

Pacific herring respond to simulated odontocete echolocation sounds

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Abstract: There has been a long-running debate as to if and how clupeoid fish, such as herring (*Clupea* sp.), respond to anthropogenic sound. Anatomical and physiological investigations have shown that members of the clupeoid suborder have highly developed hearing extending into ultrasonic frequencies and behavioural studies suggest that they respond to many sounds. However, only recently have the selective forces that have driven the evolution of this keen sense and behavioural repertoire played a major part in the debate. One explanation is the adaptation to predation from echolocating cetaceans. In this study, we investigate the responses of adult Pacific herring (*Clupea pallasii*) to broadband biosonar-type sounds with high-frequency similarities to those produced by odontocete cetaceans. Exposures to these sounds in an indoor tank and sea cage caused feeding fish to cease, drop in the water column, and begin to school actively. Fish already schooling dropped in the water column and increased their swimming speed. Exposures to electronic silence and an acoustic deterrent device for marine mammals did not elicit such responses. We discuss the potential suitability of the observed manoeuvres for avoidance of foraging odontocetes and consider their relevance for human-related fishing activities.

Résumé : Il existe depuis longtemps un débat à savoir si et dans quelle mesure les poissons clupéoïdes, tels que les harengs (*Clupea* spp.), réagissent aux sons générés par l'activité humaine. Des études anatomiques et physiologiques révèlent que les poissons du sous-ordre des clupéoïdes possèdent une ouïe bien développée qui s'étend jusque dans les ultrasons; des études comportementales montrent qu'ils réagissent à plusieurs sons. Ce n'est cependant que récemment que l'on a fait intervenir de façon importante dans le débat les forces de sélection qui ont favorisé cette ouïe fine et la gamme des comportements associés. Une explication veut que ce soit une adaptation à la prédation par écholocation des cétacés. Nous examinons donc les réactions de harengs du Pacifique (*Clupea pallasii*) à des sons de type sonar à bande large qui ont des similitudes de haute fréquence avec les sons produits par les cétacés odontocètes. Des expositions à de tels sons dans un enclos de laboratoire et dans une cage en milieu marin causent un arrêt de l'alimentation, un mouvement vers le bas de la colonne d'eau et un regroupement actif en bande. Les poissons déjà en bande se déplacent vers le bas de la colonne d'eau et augmentent leur vitesse de nage. Des expositions à un silence électronique ou à des sons générés par un appareil de dissuasion des mammifères marins ne causent pas de telles réactions. La signification des comportements observés dans l'évitement des odontocètes en quête de nourriture et leur influence sur les activités de pêche commerciale font l'objet d'une discussion.

[Traduit par la Rédaction]

Introduction

There are many reports from the fishing and research communities that some fish species, particularly Atlantic and Pacific herring (*Clupea harengus* and *Clupea pallasii*) and other clupeoids, respond to the sounds made by boats, tackle, sonar equipment, and, most recently, acoustic deterrent devices for marine mammals (Mohr 1971; Misund et al.

1996; Kraus et al. 1997). Such observations have put into question the validity of acoustically derived abundance estimates (MacLennan and Simmonds 1992) and led directly to changes in fishing practices with, for example, the construction of quieter vessels (Mitson 1995; Fernandes et al. 2000). The aversive behavioural responses have also been exploited. For example, high-frequency sounds have been used to keep clupeoid fish from power plant water intakes (Nestler et al. 1992; Ross et al. 1996). Together, the potential consequences and opportunities raised by these responses have stimulated a diverse variety of anatomical, physiological, and ethological research studies.

Physiological investigations of a clupeoid (the American shad, *Alosa sapidissima*) have shown that its hearing spans an unusually broad frequency range that stretches high into the ultrasonic (Mann et al. 1997, 1998). The mechanism behind this specialization remains unclear (Mann et al. 1998), although the paired tubular extensions that reach from the physostomous swimbladder to the bony air-filled auditory bullae are likely to be involved (Blaxter et al. 1981). Because these structures are common to clupeoids, it is thought that the other members of this suborder have similar hearing

Received 16 January 2002. Accepted 28 February 2002.

Published on the NRC Research Press Web site at <http://cjfas.nrc.ca> on 17 April 2002.

