and Ellis, 2006). Even in months when Chinook salmon may constitute less than 15% of the salmon population, the whales still forage mainly on Chinook salmon (Ford and Ellis, 2006). Visual observations of foraging killer whales strongly suggest that they depend on echolocation to detect and recognize their prey. Whales would often be observed swimming near the surface along nearly straight line tracks for minutes and then suddenly submerge and resurface several tens of meters away with a salmon in their mouths. Collection of scales after the whales bring the prey to the surface has allowed for the identification of the salmon species. Unfortunately, such selective foraging by other species of odontocetes has not been reported. The specific cues that odontocetes may use to discriminate and recognize different species of fish will not be addressed in this study; rather, the focus will be on determining if acoustic cues that can be used for species discrimination are indeed present in the echoes of fish, an important component of selective foraging.

## II. PROCEDURE

### A. Experimental geometry

This study is an extension of the work that was reported by Au *et al.* (2007) on modeling the biosonar detection range for four species of fish and the description of the procedure will be brief with only important aspects repeated. The backscatter measurements were conducted in an outdoor tank belonging to the Sea Mammal Research Company (Seamarco) at the field station of the Netherlands National Institute for Coastal and Marine Management (RIKZ) in Jacobahaven, Zeeland, The Netherlands. The surface dimension of the tank was  $7 \times 4 \text{ m}^2$  with a water depth of 2 m. Anesthetized fish subjects were constrained in a monofilament bag that was in turn attached to a monofilament net which was attached to a rotor, as shown in Fig. 1(a). The orientation system that will be used in this study is shown in Fig. 1(b) where the arrows indicate the direction of the incident acoustic signal. The fish were rotated as simulated biosonar signals of *Tursiops truncatus* and *Phocoena phocoena* were projected and the echoes collected. A monostatic system with the same transducer projecting the signals and receiving the echoes was used. Both signals are shown in Fig. 2, with the dolphin-like signal having a peak frequency of 130 kHz and the porpoise-like signal having a peak frequency of 138 kHz. The duration of the

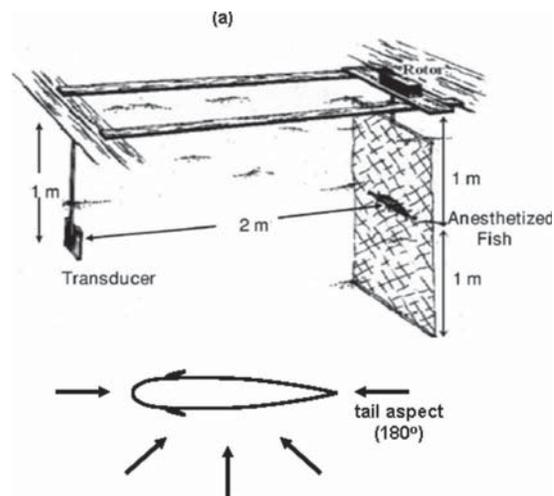


FIG. 1. (a) Experimental geometry showing a monofilament net curtain attached to a rotor with a fish subject to a monofilament net bag attached to the curtain. A monostatic echo ranging system was used in which the same transducer projected the signal and received the echoes. (b) The orientation system used in this study showing the direction of the incident signal with respect to the fish body.

dolphin-like signal was approximately  $70 \mu\text{s}$  while the porpoise-like signal was approximately  $270 \mu\text{s}$  in duration.

### B. Fish subjects

The species of fish used were Atlantic cod (*Gadus morhua*), gray mullet (*Chelon labrosus*), pollack (*Pollachius pollachius*), and sea bass (*Dicentrarchus labras*). Three fish of each species except for the pollack were examined acoustically. The lengths of the subjects were cod (29–30 cm), mullet (15–17 cm), sea bass (14–17 cm), and pollack (21 cm). These fish were on loan from “The Arsenal Aquarium,” Vlissingen, The Netherlands. They were fed to satiation each day after the measurement sessions on a diet of raw fish and in compliance with The Animal Welfare Commission of The Netherlands. After the measurements they were returned to the aquarium. Since the fish were borrowed,

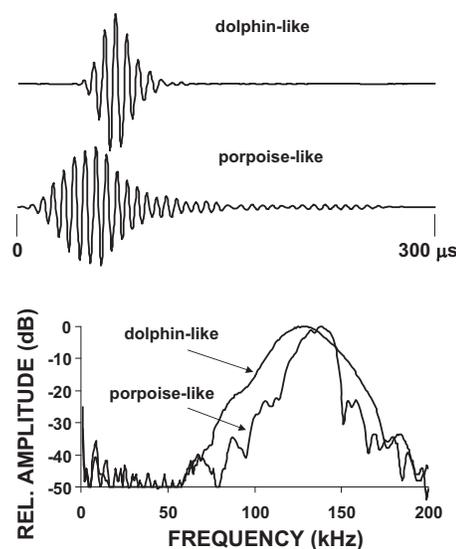


FIG. 2. The dolphin-like and porpoise-like signal waveforms and spectra.

