

# Modeling the detection range of fish by echolocating bottlenose dolphins and harbor porpoises

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The target strength as a function of aspect angle were measured for four species of fish using dolphin-like and porpoise-like echolocation signals. The polar diagram of target strength values measured from an energy flux density perspective showed considerably less fluctuation with azimuth than would a pure tone pulse. Using detection range data obtained from dolphin and porpoise echolocation experiments, the detection ranges for the Atlantic cod by echolocating dolphins and porpoises were calculated for three aspect angles of the cod. Maximum detection ranges occurred when the fish was broadside to the odontocete and minimum detection ranges occurred when the cod was in the tail aspect. Maximum and minimum detection ranges for the bottlenose dolphin in a noise-limited environment was calculated to be 93 and 70 m, respectively. In a quiet environment, maximum and minimum detection ranges for the bottlenose dolphin were calculated to be 173 and 107 m, respectively. The detection ranges for the harbor porpoise in a quiet environment were calculated to be between 15 and 27 m. The primary reason for the large differences in detection ranges between both species was attributed to the 36 dB higher source level of the bottlenose dolphin echolocation signals. © 2007 Acoustical Society of America.  
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## I. INTRODUCTION

Target detection experiments with echolocating dolphins and porpoises have been conducted for over three decades using various types of targets. The first set of target detection experiments was conducted in open waters of Kaneohe Bay, Oahu, HI, with bottlenose dolphins (*Tursiops truncatus*) by Murchison (1980) using a 7.62-cm-diam water-filled stainless steel sphere and a 2.54-cm solid steel sphere. The 50% correct detection threshold was found to be 74 m for the 2.54-cm sphere (target strength of  $-42$  dB) and 79 m for the 7.62-cm sphere (target strength of  $-28$  dB). The detection range for the 7.62-cm sphere measured by Murchison (1980) was negatively affected by the presence of an underwater shelf in the vicinity of the measured threshold range that was a source of bottom reverberation which masked the target echoes (Au and Snyder, 1980). Au and Snyder (1980) remeasured the threshold detection range with one of the bottlenose dolphins used by Murchison (1980), but in a different part of the bay and obtained a threshold range of 113 m. Thomas and Turl (1990) also used a 7.62-cm-diam water-filled stainless steel sphere and the same experimental range as Au and Snyder (1980), and measured a target detection threshold range of 119 m for a false killer whale (*Pseudorca*

*crassidens*). All of the animals in the Kaneohe Bay experiments were masked by snapping shrimp sounds (Au and Snyder, 1980). Kastelein *et al.* (1999) measured the threshold detection range of echolocating harbor porpoise (*Phocoena phocoena*) to be approximately 26 m for the same 7.62-cm sphere used by the investigators in Kaneohe Bay, and 16 m for a 5.08-cm sphere. One of the most important differences in Kastelein *et al.* (1999) experiment and the experiments in Kaneohe Bay was the absence of masking noise at the Neeltje Jans facility in The Netherlands.

The target detection experiments with captive odontocetes have been useful in understanding the basic capabilities of the echolocation systems of these animals. However, there has not been much effort transferring the basic understanding of detection ranges to how well odontocetes can detect fish in their natural habitat. In recent years, there have been some modeling studies of echolocation detection range by three species of odontocetes, *Orcinus orca* (Au *et al.*, 2004), *Pseudorca crassidens*, and *Grampus griesus* (Madsen *et al.*, 2004). Au *et al.* (2004) measured the echolocation signals of fish-eating killer whales in the waters of Vancouver Island, British Columbia, and estimated the detection ranges for a 70-cm-long Chinook salmon by echolocating killer whales to be well over 100 m under quiet conditions. Madsen *et al.* (2004) measured the echolocation signals of false killer whales and Risso's dolphin in off-shore habitat and estimated detection ranges for a 1-m-long tuna and 20- and 80-cm-long

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squid. Madsen *et al.* (2004) estimated detection ranges that varied from 80 to 210 m. The shortcoming of both of these studies is that realistic target strength values for the prey were not used. The target strength in the Au *et al.* (2004) study was based on theoretical calculations for a narrow band signal at 50 kHz using a Kirchoff ray model (Jech and Horne, 1995; Horne and Jech, 1999). The estimate of detection ranges of Madsen *et al.* (2004) were based on target strength measurements using tonal signals and they did not take into account the aspect dependence of acoustic backscatter from the fish or squid.

One of the obstacles in modeling echolocation detection ranges for different species of fish has to do with our poor understanding of how odontocete echolocation signals reflect off different fish species. Measurements of deep-dwelling snappers using simulated dolphin echolocation signals by Benoit-Bird *et al.* (2003) and Au and Benoit-Bird (2003) indicated that the echoes were about 4.5 times longer in duration than the incident signals, suggesting a very complicated backscatter process that is not well understood. They also found that the variation in target strength based on energy with angle did not fluctuate nearly as much as with tonal sonar signals. In this study we measured the acoustic backscatter of four different species of fish that are prey of bottlenose dolphins and harbor porpoises using simulated bottlenose dolphin and harbor porpoise echolocation signals in order to estimate target detection range for these species.

## II. PROCEDURE

### A. Experimental geometry

The backscatter measurements were conducted in an outdoor tank of Sea Mammal Research Company, at the field station of the Netherlands National Institute for Coastal and Marine Management (RIKZ) at Jacobahaven, Zeeland, The Netherlands, in a 7 m × 4 m rectangular tank with a water depth of 2 m. The measurement geometry is depicted in Fig. 1(a) showing a rotor with a cylindrical rod supporting a monofilament net. Fish subjects were contained in a monofilament bag that was in turn attached to the center of the monofilament net which was attached to a rotor. The fish could be placed in the bag in the two different aspects depicted in Fig. 1(b). The transducer was a custom-made circular disk with the active element being a 1-3 piezo-ceramic circular disk with a diameter of 6.4 cm and a thickness of 0.64 cm. The transducer was placed 2 m from the fish and at the same depth as the fish, which was 1 m.