J16702

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abilities. While permitting the detection of high-frequency far-field sounds, the single-receiver nature of the swimbladder-mediated reception system could possibly deny these fish the ability to perceive the bearing from which the sounds originated. Instead they would have to resort to behavioural tactics such as assessing spatial amplitude gradients. Indeed, in a limited behavioural experiment, herring did not show evidence of directionally informed responses to aversive noises at frequencies over 5 kHz (Olsen 1976).

The responses that clupeoids show to sound have received much attention. A wide variety of stimuli have been applied including low to high-frequency sine waves, square waves, recorded and actual vessel noises, sonar and echosounder outputs, and killer whale calls (Olsen 1971; Schwarz and Greer 1984; Nestler et al. 1992). The responses described generally fall into two categories: startle and avoidance. Short-duration, low-frequency sounds appear to elicit short-lived directional startle responses (Blaxter and Hoss 1981; Schwarz and Greer 1984). Higher-frequency or long-duration sounds produce avoidance responses including compaction and polarization of schools, sinking in the water column, leaving the vicinity of the sound, and being herded in front of a moving source (Schwarz and Greer 1984; Misund et al. 1996; Suuronen et al. 1997). Furthermore, reactions appear to be context specific. For example, schools of *Sardinella* reacted to vessel noise by diving but only when encountered above a depth of 20 m (Gerlotto and Freon 1988).

Despite the economic importance of these responses, their evolutionary relevance for the fish is unclear. Their hearing and behavioural repertoires have clearly not evolved as a response to human fishing activities (MacLennan and Simmonds 1992). Instead, an idea that has recently gained increasing interest is that the unusually high-frequency component of their hearing and their behaviour may be adaptations to predation from echolocating marine mammals, specifically odontocete cetaceans (Mann et al. 1997; Astrup 1999). Odontocetes typically produce intense, short duration directional signals that range in frequency from 0.3 kHz to as high as perhaps 325 kHz and durations from 40–600 μ s (Au 1993; Richardson et al. 1995). Within this range, there are several so far unexplained, but potentially niche-related, patterns of variation. Dolphins in the genus *Cephalorhynchus* and the porpoises, for example, produce relatively high-frequency, narrowband clicks, whereas killer whales (*Orcinus orca*) produce low-frequency broadband signals (Au 1993). All of these sounds are potentially detectable to clupeoids; however, the behavioural responses that they might elicit have not been specifically assessed to determine if they are of any relevance to odontocete predation.

In this study, we investigate the responses of adult Pacific herring to broadband biosonar-type sounds with high-frequency similarities to those produced by odontocete cetaceans. A combination of different clicks varying in amplitude and interpulse interval were applied to determine if the fish's responses were generalized or specific to the nature of the sound that they experienced. Sound-exposure experiments were carried out on feeding and nonfeeding fish in a large indoor tank and in a sea cage. We discuss the potential relevance of the manoeuvres observed for avoidance of predation from foraging odontocetes as well as offering a possible

explanation for the responses frequently described to human-related fishing activities.

In addition to the echolocation-type sounds, we exposed fish to an acoustic deterrent device designed to reduce by-catch of odontocete cetaceans in fishing nets. Trials at sea of the same device have given mixed results as to whether they also influence the catch of herring (Kraus et al. 1997; Trippel et al. 1999). By investigating how the sound produced by such devices impacts herring behaviour, we hoped to better understand why the results of separate but similar studies at sea have produced such different results.