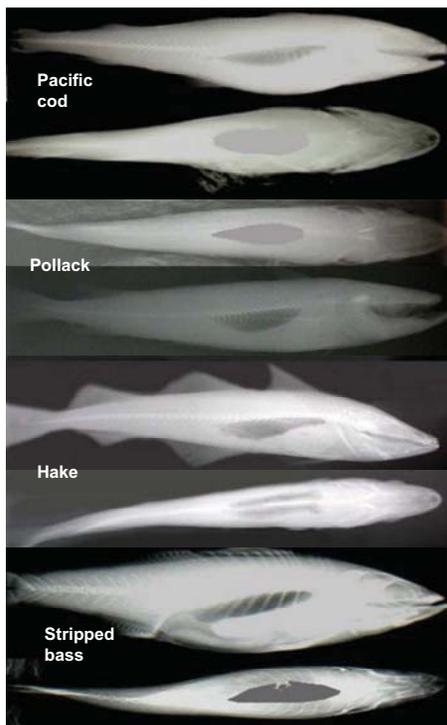


FIG. 3. (Color online) Radiograph images of four species of fish that are closely related to the Atlantic cod, mullet, and sea bass used in this study (courtesy of Dr. John Horne, U. Washington).

we did not attempt to x-ray them and risk potential injury. However, we were able to obtain radiograph images from closely related species and these are shown in Fig. 3. The images in the dorsal aspect for three of the species were digitally enhanced using PHOTOSHOP. The purpose of showing this figure is to convey to those unfamiliar with swimbladder geometry that the shape, orientation, and volume of swimbladders vary between species (Simmonds and MacLennan, 2005). Since the swimbladder is the most prominent structure affecting backscatter of acoustic signals (Foote, 1980; Foote and Ona, 1985) we expected the echoes from different fish species to have different temporal and spectral structures that could be resolved with dolphin and porpoise biosignals.

### C. Analysis with a peripheral auditory filter model

The auditory filter model of the bottlenose dolphin developed by Branstetter *et al.* (2007) was one of the tools used to examine the time-frequency characteristics of the fish echoes. The model consisted of a bank of gammatone filters, each followed by a half-wave rectifier and a low-pass filter. The output of this model resembles a spectrogram. However, unlike a spectrogram which applies the same arbitrary window lengths and shapes across frequencies (e.g., 512 point Hanning with 50% overlap), the auditory filter model incorporates the spectral and temporal resolution of bottlenose dolphin's auditory periphery. The resulting output provides a closer approximation to what the dolphin actually hears.

The auditory filter shapes of a bottlenose dolphin were measured by Lemonds (1999) at 60, 90, and 120 kHz. The shape of the auditory filters closely resembled those of a

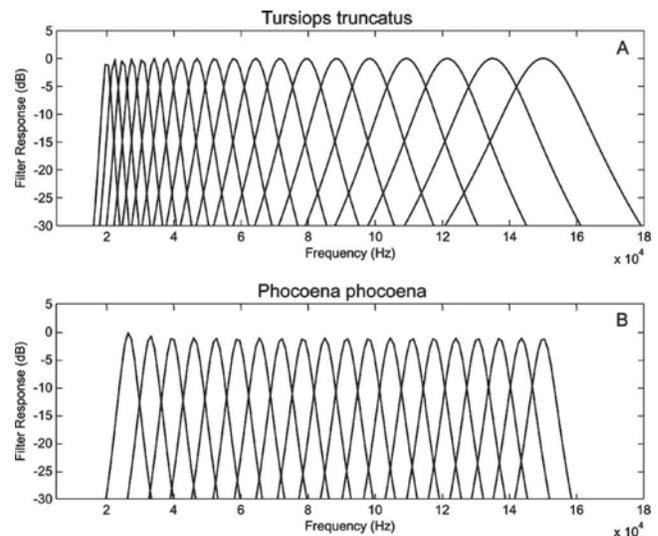


FIG. 4. Gammatone filter bank (a) modeling the auditory filterbank of a dolphin with constant  $Q$  filters using the results of Branstetter *et al.* (2007) and (b) modeling the auditory filterbank of a harbor porpoise using the results of Popov *et al.* (2006).

gammatone filter described by Patterson (1994). The impulse response of a gammatone filter is given by the equation (Patterson, 1994)

$$g_i(t) = at^{n-1} e^{-2\pi bt} \cos(2\pi f_c t - \phi), \quad (1)$$

where  $f_c$  is the center frequency of the filter,  $\phi$  is the starting phase, and  $a$ ,  $b$ , and  $n$  are the parameters determining the ramping and duration of the impulse function and consequently the width and shape of a filter (Slaney, 1993). The parameter  $b$  is related to the equivalent rectangular bandwidth (ERB), both defined by the equations

$$b = k \times \text{ERB}(f_c), \quad (2)$$

$$\text{ERB}(f_c) = \frac{f_c}{Q} + \text{min BW}, \quad (3)$$

where  $k$  is a constant and is equal to 1.019 (Patterson *et al.*, 1992),  $Q$  is the ratio of center frequency over bandwidth, and min BW is the minimum bandwidth for the low frequency channels. Since the critical ratio in dolphins approaches that of humans (Johnson, 1968) the estimated value of 24.7 for humans (Glasberg and Moore, 1990) was used in this study. Branstetter *et al.* (2007) found that a gammatone filterbank with a  $Q$  of 11.3 will produce an excellent fit to the two roex filter derived for the dolphin by Lemonds (1999) and will be used here. The gammatone filter bank that will be used to analyze the fish echoes produced by the simulated dolphin biosonar signal is shown in Fig. 4(a). In reality, the filterbank consisted of 94 frequency channels spaced between approximately 80 and 160 kHz since the spectrum of the incident signal was lower than  $-30$  dB below a frequency of approximately 70 kHz.