A monostatic echoranging system was used in which the same transducer transmitted the signals and received the echoes. The echoes were time-gated and filtered before being digitized at a sample rate of 1 MHz. A total of 1024 points were digitized per echo and stored to disk. The waveform and frequency spectra of the incident signals are shown in Fig. 2. An acoustic mirror consisting of a flat 0.63 thick aluminum plate covered with a close cell neoprene sheet was used to obtain the signals shown in Fig. 2. The dolphin-like signal had a peak frequency of 130 kHz while the porpoise-like signal had a peak frequency of 138 kHz. The duration of the dolphin-like signal was approximately 70  $\mu$ s vs 270  $\mu$ s

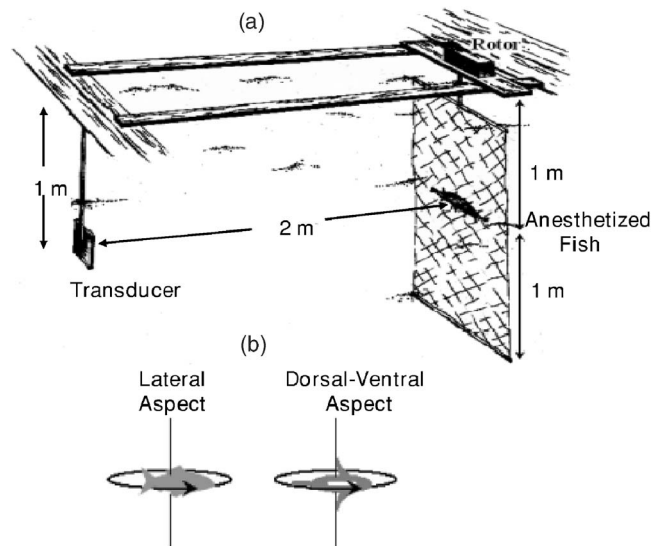


FIG. 1. (a) Fish backscatter measurement geometry showing the fish in a net bag attached to a monofilament, net supported by a rod connected to a rotor. (b) Rotational geometry of the fish.

for the porpoise-like signal. The bandwidth of the porpoise signal was clearly narrower than the dolphin-like signal. Both dolphin-like and porpoise-like signals were replicates of previously recorded signals.

### B. Fish subjects

The species of fish used were Atlantic cod (*Gadus morhua*), grey mullet (*Chelon labrosus*), pollack (*Pollachius pollachius*), and sea bass (*Dicentrarchus labras*). Three fish of each species except for the pollack were acoustically examined. The lengths of the subjects were cod (29 to 30 cm), mullet (15–17 cm), and sea bass (14–17 cm). Only one pollack having a length of 21 cm was used. Acoustic backscatter from the Atlantic cod has been studied fairly intensely by Clay and Horne (1994) and will therefore be used as our model fish in detection range calculations. These fishes were on loan from “The Arsenaal Aquarium,” Vlissingen, The Netherlands. The Animal Welfare Commission of The Netherlands stipulated that the fish must feed readily in captivity, so they had to come from aquaria though all were originally wild-caught. They were fed to satiation each day after the sessions on a diet of raw fish. Fish were returned to the aquarium following the experiment to comply with animal care regulations. Three fish per species were used to ensure that the backscatter results were consistent and repeatable. We did not expect the target strength to vary much since the lengths within a species varied very little. Each fish was anesthetized by placing it in a bath containing 1 mL of 2-phenoxy-ethanol per 10 L of seawater. Once anesthetized, the fish was enclosed in the fitted monofilament net bag to restrain its movements and the net bag was mounted to the monofilament net. Echoes from the fish were collected as a function of azimuth. The rotor incremented approximately 2.2° after each transmission and reception cycle until the fish was rotated through 360°. Most of the measurements were done with the fish in the lateral aspect having its dorsal surface aligned upwards and the ventral surface pointing down-

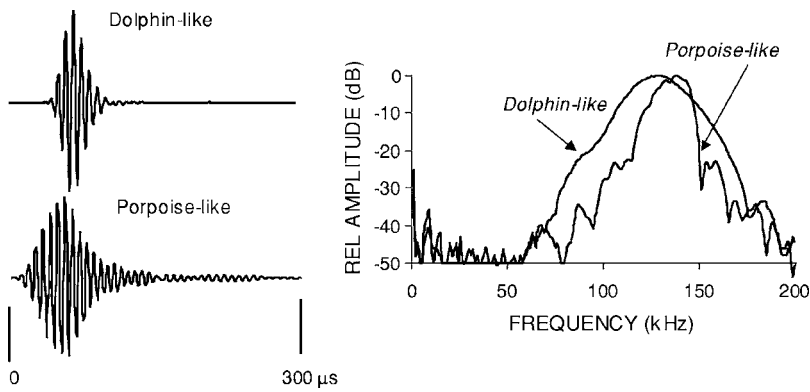


FIG. 2. Simulated bottlenose dolphin and harbor porpoise echolocation signals in the time and frequency domains.

wards although some measurements were also done in the dorsal-ventral plane [Fig. 1(b)].

### III. RESULTS

#### A. Fish backscatter

Examples of echo waveforms obtained with both the dolphin-like and porpoise-like signals for a cod in the lateral plane are shown in Fig. 3 for three different aspect angles of the fish; broadside ( $90^\circ$ ),  $135^\circ$  or  $45^\circ$  from the broadside and tail aspects, and the tail aspects ( $180^\circ$ ). At broadside, the echo is relatively simple with a single large highlight followed by a much smaller highlight, where the major highlight is probably a reflection off the surface of the swim bladder. Highlights are local maxima within the structure of the echoes. The swimbladder of a fish is the structure having the most dominant influence on the echo intensity (Foote, 1980; Foote and Ona, 1985). As the aspect angle changes from broadside, the echo structure becomes extremely complex, with many highlights and an elongated duration much

longer than that of the incident signals. The amplitude of each echo is normalized to its maximum value in Fig. 3 so that the structure of the echoes can be readily seen. Otherwise, the amplitude of the echoes at  $135^\circ$  and tail aspect would be at least 1/4 of what is shown. More highlights can be seen for the dolphin-like signal than the porpoise signal for the  $135^\circ$  and tail aspect. This is the result of the dolphin-like signal having a better range resolution capability by virtue of its broader bandwidth than the porpoise-like signal. Nevertheless, the echo structure of the porpoise-like echoes is still very complex.