Methods

Fish and maintenance

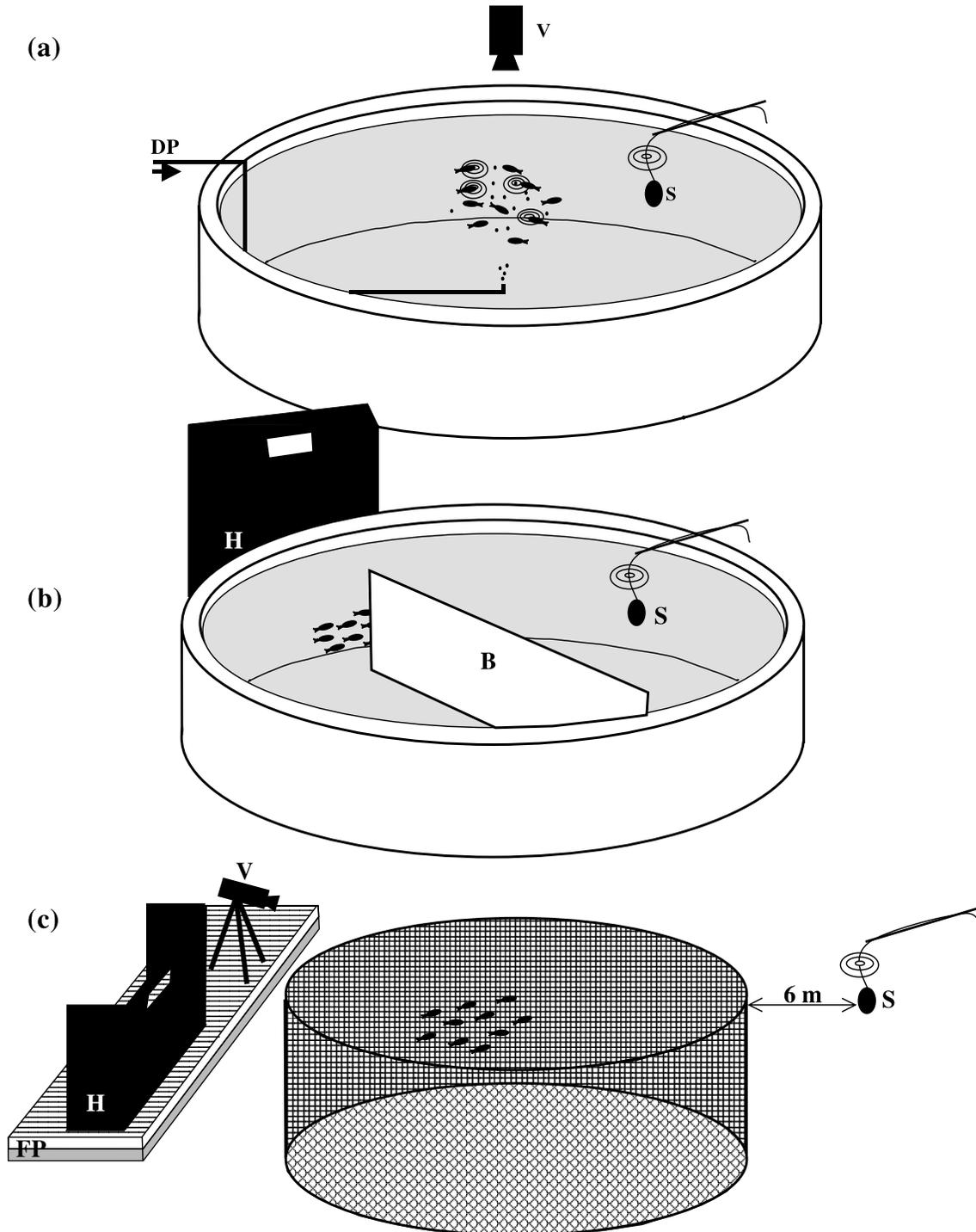
Adult Pacific herring were caught in early March of 1999 and 2000 during Canadian Department of Fisheries and Oceans spawning stock assessment surveys in Barkley Sound, B.C. (048°58'N, 125°22'W). Fish ranged in length from 14.9 to 26.2 cm, with the fish caught in 1999 being slightly larger than those caught in 2000 (mean fork length year 1999: 20.6 cm, standard error (SE) 1.4, $n = 200$; year 2000: 19.5 cm, SE 1.5, $n = 200$). Following capture, they were transferred to adjacent on-land holding facilities at the Bamfield Marine Sciences Centre, B.C. (048°50'N, 125°08'W). Fish were held in circular holding tanks (average 1.6 m diameter and 1 m deep), supplied with fresh seawater and fed on freeze-dried or frozen euphausiids.

Experiment 1: impacts of sound exposures on feeding behaviour

To evaluate the impacts of odontocete echolocation-type sounds on the feeding behaviour of adult herring, small groups were placed in a test tank and subjected to computer-generated sounds during feeding. Each trial was conducted in a large, circular, concrete, indoor test tank (9.18 m across and 2.15 m deep, Fig. 1a). Ten fish per trial were allowed to acclimate overnight before being tested the following day. During daylight hours, the water was illuminated from above with five ceiling-mounted 500-W lamps (maximum in-water light levels 16.2 μ mol·m⁻²·s⁻¹). During the hours of natural darkness, the lights were extinguished. Water temperatures ranged from 8 to 12°C during the study.