Popov *et al.* (2006) used a tone-tone masking paradigm with the envelope-following response evoked potential technique to measure the auditory filter shapes of *Phocoena phocoena* and *Neophocaena phocaenoides*. They described their results in terms of the roex function of Patterson *et al.* (1992)

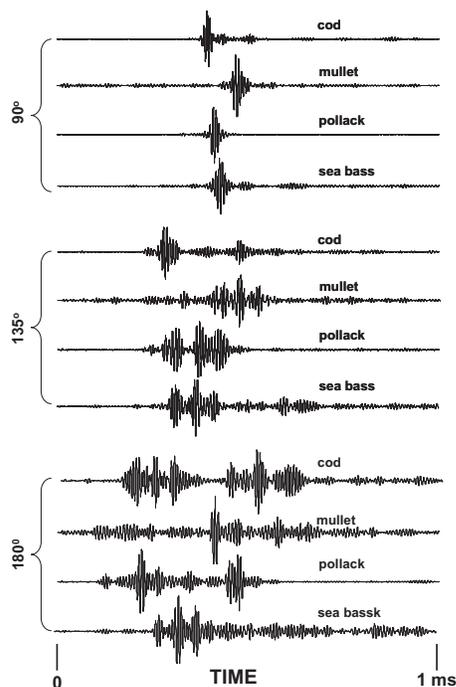


FIG. 5. Echo waveforms using the dolphin-like biosonar signal for the four species of fish examined at the broadside, 135°, and tail aspects. Each waveform was normalized.

and estimated  $Q$  values of approximately 10 at 30 kHz to approximately 40 at 150 kHz, varying with center frequency according to the equation

$$Q = q_0 f_c^k, \quad (4)$$

where  $q_0$  is a quality at  $f_c=1$ , and  $k$  determined the degree of  $Q$  dependency on  $f_c$ . Constant bandwidth filters would have  $k=0$  and constant  $Q$  filters would have  $k=1$ . Popov *et al.* (2006) found that  $k$  between 0.83 and 0.86 fit their threshold results best. The gammatone filter bank with  $Q$  values that varied according to Eq. (4) was used to analyze the results from the porpoise-like biosonar signal shown in Fig. 4(b).

### III. RESULTS

Polar plots of the target strength (based on the energy flux density in the echoes and incident signal) as a function of the aspect angle from 0° to 360° were shown in the previous publication of Au *et al.* (2007). The polar plots of target strength were in general very similar in shape for all the specimens measured and would probably not provide much information on the species of fish producing the echoes.

Examples of the echo waveforms generated with the simulated dolphin biosonar signal for the four fish species are shown in Fig. 5 at aspect angles of 90° (broadside aspect), 135°, and 180° (tail aspect). Each waveform is normalized to its maximum value. The simplest echoes occurred at the broadside aspect and consisted mainly of the specular reflection from the surface of the swimbladder facing the transducer and some secondary components from other structures in the fish. Even at the broadside aspect, the echo waveforms can be distinguished from one another. As the

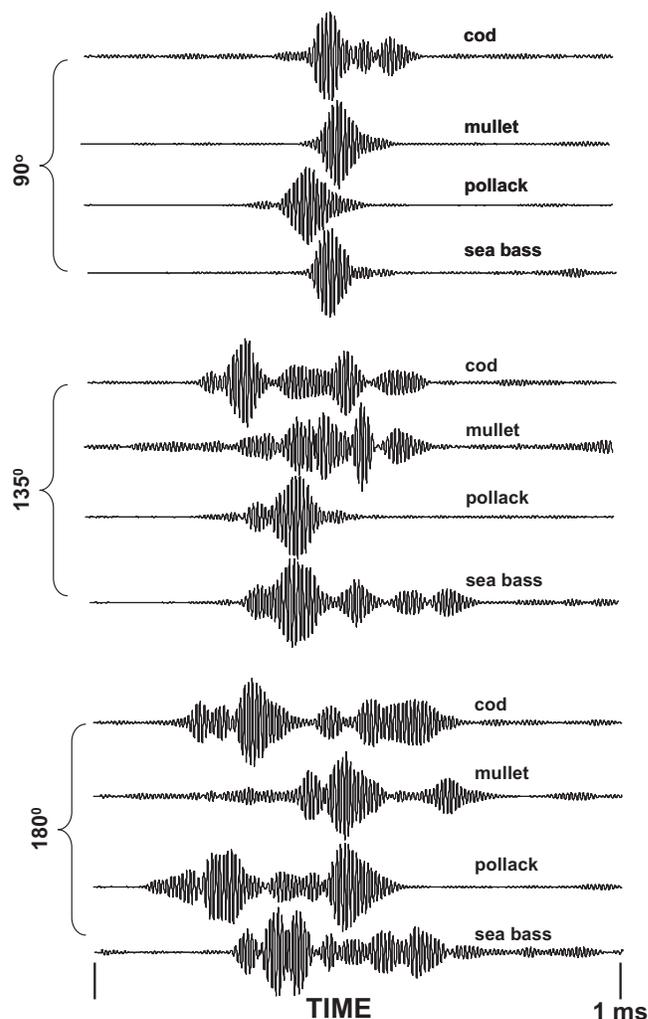


FIG. 6. Echo waveforms using the porpoise-like biosonar signal for the four species of fish examined at the broadside, 135°, and tail aspects. Each waveform was normalized.