Typical variations in target strength as a function of the aspect angle of a cod in the lateral plane are shown in Fig. 4. Target strengths based on both the energy in the echoes (dark line) and peak amplitude for a tonal signal (light line) are included. The target strength for a tonal signal fluctuated considerably with azimuth, having deep nulls. On the other hand, the target strength based on energy for a broadband click had considerably less fluctuation with azimuth, and did not have the deep sharp nulls that were present for the tonal signal. The tonal results were obtained by using the values of the incident and reflected signal at a frequency of 130 kHz. The difference between the maximum and minimum values

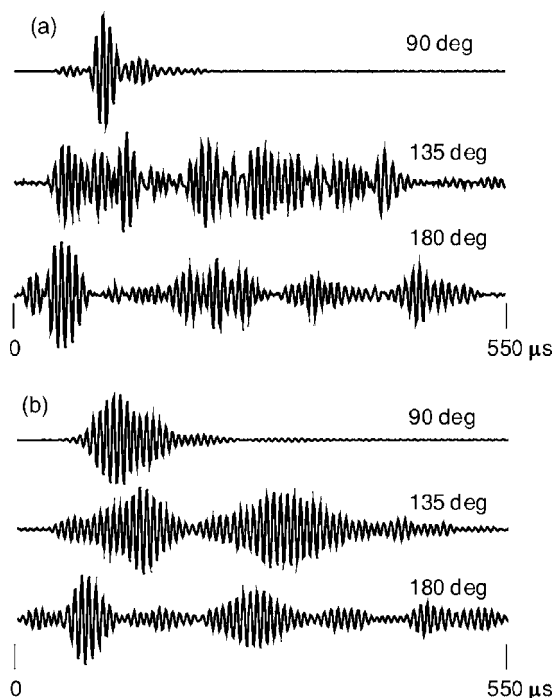


FIG. 3. Backscatter signal wave form for different aspect angles and for the two simulated echolocation signals used in this study.

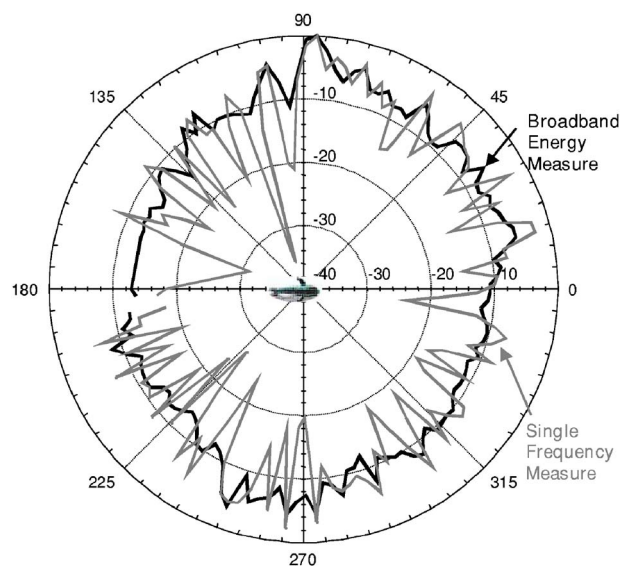


FIG. 4. (Color online) Polar diagram of the target strength determined on the basis of energy flux density of a simulated dolphin echolocation signal (black line) and the target strength based on a single frequency of 130 kHz.

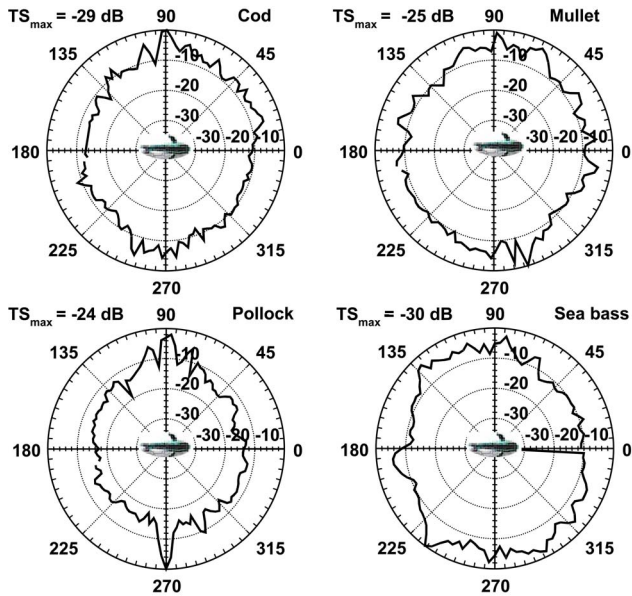


FIG. 5. (Color online) Polar diagram of the target strength in the lateral plane for the four fish species. The data were obtained with a simulated bottlenose dolphin echolocation signal.

of the target strength based on energy was about 13 dB compared to over 30 dB for the tonal signal. These results are similar to those of Benoit-Bird *et al.* (2003), who also compared target strength versus azimuth for snappers using target strength values based on energy in broadband clicks and on the peak values of tonal signals.

The target strength of the four species of fish is shown in polar form in Fig. 5 for the dolphin-like echolocation signal and in Fig. 6 for the porpoise-like signal. The polar plots are normalized with the maximum value of the target strength indicated next to each plot. The maximum values typically occurred when the fish was at a broadside aspect (90° and

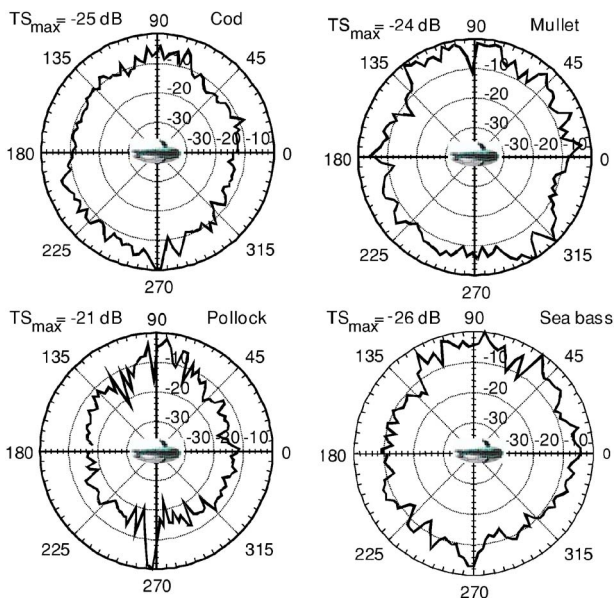


FIG. 6. (Color online) Polar diagram of the target strength in the lateral plane for the four fish species. The data were obtained with a simulated harbor porpoise echolocation signal.