Immediately before each test, freeze-dried krill were delivered to the centre of the tank using a remotely operated pipe system running along the bottom (Fig. 1a). Once delivered, the food quickly rose through the water column to float at the surface. Behaviour of the fish was recorded using a Hi-8 video camera (Handycam CCD-V101, Sony Corporation, Japan) mounted on the ceiling 3.5 m above the centre of the tank. Fish were allowed to feed undisturbed for three minutes before a three-minute sound exposure was presented. Sounds were played through an Oceanears DRS-8 underwater speaker (Ocean Engineering Enterprises, North Canton, Ohio) powered by a 50-W amplifier and signals were generated with a laptop computer running Cooledit software (Syntrillium Software, Phoenix, Ariz.). The speaker was suspended at a depth of 1 m and held 2.3 m from the sidewall of the tank (Fig. 1a). Three sound types were presented as follows: (A) Control: a three minute flat waveform including the incidental noise generated by the computer,

Fig. 1. Experimental set-up. (a) Experiment 1. Fish in an indoor concrete tank were fed floating food in the centre via a delivery pipe (DP). Their behaviour was recorded with an overhead video camera (V) and sounds played through an underwater speaker (S). (b) Experiment 2. Fish circuiting the same tank were observed from a hide (H) and their time between gateways (formed by a baffle (B) and the tank walls) were recorded. Sounds were played with a speaker (S). (c) Experiment 3. Fish in a net pen tethered in open water were filmed (V) from a floating pontoon (FP) and observed from behind a hide (H). Sounds were played with an underwater speaker (S) 6 m from the outside perimeter of the net pen. For clarity, fish in (a), (b), and (c) are drawn larger than scale.



amplifier, and speaker. (B) Click trains: because tapes of foraging odontocetes recorded in the wild potentially contain sounds from other organisms and processes, tapes of foraging odontocetes could not be directly played to the fish. In-

stead, tapes of foraging schools of killer whales were used to determine a temporal distribution of echolocation clicks (inter-click intervals: mean = 0.2, max = 7.8, min = 0.03, SD = 0.35 s) and then simulated broadband echolocation-

type pulses (see below) of constant amplitude were created in the same temporal sequence. (C) Regular clicks: the same echolocation signals as the click trains were used, but with a regular time interval between each click. The inter-click interval was 0.2 s, which for a single odontocete would represent a foraging horizon of approximately 120 m (Au 1993).

To reduce the potential for pseudoreplication, three different versions of the click trains and regular clicks were constructed and used during the replicates (Hopp and Morton 1998). Ten groups of fish were tested in 1999 and the order of the sound exposures was assorted between trials in ABC, BCA, CAB, BAC, etc. fashion. Fish were allowed up to an hour between sound exposures to resume normal behaviour and each group was subjected to the sounds only once. The video tapes that resulted from these trials were used to document feeding rates, proximity to the food patch, rates of turning, and school polarization before and during the sound exposures (columns 1 and 2 in Table 1).

Click characteristics

Because of the interspecies variation in echolocation sound characteristics among odontocete cetaceans and the potential that these specializations developed as a counter to the evolving detection systems of their fish prey (analogous to the bat–moth arms race, Fenton et al. 1998), generalized broadband, medium-duration odontocete-type echolocation signals were constructed for this study. Again, three versions were generated to reduce potential pseudoreplication (Hopp and Morton 1998). These waveforms were modified slightly by both the sound production equipment and the tank itself. In consequence, the actual clicks that the fish received were composed of 370- to 390- μ s broadband pulses with 2350–13 900 μ s of subsequent reverberation (Fig. 2). In each click the initial pulse had energy in frequencies from 1.3 to 140 kHz with a peak at 6–7 kHz. Reverberation tended to be at frequencies below 20 kHz. Amplitudes were recorded with a calibrated hydrophone (Cetacean Research Technology, C50a) at 264 locations in the tank (over a grid of 88 points and at three depths (0.3, 1.0, and 1.7 m)). At 1 m, peak-to-peak sound-pressure levels (SPLs) of individual clicks ranged from 157 to 169 dB re 1 μ Pa (relative to one microPascal). On average, SPLs were 3 dB quieter on the side of the tank opposite the speaker; however, there was a complex pattern of troughs and peaks in SPL in different parts of the tank such that there was no relationship between SPL and proximity to the speaker for fish swimming around the perimeter (ordinary least squares regression $r^2 = 0.07$, $P = 0.1$, $n = 36$).