aspect angle increased away from the broadside aspect, the echoes became longer in duration and more complex in structure as seen by the presence of more and larger secondary echo components. The difference in the echo structure between species became more distinguishable at these aspect angles than at the broadside aspect. Differences between the echoes from the four fish species at 135° and 180° include differences in the number of secondary echo components (highlights) and differences in the relative amplitude and spacing between the highlights. At the tail aspect, the echo duration was the longest which is consistent with typical swimbladder geometry. The x-ray images from the dorsal aspects in Fig. 3 show that the swimbladders are aligned with the longitudinal axis of the fish and are typically tilted dorso-ventrally. Therefore, the incident signal entering a fish from the tail aspect will travel the maximum distance propagating from the tail-end of the swimbladder to the front-end.

A similar set of echo results as in Fig. 5 but for a porpoise-like biosonar signal is shown in Fig. 6. Even with a longer and narrower biosonar signal, the echoes returning to a porpoise show differences between species that could provide discrimination cues. At the broadside aspects, the secondary echo components are not resolvable with the narrow

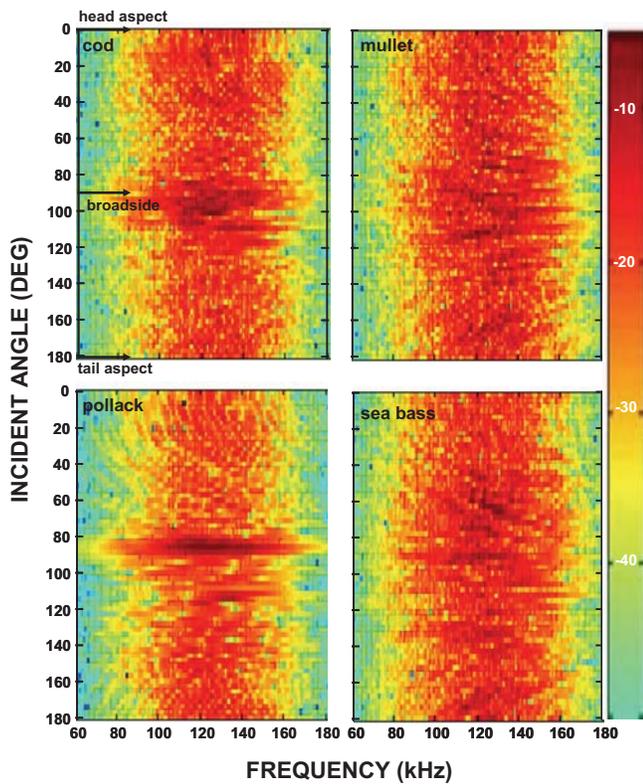


FIG. 7. (Color online) Polargrams (frequency spectra versus polar angle of the echoes) for the four species of fish obtained with the dolphin-like biosonar signal. The frequency spectra for different polar angles are shown with the amplitude color coded according to the color bar on the right.

band porpoise-like signal, except for the cod. As in the dolphin signal case, the differences become more pronounced as the aspect angle was increased from the broadside orientation. The same types of differences involving the number of highlights, the relative amplitude of highlights, and the time delay between highlights existed for the porpoise signal as observed in the dolphin signal.

Polargrams, which are the frequency spectra of the echoes as a function of the polar angle about one side of each fish species, are shown in Fig. 7 for the dolphin-like biosonar signal and in Fig. 8 for the porpoise-like biosonar signal. The amplitude of each spectrum is coded in color as shown in the color bar to one side of the figure. A similar kind of polargram can be drawn in which the envelope of the echo for each polar angle can be drawn as was done by Reeder *et al.* (2004). Perhaps the best way to visualize the polargrams is to step back and look at the pattern of changes in the spectra as the polar angle varies. Each polargram has a slightly different manner in which the echo spectra change with angle and this pattern may be used by dolphins and porpoises to discriminate a specific species of fish. One feature of the polargrams is the presence of diagonal stripes that indicate how information from different frequencies varies in a pattern as the fish aspect angle changed. These are caused by changes in the high-light separation time as the polar angle changes which will cause local maxima and minima in the spectrum to shift. The shift in local maxima and minima in the spectrum is reflected by the diagonal stripes. The polargrams