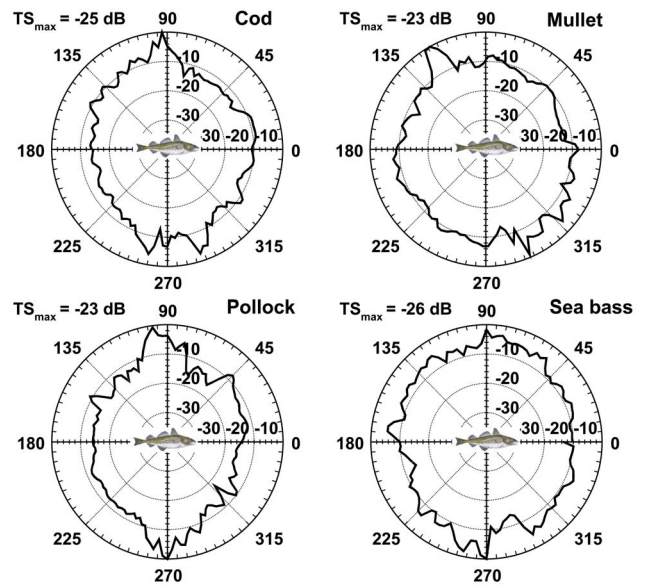


FIG. 7. (Color online) Polar diagram of the target strength in the dorsal-tilt plane for the four fish species. The data were obtained with a simulated bottlenose dolphin echolocation signal.

270°). The minimum values typically occurred in the tail aspect orientation. The maximum target strengths obtained with the porpoise-like signal were 1–3 dB larger in value than the values obtained using the dolphin-like signal. The polar diagrams of target strength are similar between the dolphin-like and porpoise-like echolocation signals for a given species. The pollack had the most unusual variation of target strength with azimuth, showing a major lobe at 270°. We cannot state with certainty why the pollack backscatter had this lobe, however, the probability is fairly high that the shape of the swim bladder was the major contributor to the presence of the lobe. Unfortunately, the fishes had to be returned to The Arsenal Aquarium and were not available for x-ray measurements. There are also some minor differences in the maximum target strength values for the two types of signals and these differences were probably caused by the signals having different peak frequencies. Target strength of fish generally increases with frequency and the 9 kHz higher peak frequency of the porpoise signal may have contributed to the slightly higher target strength values for the porpoise signal.

The polar diagrams of the target strength in the dorsal-ventral plane for the four species of fish that were obtained with the dolphin-like echolocation signal are shown in Fig. 7. The angle of maximum reflection probably occurred when the incident signal was perpendicular to the longitudinal axis of the swimbladder (Benoit-Bird *et al.*, 2003), which in most fishes is tilted slightly. The minimum target strength occurred close to the tail and head aspects. For the tail and head aspects, the target strength with the fish rotated in the lateral plane should be the same as in the dorsal-tilt plane. Any differences were probably caused by slight misalignment of the fish when mounted to the monofilament net. The polar plots of the target strength in the dorsal-ventral plane measured with the porpoise-like signals were similar to the plots in Fig. 7 and are not shown.

## B. Modeling fish detection ranges by echolocating odontocetes

### 1. Atlantic bottlenose dolphin

The results of Murchison (1980) using a 2.54-cm-diam solid steel sphere and the results of Au and Snyder (1980) using a 7.62-cm water-filled stainless steel sphere were used to calculate the bottlenose echolocation detection ranges searching for a cod. Kaneohe Bay has a large population of snapping shrimps which produced noise that limited the dolphins' detection capability, i.e., a noise-limited environment (Au *et al.*, 1974; Au and Snyder, 1980). In order to determine the detection ranges for a fish using the results of Murchison (1980) and Au and Snyder (1980), the noise-limited transient form of the sonar equation should be used (Urick, 1983). The transient form of the sonar equation (expressed in dB) that is applicable to a dolphin can be expressed as

$$DT_E = SE - 2TL + TS_E - (NL - DI), \quad (1)$$

where  $DT_E$  is the detection threshold,  $SE$  is the source energy flux density,  $TL$  is the one-way transmission loss,  $TS_E$  is the target strength based on energy,  $NL$  is the ambient noise spectral density, and  $DI$  is the receiving directivity index at the peak-frequency of the dolphin's echolocation signal. Assuming simple spherical spreading loss propagation, the one-way transmission loss can be expressed as

$$TL = 20 \log R + \alpha R, \quad (2)$$

where  $R$  is range in meters and  $\alpha$  is the sound absorption coefficient in dB/m at the peak frequency of the animal's echolocation signal. If we assume that the dolphin uses echolocation signals having similar source levels for both an artificial steel sphere and a fish, then the results obtained with the steel sphere can be used to predict the performance of a dolphin echolocating a fish. This can be done by equating Eq. (1) for a fish to the same equation, but for a sphere and using Eq. (2). Therefore, we obtain the following equation that can be used to determine the threshold detection range for a fish:

$$40 \log R + 2\alpha R = TS_{E_{fish}} - TS_{E_{sphere}} + 2TL_{sphere}. \quad (3)$$