Experiment 2: impacts of sound exposures on nonfeeding behaviour

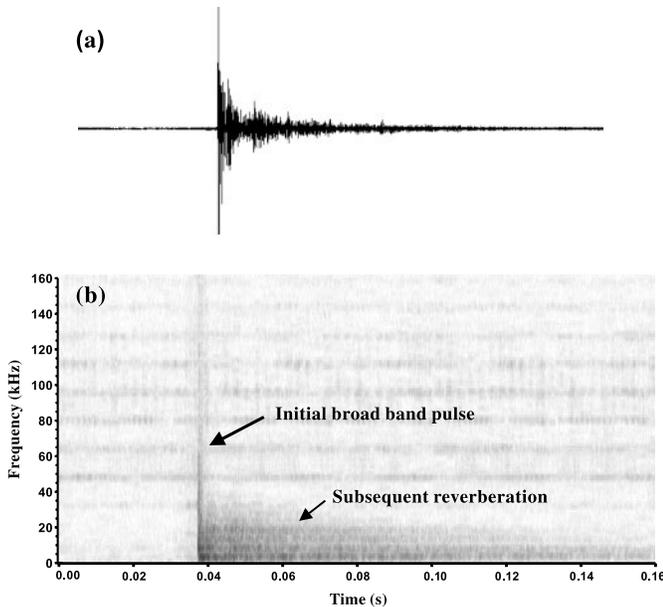
To quantify the impacts of the clicks on the nonfeeding behaviour of adult herring, small groups were subjected to sounds in the indoor test tank in the absence of food. The set-up was as for experiment 1, except for the following. An opaque vertical baffle was erected to bisect the tank leaving gateways (1.45-m wide) between the ends of the baffle and the tank walls (Fig. 1b). Instead of using a camera, behaviour was recorded by a seated observer concealed by a hide. In the absence of food, fish would circuit the perimeter of the tank passing through the two gateways on each circuit.

Table 1. Comparison of the behaviour of groups of feeding fish before and during sound exposures ($n = 10$).

Activity	Measure used	Control		Click trains		Regular clicks	
		<i>b</i>	<i>d</i>	<i>b</i>	<i>d</i>	<i>b</i>	<i>d</i>
Feeding rate	Total no. of strikes at surface food per minute	26.3	26.8	23.8	23.8	16.5	16.5
				$z = -1.066$	$z = -2.80$	$z = -2.80$	$z = -2.80$
				$P = 0.29$ (NS)	$P < 0.01$ (**)	$P < 0.01$ (**)	$P < 0.01$ (**)
Residence at food patch	No. of fish in portion of tank where food was delivered	3.7	5.3	4	4	3.2	3.2
				$z = -1.36$	$z = -2.60$	$z = -2.60$	$z = -2.80$
				$P = 0.17$ (NS)	$P < 0.01$ (**)	$P < 0.01$ (**)	$P < 0.01$ (**)
Changes in direction	No. of direction changes ($>20^\circ$) by randomly chosen fish over 2 s	1.7	2.0	1.5	1.5	1.7	1.7
				$z = -0.8$	$z = -2.80$	$z = -2.80$	$z = -2.80$
				$P = 0.41$ (NS)	$P < 0.01$ (**)	$P < 0.01$ (**)	$P < 0.01$ (**)
School polarization	Relative orientation of pairs of fish chosen at random (range 0–180°)	87.0	71.3	83.8	83.8	78.5	78.5
				$z = -0.15$	$z = -2.70$	$z = -2.70$	$z = -1.99$
				$P = 0.88$ (NS)	$P < 0.01$ (**)	$P < 0.01$ (**)	$P < 0.05$ (*)

Note: Comparisons performed using the Wilcoxon test for matched pairs with the before and during exposure values making up each pairing. The variables *b* and *d* represent median values before and during exposures, respectively. NS, not significant; *, significant at a 95% confidence level; **, significant at a 99% confidence level.

Fig. 2. (a) Time waveform and (b) spectral plots of a typical click recorded in the test tank. Measurement taken at 1 m from the speaker with a calibrated hydrophone (Cetacean Research Technology C50a, Seattle, Wash.) and data acquisition equipment (Digidata 1200B, Axon Instruments, Union City, Calif.). Sampling rate 333 kHz. Spectral plot analysis bandwidth 650 Hz.