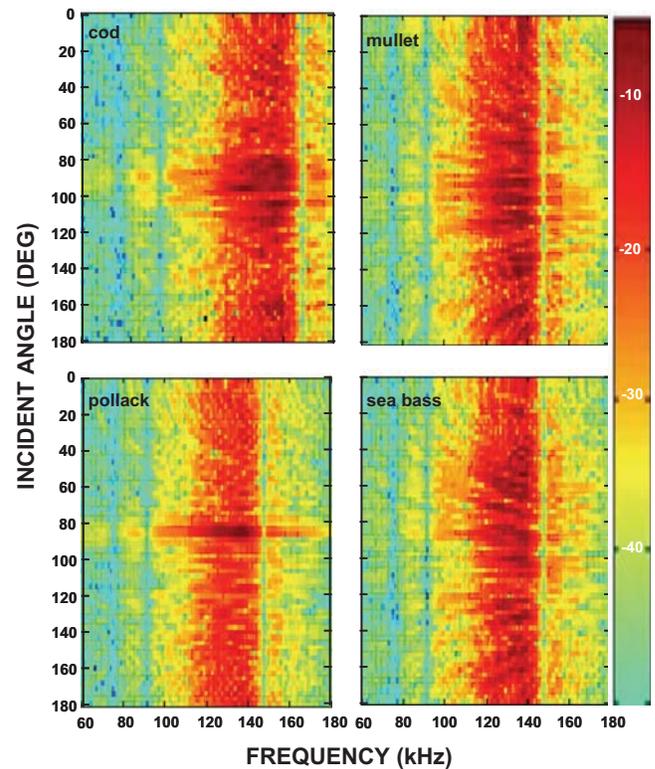


FIG. 8. (Color online) Polargrams for the four species of fish obtained with the porpoise-like biosonar signal. The frequency spectra for different polar angles are shown with the amplitude color coded according to the color bar on the right.

clearly show differences in the spectra of the echoes from the different fish species that can be utilized by dolphins and porpoises in discriminating between these four species of fish. In a natural situation, the predator-prey geometry will constantly change from ping to ping and the polargram can be used to gain an appreciation of how the spectra of the echoes will change as the predator-prey geometry changes continuously and dynamically.

The time-frequency representations of the echoes (Fig. 5) from the four fish species produced by analyzing the echoes with the gammatone filter bank of Fig. 4(a) are shown in Figs. 9 and 10 for the broadside and 135° incident angles, respectively. The frequency values along the vertical axis correspond to the center frequencies of some of the individual gammatone filters shown in Fig. 4(a). The time-frequency representations show how the spectra of the echoes develop as a function of time as the echoes propagate into the dolphin auditory system. Even for the broadside aspect, differences in the time-frequency representations can be seen between species. The time-frequency plot for the mullet and sea bass had the narrowest frequency extent. The frequency extent of the cod and pollack was similar and larger than for the mullet and sea bass. The differences become more apparent for the 135° aspect angle. Time-frequency representations of echoes (Fig. 6) associated with the porpoise signal and porpoise hearing model for the broadside and 135° aspects are shown in Figs. 11 and 12, respectively. Differences in the time-frequency plots are obvious and are likely exploited by porpoises to discriminate between different fish species. As would be expected, the time-frequency

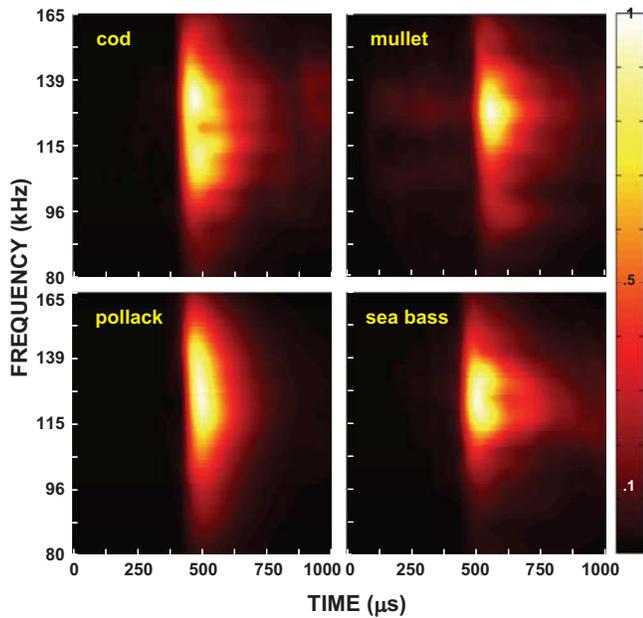


FIG. 9. (Color online) Time-frequency representation of the echoes using the dolphin-like biosonar signal at the broadside aspect.

plots for the porpoise signal are different from those for the dolphin because of the different incident signals and gamma-tone filter bandwidths.

#### IV. DISCUSSION AND CONCLUSIONS

The results obtained in this study resembled the broadband measurements performed by Au and Benoit-Bird (2003) for deep dwelling snappers (commercially referred to as bottom fish) in Hawaiian waters. In both studies, the echo structures were complex with many echo components originating from different parts of the fish anatomy. Reeder *et al.* (2004) focused on the backscatter process using broadband

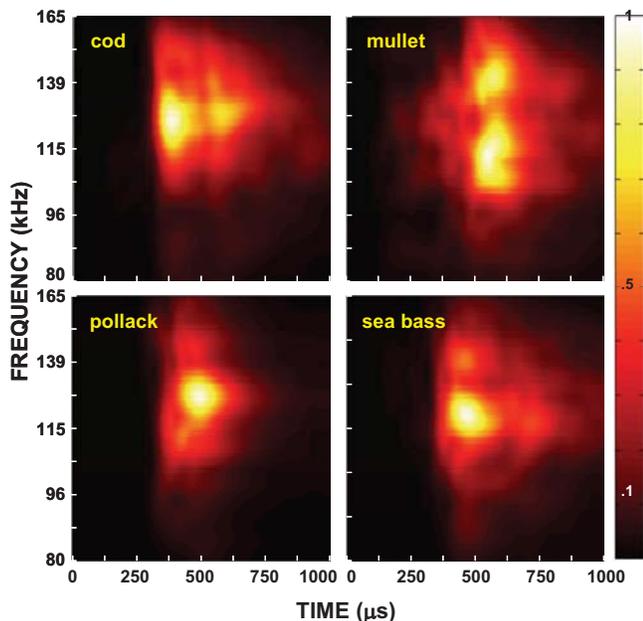


FIG. 10. (Color online) Time-frequency representation of the echoes using the dolphin-like biosonar signal at the 135° aspect.