This is a transcendental equation and does not have a closed form solution. The solution must be determined by iteration, inserting a value for  $R$  and determining if the value of the left side of the equation matches the right side. If the left side is larger then a smaller  $R$  is chosen on the next iteration until the appropriate  $R$  is determined. However, it should be noted that the 2.54-cm results of Murchison and the 7.62 cm of Au and Snyder did not agree completely when transient form of the sonar equation was applied to their results; there was approximately a 2.5-dB difference in the calculated value of the detection threshold for the range where the animal's threshold occurred. Both experiments were performed with the same animal but about 2 years apart (Au and Snyder, 1980). However, considering this time interval between both experiments, the 2.5-dB discrepancy was considered rather minor and both results were considered remarkably close for psychophysical experiments,

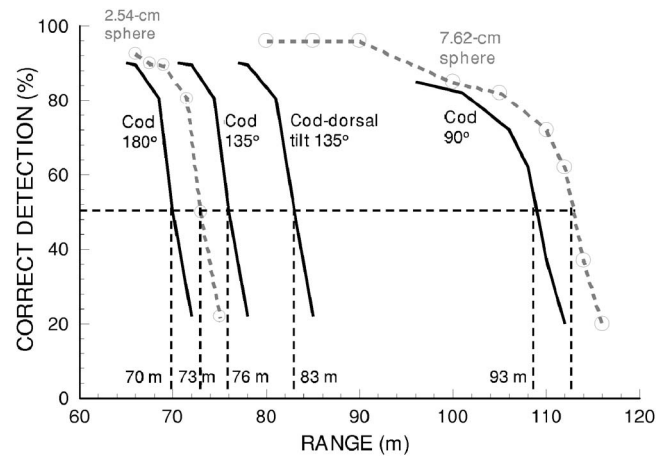


FIG. 8. Predicted correct detection performance for a bottlenose dolphin echolocating on a 30-cm-long Atlantic Cod in a noise-limited environment. The actual bottlenose dolphin performance curves with real water-filled spheres are shown by the dark gray curves. The 50% correct detection threshold ranges are shown for different aspects of the fish.

which often have very large variations (Au, 1993).

In order to estimate the detection range the backscatter results for cod at different aspect angles were used. When the fish target strength at a particular aspect angle is closer to the target strength of the 2.54-cm sphere then Murchison's results were used and when the fish target strength is closer to that of the 7.62-cm sphere then Au and Snyder's results were used. The target strength for the cod in the lateral plane at broadside ( $90^\circ$ ) was  $-29$  dB (Fig. 5), at  $135^\circ$  it was approximately  $-41$  dB, at tail aspect ( $180^\circ$ ) it was approximately  $-43$  dB, and in the dorsal-ventral plane (Fig. 7) at  $135^\circ$  it was approximately  $-39$  dB. Applying Eqs. (2) and (3) the detection performance curves for the cod were calculated and the results are shown in Fig. 8. The 50% correct detection threshold is shown for the three aspect angles of the cod in the lateral plane and for  $135^\circ$  in the dorsal-ventral plane. The detection threshold range is maximum at the broadside ( $90^\circ$ ) aspect with a value of 93 m and minimum at the tail aspect ( $180^\circ$ ) with a value of 70 m in a noise-limited environment.

Au *et al.* (2002) determined the nonmasked detection threshold of an Atlantic bottlenose dolphin using two broadband signals resembling the echoes from a 7.62-cm water-filled sphere. They obtained an average energy flux detection threshold of 33.1 dB re  $1 \mu\text{Pa}^2 \text{s}$ . In order to calculate the detection range for any target the energy flux density of the echo must be determined using

$$EE = SE - 2TL + TS_E, \quad (4)$$

where  $EE$  is the energy flux density of the echo,  $SE$  is the source energy flux density, and  $TL$  is defined by Eq. (3). Assuming an echolocating dolphin emitting a signal with an average source level of 222 dB re  $1 \mu\text{Pa}$  (Au *et al.* 1980) which equated to a source energy flux density of 167 dB re  $1 \mu\text{Pa}^2 \text{s}$  and inserting the appropriate values into Eq. (4), the threshold detection range can be expressed as

$$40 \log(R) + 2\alpha R = 133.9 + TS_E. \quad (5)$$

Au *et al.* (2002) calculated the threshold range of a bottlenose dolphin searching for a 7.62-cm sphere to be approxi-

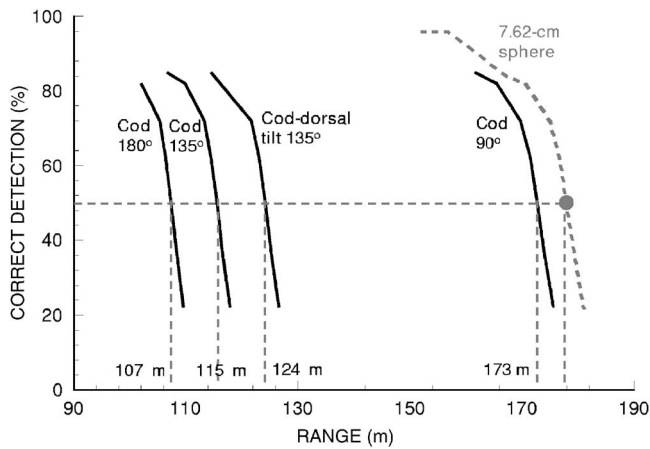


FIG. 9. Predicted correct detection performance for a harbor porpoise echolocating on a 30-cm-long Atlantic Cod. The actual harbor porpoise performance curves with real water-filled spheres are shown by the dark gray curves. The 50% correct detection threshold ranges are shown for different aspects of the fish.

mately 178 m. We also used the shape of the performance curve for the 7.62-cm sphere shown in Fig. 8 (dashed gray line) to estimate a performance curve for detection of the sphere as a function of range in a nonmasking condition.

The same procedure can be used here for calculating the detection range for a single fish in a quiet environment. Using the same cod aspect angles and the corresponding target strength values, the results of this calculation are shown in Fig. 9. The largest threshold detection range of 173 m occurred when the cod is broadside to the dolphin and the lowest threshold detection range of 107 m occurred at the tail-aspect angle. These detection ranges are considerably larger in a quiet environment than in a noise-limited environment. The lowest threshold detection range in the quiet environment was larger than the highest threshold detection range in the noise-limited environment (107 m vs 93 m). The maximum threshold detection range in the quiet environment is almost double the corresponding range for the noise-limited environment (173 m vs 93 m). These results clearly demonstrate how ambient noise produced by snapping shrimp can severely limit the echolocation detection range of a dolphin.