Each minute, the observer recorded their behaviour, specifically the number of schools formed, their estimated depth in the water column, and how many fish were on either side of the tank. Swimming speeds were calculated from the times that the lead fish in the fastest moving school passed between the two gateways on each circuit. The baffle was positioned so that the observer could see the fish at all times and so that the speaker (positioned as experiment 1) was centred on one side of the bisected tank.

In each trial, the behaviour of 10 fish 15 min before and 15 min after each sound exposure was recorded, as well as their behaviour during the transmission period. In the summer of 1999, the three sound types used in experiment 1 were played to 16 groups for durations of 15 min.

In the spring of 2000, five additional sounds were presented to 16 new groups. (D) Regular clicks short: as regular clicks, but played for 3 minutes; (E) increasing amplitude clicks: as regular clicks with a constant inter-click interval of 0.2 s, but clicks sequentially increasing in amplitude; initial clicks began at 130 dB re 1 μ Pa at 1m and steadily increased to reach 169 dB by the ninth minute and remained at 169 dB for a further 5 min; (F) decreasing amplitude clicks: reversed version of increasing amplitude clicks; (G) variable amplitude clicks: as increasing amplitude clicks, but clicks in random order so that the amplitude of each click was unrelated to those preceding or following; (H) pinger: an acoustic deterrent device (Dukane NetMark 1000), positioned by the speaker, turned on for 15 min. The pinger produced 0.3-s pulses at a peak frequency of 10–11 kHz every 4 s at an SPL of between 133 and 145 dB re 1 μ Pa at 1 m (Trippel et al. 1999). Batteries were replaced if their output dropped below 6 volts. As with Experiment 1, three versions of each sound exposure were constructed and three different pingers used

to reduce any impacts of pseudoreplication (Hopp and Morton 1998).

Experiment 3: repetition of experiment 2 in a free-field environment

Because of the potential impact of the test tank on the acoustic characteristics of the sound exposures, the procedure used in experiment 2 was repeated in a free-field environment in the summer of 2000. A 2.9-m diameter, 1.5-m deep sea cage was constructed from 1-mm net twine (3-cm mesh) and 21-mm plastic hose and suspended in a sheltered inlet off Barkley Sound (Fig. 1c). Minimum water depth under the sea pen was 3 m and the bottom was soft mud. The behaviour of the fish was recorded both by a hidden observer and a Hi-8 video camera. Ten separate groups were filmed for 3 min without intervention, then subjected to a 3-min sound exposure of either click trains ($n = 3$) or regular clicks ($n = 7$). The speaker used in earlier experiments was held 1 m below the surface and 6 m from the outside of the cage to minimize near-field effects (Enger and Andersen 1967). Subsequent double-blind analyses of the videotape were carried out such that the analyst was unaware of the sound exposure type.

Results

Exposures to odontocete echolocation-type sounds elicited changes in the behaviour of both feeding and nonfeeding fish, whereas the control (electronic silence) and an acoustic deterrent device for marine mammals did not.

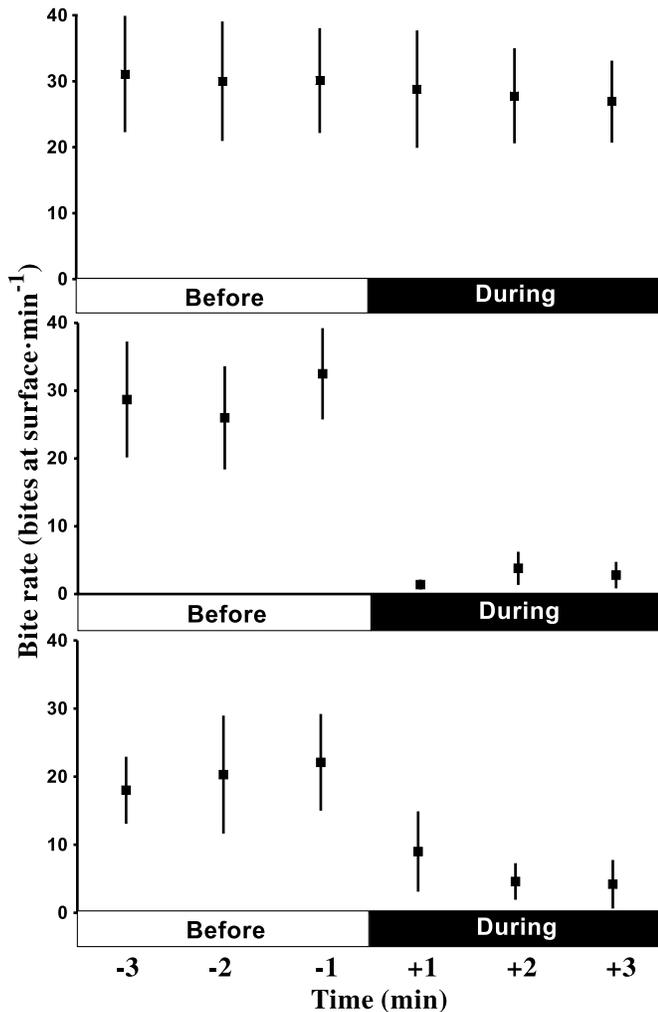
Experiment 1: impacts of sound exposures on feeding behaviour