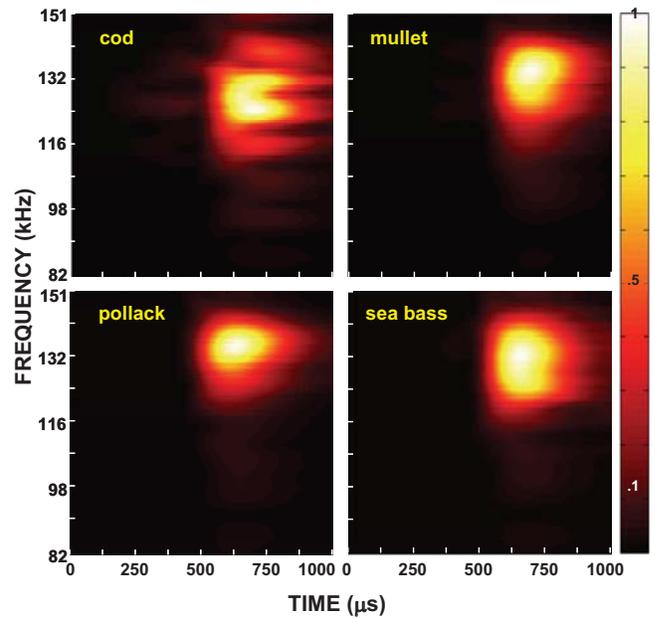


FIG. 11. (Color online) Time-frequency representation of the echoes using the porpoise-like biosonar signal at the broadside aspect.

frequency modulated signals to measure the echoes from the fish, alewife, and were able to identify some of the sources of the secondary reflections which should be similar for the fish used in this study. The results in this study were analyzed and discussed from both an echo structure perspective in the time domain and in the frequency domain with the polargrams and in both domains simultaneously with the time-frequency hearing model plots. The multiple highlight feature of the echoes made analysis and interpretation in the time domain very insightful because the secondary echoes could be easily observed.

The polargrams showing how the frequency spectra of the echoes changed with the aspect angle of the fish also

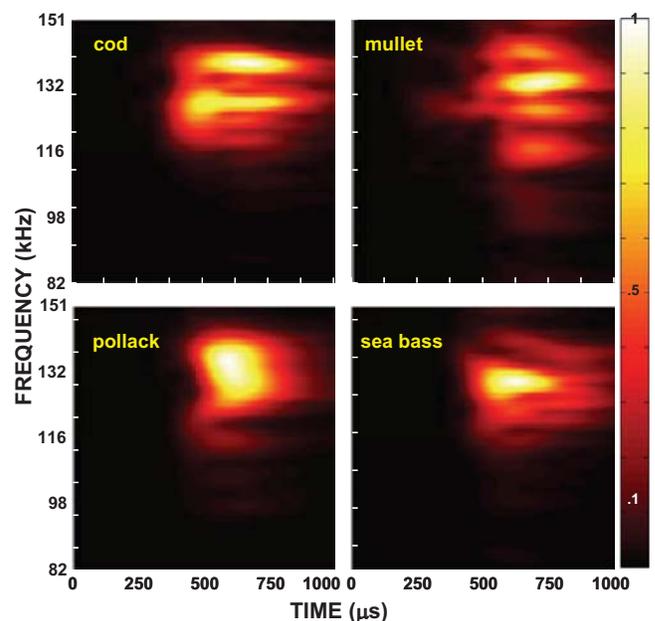


FIG. 12. (Color online) Time-frequency representation of the echoes using the porpoise-like biosonar signal at the 135° aspect.

provide insights into the differences between species because one can see how certain frequency peaks vary as a function of aspect angle. Therefore, whether the data are analyzed in the time or frequency domain is immaterial because species difference cues can easily be seen in both domains. However, the polargrams have the advantage of being compact, allowing the effects of aspect to be readily seen for all aspects on one side of the fish. Reeder *et al.* (2004) presented graphs similar to polargrams plotting the compressed pulse output (CPO) as a function of time-delay as the aspect angle changed. The CPO at any given angle is the envelope of the cross-correlation function between the echo from the subject with an echo from a calibrated sphere. Just as in the polargram, there were peaks in the CPO that varied as a function of the aspect angle. Combining the time and frequency information is likely most appropriate because the auditory system of mammals probably utilizes simultaneous time-frequency information rather than information in only one domain. A future follow-up to this study is to use the echoes collected in this study in a dolphin auditory model with a classification algorithm (e.g., Au, 1994; Branstetter *et al.*, 2007) as well as in a human listener experiment as has been done for echoes done with other targets (Au, 1993; Delong *et al.*, 2007).

The time-frequency representations based on the gammatone filter banks modeled the processing of the echoes by the auditory periphery. The results from only two aspect angles strongly suggest that the echoes from the four species contain sufficient species-specific information to facilitate discrimination by echolocating odontocetes. Although auditory images from only two angles are presented for brevity, similar species-specific patterns are apparent at different fish orientations.