We can generalize the threshold detection range by calculating the threshold detection range as a function of target strength. Using the threshold values and the corresponding target strength used to generate Figs. 8 and 9, the generalized threshold detection ranges that can be applied for any fish of known broadband target strength are shown in Fig. 10. A linear curve fit of the points for the quiet condition is given by

$$\text{nonmasked threshold range} = 4.75TS_E + 310.10 \text{ m.} \quad (6)$$

Similarly, for the noise-limited condition of Kaneohe Bay, the linear curve fit is given by

$$\text{noise-limited threshold range} = 1.52TS_E + 138.15 \text{ m} \quad (7)$$

with  $r^2$  values of 1.00 for the nonmasked curve and 0.96 for the noise-masked curve.

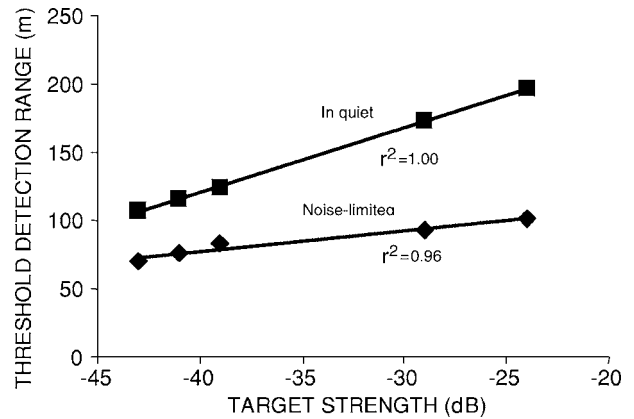


FIG. 10. Predicted echolocation detection threshold range as a function of target strength for the Atlantic bottlenose dolphin in a quiet environment and in noise masking environment where the masking noise is produced by snapping shrimps.

## 2. Harbor porpoise

Kastelein *et al.* (1999) used a 5.08- and a 7.62-cm-diam water-filled sphere to measure the echolocation detection capability of a harbor porpoise (*Phocoena phocoena*) in a large open pen at Neeltje Jans, The Netherlands. The 5.08-cm sphere had a target strength of  $-36$  dB and the 7.62-cm sphere had a target strength of  $-26$  dB. The correct detection threshold ranges were 16 and 26 m, respectively. Using Eq. (4) and assuming that the harbor porpoise used the same source level while searching for the two targets, the echo energy flux density of the echoes for both spheres at their respective threshold range agreed within 1 dB. We again used the cod as our fish of interest and the target strength values shown in Fig. 6, which are  $-25$  dB at broadside ( $90^\circ$ ),  $-35$  dB at  $135^\circ$ , and  $-36$  dB for the tail aspect ( $180^\circ$ ). The detection performance of the harbor porpoise can be calculated with Eq. (2) and the results are shown in Fig. 11, for detection in the lateral plane. The detection threshold range is maximum at the broadside ( $90^\circ$ ) aspect with a value of 27 m and minimum at the tail-aspect ( $180^\circ$ )

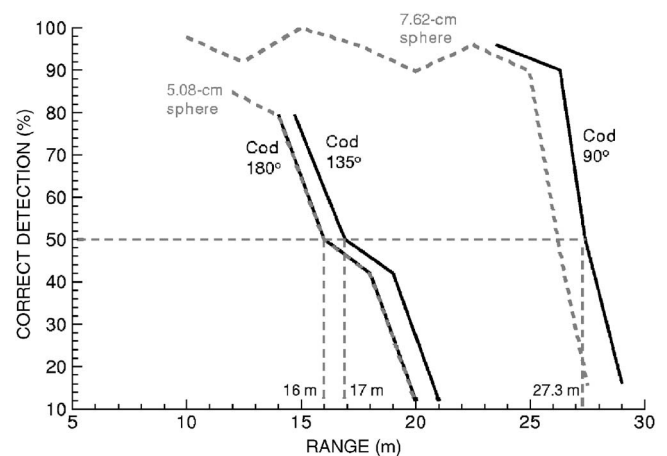


FIG. 11. Predicted correct detection performance for a harbor porpoise echolocating on a 30-cm-long Atlantic Cod. The actual harbor porpoise performance curves with real water-filled spheres are shown by the dark gray curves. The 50% correct detection threshold ranges are shown for different aspects of the fish.

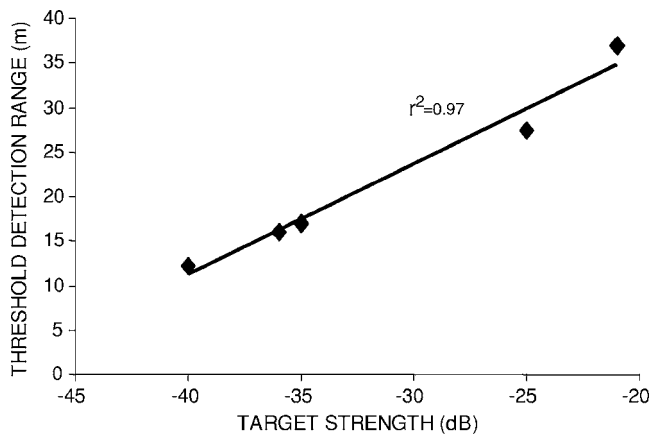


FIG. 12. Predicted echolocation detection threshold range as a function of target strength for the harbor porpoise in a quiet environment.

with a value of 16 m in a quiet environment. The target strength for the cod at tail aspect was the same as the 5.08-cm sphere so that both detection performance curves were the same.

We generalized the threshold detection range for *Phocoena phocoena* by plotting the threshold detection range as a function of the target strength. The results are shown in Fig. 12 with a linear curve fitted to the calculated values. The equation of the fitted curve is

$$\text{nonmasked threshold range} = 1.25 \text{ TS}_E + 61.10 \text{ m} \quad (8)$$

with an  $r^2$  value of 0.97. Equation (8) can be used in conjunction with the target strength values shown in polar form for any of the four species to determine the echolocation threshold detection range for *Phocoena phocoena* in a non-masked environment.