In 1999, 10 separate groups of herring were exposed to sounds while feeding. No measurable changes in behaviour were detected in response to the control sound. The number of strikes at surface food, the number of individuals directly under the food patch, the frequency of sharp changes in direction, and the fishes' relative orientation to one another (polarization) showed no significant difference during exposure to the control sound as compared with before the production of the control sound (Table 1). In contrast, the behaviour of fish changed during the click trains and regular clicks. Some groups severely reduced their feeding activity while all others (8 out of 10 click trains; 7 out of 10 regular clicks) stopped feeding entirely (Fig. 3). Instead, fish appeared to actively school near the bottom of the tank and become more polarized (by converging their swimming trajectories; Fig. 4), turn less frequently, and spend less time in the part of the tank containing the surface food patch (Table 1).

Experiment 2: impacts of sound exposures on nonfeeding behaviour

None of the 1999 treatments (control, click train, or regular click sounds) had any significant impact on the number of schools the fish formed, the proportion of time spent on the with- or without-speaker sides of the tank, or the frequency with which fish changed from clockwise to counter-clockwise swimming (Table 2). Neither fast-start startle responses nor the ejection of air bubbles was observed in any of the trials. However, in contrast to the controls, the click

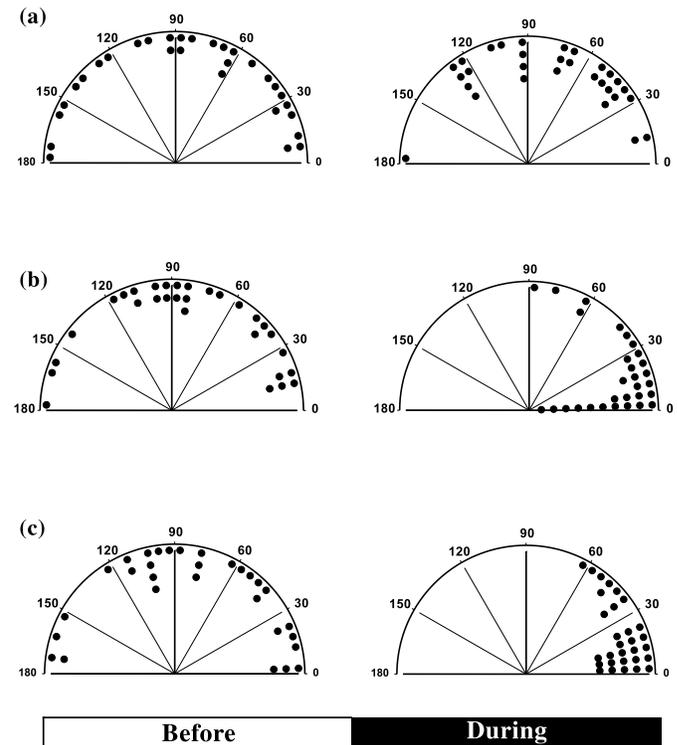
Fig. 3. Frequency with which fish took food from the water surface before and during (a) control, (b) click train, and (c) regular click exposures. Mean \pm 1 SE bars shown.