Species-specific differences in the echo structure of backscattered acoustic signals from the four species of fish used in this study are apparent. The data indicate that the echo structures vary in amplitude, time separation between highlights, number of highlights, and overall duration depending on the angle of incident of echolocation signals. These results suggest a very complex backscattering process with various types of aspect-dependent information available. So the most obvious question is whether or not a dolphin or porpoise can handle the aspect-dependent fluctuations associated with reflections from different species of fish. From a slightly different perspective one could ask whether or not a dolphin or porpoise can generalize from fluctuating broadband echoes the species of a potential prey. The task for an odontocete is to detect, localize, recognize, and track a moving prey. Since both predator and prey move, the acoustic geometry will be continuously and dynamically changing, causing the echo structure to fluctuate from ping-to-ping. If an odontocete utilizes the echo structure information to hunt for specific prey, the odontocete auditory classification scheme would need to match and generalize a large variety of echo exemplars (some of which will be novel) to specific species categories. Such a generalization capability is not out of the question and has been demonstrated by a dolphin matching three dimensional, aspect-dependent targets (Helweg *et al.*, 1996) that were allowed to freely rotate,

resulting in within target echo variability. Despite the large variability of within target echoes, the dolphin was successful at discriminating between the targets.

Just as the aspect-dependent echoes could be discriminated by echolocating *Tursiops truncatus* in study of Helweg *et al.* (1996) it would not be far-fetched to assume that the same will be true for aspect-dependent echoes from fishes. However, in order to unequivocally demonstrate the capability for aspect-dependent discrimination of fish echoes, a rigorous psychophysical study would be needed. Such an experiment can be conducted with electronic generated phantom echoes (Aubauer *et al.* 2000; Ibsen *et al.*, 2007). The apparent aspect of fish echoes could be varied from ping-to-ping in a similar manner, as was done by Delong *et al.* (2007) for human listening experiments using echoes generated by simulated dolphin clicks and rotating targets.

It should be emphasized that although our results suggest that intraspecies difference in the echo structure exists for the four species examined, this type of information is probably not the only information used by an echolocating predator to detect, localize, and recognize specific species. There are potentially a multitude of cues that would be available through the echolocation process. The swimming behavior and dynamics of potential prey can be determined by examining the change in the echo amplitude and timing as well as the echo structure from ping-to-ping. The depth of potential prey could also be determined by the echolocation process. An odontocete will no doubt use as many available cues that are present. Furthermore, different cues may have different weights depending if the odontocetes forage in relatively open waters or in shallow waters, the variety of species present in the habitat, and the relative food value of these species.

## ACKNOWLEDGMENTS

We thank Sander van der Hel for assistance in conducting the experiments. Jan van der Veen, Sea aquarium "het Arsenaal," The Netherlands, lent us the study animals. Gijs Rutjes (Coppens International) provided some of the sea bass. We thank Brigitte Kastelein and the volunteers for logistical support. The facilities of the research station were made available, thanks to Dick Vethaak (RIKZ), Roeland Allewijn (RIKZ), and Wanda Zevenboom (North Sea Directorate). This work was supported by the US Office of Naval Research, Mardi Hastings, Program Manager, and the Netherlands Ministry for Agriculture, Nature, and Food Quality (DKW-program 418: North Sea and Coast). This project complied with the Dutch standards for animal experiments (Chris Pool, Head of the Committee for Animal Experiments of RIKZ) and was conducted under University of Hawaii Animal Care Protocol 04-019. This is HIMB Contribution No. 1343.

Au, W. W. L. (1993). *The Sonar of Dolphins* (Springer, New York).

Au, W. W. L. (1994). "Comparison of sonar discrimination: Dolphin and an artificial neural network," *J. Acoust. Soc. Am.* **95**, 2728–2735.