#### IV. DISCUSSION AND CONCLUSIONS

The target strength of several species of fish was measured with simulated odontocete echolocation signals as a function of fish aspect angle, in order to estimate how far dolphins and porpoises can detect fish prey by echolocation. The results obtained in this study pertained to the detection of a single fish. This would represent the most difficult detection task a foraging odontocete would confront. If there is a cluster of fishes, the target strength of the cluster would be greater than that of the single fish. The amount of increase in target strength would depend on the orientation of the fish to one another and the spacing between them. How a greater target strength would increase the detection range of an echolocating odontocete is far from obvious. The critical issue is knowing what the integration time of the animal's auditory system that should be used in such a situation where there are echoes from more than one fish. Johnson (1968) used pure tone signals of different duration to measure the integration time of a bottlenose dolphin. The integration time varied with frequency and was greater than 5 ms for a 100-kHz signal. Au *et al.* (1988) used a phantom echo system and broadband replica of the dolphin's emitted signal and measured an integration time of 264  $\mu\text{s}$ , which is considerably shorter than the integration time determined with

narrow band signals. However, the results of Au *et al.* (1988) may not be applicable here since their phantom echoes had gaps in them, i.e., two replicas of the outgoing signal separated by a silent period was played back to the animal. The waveform of an echo from a cluster of fishes would not have gaps in it but would be similar to the wave forms shown in Fig. 3 for the 135° and 180° aspects, only longer.

The minimum detection range of 70 m for a single cod in the tail aspect in a noise-masked environment seems to be large enough that a bottlenose dolphin would need to expend energy to close the separation distance and not alert the fish by its swimming motion. It would seem that in most cases a dolphin would definitely be more interested in prey at closer ranges. The maximum detection range of 93 m for a cod at broadside seems to suggest that dolphins really should not have much problem detecting prey by echolocation, even in a noise-limited environment, in order to maintain their dietary requirements (Kastelein *et al.*, 2002, 2003) assuming that a sufficient amount of prey is in the area. The noise condition in Kaneohe Bay is not atypical for many shallow off-shore waters from the temperate zone to the equator. Snapping shrimps are found throughout the world in shallow coastal waters (depth less than 60 m) at latitudes between approximately  $\pm 35^\circ$ . The detection problem may be more affected by bottom reverberation rather than by ambient noise or a combination of reverberation and noise. The effects of reverberation will be considered in a later study.

Snapping shrimps produce high intensity sounds by creating a bubble in the process of rapidly closing their large claw, and the bubble eventually cavitates creating an almost impulsive sound (Versluis *et al.*, 2000). However, at depths beyond about 60 m, the cavitation progress would probably not be possible. Therefore, as water depth progressively increases beyond about 60 m, snapping shrimp noise in temperate waters should also progressively decrease in intensity so that in sufficiently deep waters the environment becomes nonmasking. In such an environment, the minimum detection range for the bottlenose dolphin increases to about 107 m. The maximum detection range is at about 178 m. These are very long ranges and a foraging echolocating dolphin may not pay much attention to these long range echoes but would probably concentrate on closer prey if they are present.

Harbor porpoises are found in cool temperate and sub-polar coastal waters of the northern hemisphere (Jefferson *et al.*, 1993) and are not exposed to snapping shrimp noise. Since the echolocation signals are very high in frequency, there are not many noise sources that have frequency components overlapping with harbor porpoise echolocation frequencies. Therefore, the sonar system of harbor porpoises should not be limited by natural ambient noise. Nevertheless, the minimum threshold detection range of 16 m for a cod by an echolocating harbor porpoise is much smaller than the corresponding minimum detection range for a bottlenose dolphin in a noise-limited environment, about 0.22 that of a bottlenose dolphin. The limited echolocation detection range would make it difficult, if not impossible, for harbor porpoise to inhabit a noisy environment such as Kaneohe Bay. This limited sonar range may be one of the most important reasons for harbor porpoise not being usually found in lower

latitude waters inhabited by snapping shrimp. In such a noisy environment, the harbor porpoise echolocation system would be severely limited or even nonfunctional.

It is interesting that even with its limited echolocation range, harbor porpoises are able to adequately detect and forage on different types of fish. This suggests that the coastal waters that harbor porpoise inhabit have high densities and number of fishes. The bottlenose dolphin in a noisy environment can detect a fish at distances anywhere from 3.4 to 4.4 times longer than the harbor porpoise. In a quiet environment, the bottlenose dolphin could probably detect a fish at a distances anywhere from 6.3 to 6.7 times further than the harbor porpoise. Bottlenose dolphins may need the longer range detection capability perhaps because of a possible lower density of prey or less fish biomass in their habitat compared to that of harbor porpoises.

The large difference in detection ranges between the bottlenose dolphin and the harbor porpoise can probably be attributed to the difference in source level of echolocation signals emitted by both species. In the modeling of the bottlenose dolphin detection range for a cod in a quiet environment, a source level of 222 dB re 1  $\mu\text{Pa}$ , which translates to a source energy flux of 167 dB re 1  $\mu\text{Pa}^2 \text{ s}$ , was used. Unfortunately, the echolocation signals of the harbor porpoise were not measured during the range threshold experiment of Kastelein *et al.* (1999). Au *et al.* (1999) measured source levels in the same test pen and from the same porpoise used by Kastelein *et al.* (1999) and obtained an average value of 167.5 dB. However, the target used in the Au *et al.* (1999) study had about a 10 dB greater target strength than that of the 5.08-cm diameter sphere used by Kastelein *et al.* (1999) and the target range was much shorter (7–9 m) than in the target detection experiment. In a latter study to determine the capability of a harbor porpoise to detect a target in noise, we measured an average source level of 186 dB re 1  $\mu\text{Pa}$  (unpublished data). This is a rather surprising result and is the highest measured source levels for harbor porpoises to date. However, researchers at the Kerteminde facility in Denmark have recorded echolocation signals of a free swimming *Phocoena phocoena* having amplitudes comparable with these results. Having the porpoise echolocate in the presence of masking noise probably induced the animal to emit higher amplitude signals with peak-to-peak amplitude between 184 and 190 dB. Therefore, the bottlenose dolphin may be using an average source level that was about 36 dB higher in amplitude than that of the harbor porpoise. A 36-dB difference would explain most of the difference between the maximum detection range in a quiet environment between a bottlenose dolphin and a harbor porpoise. The porpoise minimum detection threshold range for the cod was 16 m (see Fig. 11), which corresponds to a two-way transmission loss of 49.3 dB. Add 36 dB to this two-way transmission loss and we have a new two-way transmission loss of 85.3 dB, which corresponds to a range of approximately 95 m, using an absorption coefficient at 130 kHz of 0.038 dB/m, which is appropriate for water temperatures between 15 and 21 °C. The dolphin minimum detection range for a cod in Fig. 9 is 107 m. The minimum detection ranges for the bottlenose dolphin and the harbor porpoise in a quiet

environment do not match up perfectly when adjusted for differences in the source levels, so other factors must be taken into consideration. One other obvious factor is the difference in hearing sensitivities between the two species or even within a species.

The use of broadband clicks for echolocation is an important part of the echolocation process. There are other types of signals that may provide long detection ranges, but longer detection ranges would not necessarily be an advantage in foraging. The detection ranges that both the dolphin and porpoise can achieve are sufficient for their needs in their ecological niches. The low amount of variation in the reflectivity as a function of azimuth when considered from an energy flux density perspective, compared to the large variation obtained with tonal pulses has the advantage of minimizing the variations of the echo energy as the fish orientation with respect to a dolphin changes. Such changes in prey orientation are to be expected in a dynamic situation in which the both the dolphin and the prey are constantly moving.

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- Au, W. W. L., Floyd, R. W., Penner, R. H., and Murchison, A. E. (1974). “Measurement of Echolocation Signals of the Atlantic Bottlenose Dolphin, *Tursiops truncatus* Montagu, in Open Waters,” *J. Acoust. Soc. Am.* **56**, 1280–1290.
- Au, W. W. L. (1993). *The Sonar of Dolphins* (Springer-Verlag, New York).
- 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 Dolphins,” *J. Acoust. Soc. Am.* **83**, 662–668.
- Au, W. W. L., Kastelein, R. A., Rippe, T., and Schooneman, N. M. (1999). “Transmission beam pattern and echolocation signals of a Harbor Porpoise (*Phocoena phocoena*)” *J. Acoust. Soc. Am.* **106**, 3699–3705.
- Au, W. W. L., Lemonds, D. W., Vlachos, S., Nachtigall, P. E., and Roitblat, H. L. (2002). “Atlantic bottlenose dolphin hearing threshold for brief broadband signals,” *J. Comp. Psychol.* **116**, 151–157.
- Au, W. W. L., and Benoit-Bird, K. (2003). “Acoustic backscattering by Hawaiian Lutjanid snappers. II. Broadband temporal and spectral structure,” *J. Acoust. Soc. Am.* **114**, 2767–2774.
- Au, W. W. L., Ford, J. K. B., Home, 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.



- Benoit-Bird, K. J., Au, W. W. L., and Kelley, C. D. (2003). "Acoustic backscattering by Hawaiian Lutjanid snappers. I. Target strength and swimbladder characteristics," *J. Acoust. Soc. Am.* **114**, 2757–2766.
- Clay, C. S., and Horne, J. K. (1994). "Acoustic models of fish. The Atlantic cod (*Gadus morhua*)," *J. Acoust. Soc. Am.* **96**, 1661–1668.
- Foote, K. G. (1980). "Importance of 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.
- Horne, J. K., and Jech, J. M. (1999). "Multi-frequency estimates of fish abundance: Constraints of rather high frequencies," *ICES J. Mar. Sci.* **56**, 1054–1199.
- Jech, J. M., and Horne, J. K. (1995). "Application of three sound scattering models to threadfin shad (*Dorosoma petenese*)," *J. Acoust. Soc. Am.* **98**, 2262–2269.
- Jefferson, T. A., Leatherwood, S., and Webber, M. A. (1993). *FAQ Species Identification Guide. Marine Mammals of the World* (UNEP/FAO, Rome), 320 pp.
- Johnson, S. C. (1968). "Relation between absolute threshold and duration of tone pulses in the bottlenosed porpoise," *J. Acoust. Soc. Am.* **43**, 757–763.
- Kastelein, R. A., Au, W. W. L., Rippe, T., and Schooneman, N. M. (1999). "Target detection by an echolocating harbor porpoise (*Phocoena phocaena*)," *J. Acoust. Soc. Am.* **105**, 2493–2498.
- Kastelein, R. A., Vaughan, N., Walton, S., and Wiepkema, P. R. (2002). "Food intake and body measurements of Atlantic bottlenose dolphins (*Tursiops truncatus*) in captivity," *Mar. Environ. Res.* **53**, 199–218.
- Kastelein, R. A., Staal, C., and Wiepkema, P. R. (2003). "Food consumption, food passage time, and body measurements of captive bottlenose dolphins (*Tursiops truncatus*)," *Aquat. Mamm.* **29**, 53–66.
- Murchison, A. E. (1980). "Maximum detection range and range resolution in echolocating bottlenose porpoise (*Tursiops truncatus*)," in *Animal Sonar Systems*, edited by R. G. Busnel and J. F. Fish (Plenum, New York) pp. 43–70.
- 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. Exper. Biol.* **207**, 1811–1823.
- Thomas, J. A., and Turl, C. W. (1990). "Echolocation characteristics and range detection threshold of a false killer whale (*Pseudorca crassidens*)," in *Sensory Abilities of Cetaceans: Laboratory and Field Evidence*, edited by J. A. Thomas and R. A. Kastelein (Plenum, New York), pp. 321–334.
- Urick, R. J. (1983). *Principles of Underwater Sounds*. 3rd ed. (McGraw Hill, New York).
- Verluis, M., Schmitz, B., von der Heydt, A., and Lohse, D. (2000). "How snapping shrimp snap: Through cavitating bubbles," *Science* **269**, 2114–2117.

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