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., and Hastings, M. C. (2008). *Principles of Marine Bioacoustics* (Springer-Verlag, New York).
- Au, W. W. L., and Pawloski, D. (1992). "Cylinder wall thickness difference discrimination by an echolocating Atlantic bottlenose dolphin," *J. Comp. Physiol., A* **172**, 41–47.
- Au, W. W. L., and Turl, C. W. (1991). "Material composition discrimination of cylinders at different aspect angles by an echolocating dolphin," *J. Acoust. Soc. Am.* **89**, 2448–2451.
- 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.
- Au, W. W. L., Schusterman, R., and Kersting, D. A. (1980). "Sphere-cylinder discrimination via echolocation by *Tursiops truncatus*," in *Animal Sonar Systems*, edited by R. G. Busnel and J. F. Fish (Plenum, New York), pp. 859–862.
- Au, W. W. L., Ford, J. K. B., Horne, J. K., and Newman-Allman, K. A. (2004). "Echolocation signals of free-ranging killer whales (*Orcinus orca*) and modeling of foraging for chinook salmon (*Oncorhynchus tshawytscha*)," *J. Acoust. Soc. Am.* **56**, 1280–1290.
- Aubauer, R., Au, W. W. L., Nachtigall, P. E., Pawloski, J. L., Pawloski, D. A., and DeLong, C. (2000). "Classification of electronically generated phantom targets by an Atlantic bottlenose dolphin (*Tursiops truncatus*)," *J. Acoust. Soc. Am.* **107**, 2750–2754.
- Barta, R. E. (1969). "Acoustical pattern discrimination by an Atlantic bottlenose dolphin," Naval Undersea Center, San Diego, CA.
- Branstetter, B. K., Mecado, E., III, and Au, W. W. L. (2007). "Representing multiple discrimination cues in a computational model of the bottlenose dolphin auditory system," *J. Acoust. Soc. Am.* **122**, 2459–2468.
- Busnel, R.-G., and Dziedzic, A. (1967). "Resultats metrologiques experimentaux de l'echolocaition chez le *Phocaena phocaena* et leur comparaison avec cues de cdrtaines chauves—souris," in *Animal Sonar Systems: Biology and Bionics*, edited by R. G. Busnel (Laboratoire de Physiologie Acoustique, Jouy-en-Josas, France), Vol. **1**, pp. 307–335.
- DeLong, C., Au, W., Harley, H., Roitblat, H., and Pytka, L. (2007). "Human listeners provide insights into echo features used by dolphins to discriminate among objects," *J. Comp. Psychol.* **121**, 306–319.
- Evans, W. W., and Powell, B. A. (1967). "Discrimination of different metallic plates by an echolocating delphinid," in *Animal Sonar Systems: Biology and Bionics*, edited by R. G. Busnel (Laboratoire de Physiologie Acoustique, Jouy-en-Josas, France), pp. 363–382.
- 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., and Ona, E. (1985). "Swimbladder cross sections and acoustic target strengths of 13 pollack and 2 saithe," *Fiskeridir. Skr., Ser. Havunders.* **18**, 1–57.
- Ford, J. K. B., and Ellis, G. M. (2006). "Selective foraging by fish-eating killer whales *Orcinus orca* in British Columbia," *Mar. Ecol.: Prog. Ser.* **316**, 185–199.
- Glasberg, B. R., and Moore, B. C. J. (1990). "Derivation of auditory filter shapes from notched-noise data," *Hear. Res.* **47**, 103–138.
- Helweg, D. A., Au, W. W. L., Roitblat, H. L., and Nachtigall, P. E. (1996). "Acoustic basis for recognition of aspect-dependent three-dimensional targets by an echolocating bottlenose dolphin," *J. Acoust. Soc. Am.* **99**, 2409–2420.
- Ibsen, S. D., Au, W. W. L., Nachtigall, P. E., Delong, C. D., and Breeze, M. (2007). "Changes in signal parameters over time for an echolocating Atlantic bottlenose dolphin performing the same target discrimination task," *J. Acoust. Soc. Am.* **122**, 2446–2450.
- Johnson, C. S. (1968). "Masked tonal thresholds in the bottlenose porpoise," *J. Acoust. Soc. Am.* **44**, 965–967.
- Kellogg, W. N. (1958). "Echo ranging in the porpoise," *Science* **128**, 982–988.
- Lemons, D. W. (1999). "Auditory filter shapes in an Atlantic bottlenose dolphin (*Tursiops truncatus*)," Ph.D. dissertation, University of Hawaii at Manoa.
- Madsen, P. T., Kerr, I., and Payne, R. (2004). "Echolocation clicks of two free-ranging delphinids with different food preferences: False killer whales (*Pseudorca crassidens*) and Risso's dolphin (*Grampus griseus*)," *J. Exp. Biol.* **207**, 1811–1823.
- Nachtigall, P. E. (1980). "Odontocete echolocation performance on object size, shape and material," in *Animal Sonar Systems*, edited by R. G. Busnel and J. F. Fish (Plenum, New York), pp. 71–95.
- Norris, K. S., Prescott, J. H., Asa-Dorian, P. V., and Perkins, P. (1961). "An experimental demonstrated echolocation behavior I the porpoise, *Tursiops truncatus* (Montagu)," *Biol. Bull.* **120**, 163–176.
- Pack, A. A., Herman, L. M., Hoffman-kuhnt, M., and Branstetter, B. K. (2002). "The object behind the echo: Dolphins (*Tursiops truncatus*) perceive object shape globally through echolocation," *Behav. Processes* **58**, 1–26.
- Patterson, R. D. (1994). "The sound of a sinusoid: Spectral models," *J. Acoust. Soc. Am.* **96**, 1409–1418.
- Patterson, R. D., Robinson, K., Holdsworth, J., McKeown, D., Zhang, C., and Allerhand, M. H. (1992). *Complex Sounds and Auditory Images* (Pergamon, Oxford).
- Popov, V. V., Supin, A. Ya., Ding, W., and Wang, K. (2006). "Nonconstant quality of auditory filters in the porpoises, *Phocoena phocoena* and *Neophocaena phocenoides* (Cetacea, Phocoenidae)," *J. Acoust. Soc. Am.* **119**, 3173–3180.
- Reeder, B. D., Jech, J. M., and Stanton, T. K. (2004). "Broadband acoustic backscatter and high-resolution morphology of fish: Measurement and modeling," *J. Acoust. Soc. Am.* **116**, 747–761.
- Schevill, W. E., and Lawrence, B. (1956). "Food-finding by a captive porpoise (*Tursiops truncatus*)," *Breviora (Mus. Comp. Zool, Harvard)* **53**, 1–15.
- Simmonds, J., and MacLennan, D. (2005). *Fisheries Acoustics: Theory and Practice*, 2nd ed. (Blackwell, Oxford, UK).
- Slaney, M. (1993). "An efficient implementation of the Patterson-Holdsworth filter bank," Apple Technical Report No. 35, Advanced Technology Group, Apple Computer, Inc., Cupertino, CA.