train and regular click exposures had a significant, sustained impact on swimming speeds and depths chosen by the fish (Table 2; Figs. 5a–5c and 6a–6c). In response to click trains, the fish increased their swim speeds within a minute of the start of the exposure, reaching peak speeds two minutes later and swimming 1.70 times faster than pretreatment. Swimming speeds during the rest of the exposure gradually declined towards those measured before the treatment. Speeds after the exposure were similar to those before it. The regular clicks elicited a similar response, although the maximal swim speeds were reached more abruptly (within two minutes of the start of the exposure) and the increase was slightly smaller in magnitude (1.45 times pretreatment). Changes in depth were equally dramatic (Fig. 6a–6c). Within two minutes of the start of the click train and regular click exposures all groups had left the water column to circuit the tank at its bottom. As the exposures continued, groups gradually re-entered the water column and reached pretreatment depths shortly after the exposures finished.

The 3-min exposures to regular clicks in 2000 elicited a similar response to the 15-min exposures to regular clicks; however, the duration of the changes in swim speed and

Fig. 4. Group polarisation before (left) and during (right) (a) control, (b) click train, and (c) regular click exposures. Once per minute in each trial, all fish visible on the video screen were assigned numbers and two chosen with a random number table. Their relative orientation to each other (0°, same; 180°, opposite trajectory) was then measured from the screen.



depth differed (compare Figs. 5c versus 5d and 6c versus 6d). The elevation in swim speed continued past the end of the 3-min exposures, returning to normal levels approximately 4–5 min later and approximately nine minutes earlier than in the 15-minute exposures. The period of decrease in swimming depth was similarly foreshortened compared with the longer exposures. The magnitude of change in swimming speed was similar between the 3-min (year 2000) and the 15-min (year 1999) trials, at 1.32 versus 1.45 times pretreatment speeds, respectively. However, the actual pretreatment and during-treatment speeds were higher in 2000 (0.53 m · s⁻¹) than in 1999 (0.43 m · s⁻¹).

The exposures to clicks of varying amplitude, like those of constant amplitude, all had impacts on the swimming speeds and depth choices of the fish (Figs. 5e–5g and 6e–6g). The increasing-amplitude click exposures had the smallest impact, producing only minor changes, whereas the decreasing-amplitude click exposures had more effect, particularly in the first few minutes of treatment. The variable amplitude clicks exposures (which were composed of the same clicks as the previous two treatments but in a random order) elicited a major and sustained change in swimming speed (peaking at 1.43× pretreatment speed) and a

Table 2. Impacts of sound exposures (1999) and pinger (2000) on nonfeeding fish ($n = 16$).

Activity	Measure used	Control		Click trains		Regular clicks		Pinger	
		b	d	b	d	b	d	b	d
No. of schools	No. of schools made by the 10 fish each minute	$b = 1.0$ $d = 1.1$	$z = -1.07$ $P = 0.28$ (NS)	$b = 1.2$ $d = 1.3$	$z = -0.06$ $P = 0.95$ (NS)	$b = 1.2$ $d = 1.2$	$z = -0.77$ $P = 0.44$ (NS)	$b = 1.1$ $d = 1.1$	$z = -1.25$ $P = 0.21$ (NS)
Avoidance of speaker	No. of fish each minute on non-speaker side of tank	$b = 5.2$ $d = 5.1$	$z = -0.70$ $P = 0.49$ (NS)	$b = 5.0$ $d = 5.0$	$z = -0.88$ $P = 0.38$ (NS)	$b = 5.3$ $d = 4.8$	$z = -0.96$ $P = 0.34$ (NS)	$b = 4.9$ $d = 5.5$	$z = -0.54$ $P = 0.59$ (NS)
Reversals in direction	Switches between clockwise and counter-clockwise swimming	$tb = 13$ $td = 7$	$z = -0.84$ $P = 0.40$ (NS)	$tb = 7$ $td = 12$	$z = -1.18$ $P = 0.24$ (NS)	$tb = 15$ $td = 12$	$z = -0.34$ $P = 0.74$ (NS)	$tb = 3$ $td = 2$	$z = -0.44$ $P = 0.65$ (NS)
Swimming speed	Time between gateways (converted to $m \cdot s^{-1}$)	$b = 0.3$ $d = 0.2$	$z = -0.70$ $P = 0.48$ (NS)	$b = 0.2$ $d = 0.4$	$z = -2.74$ $P < 0.01$ (**)	$b = 0.3$ $d = 0.4$	$z = -3.39$ $P < 0.001$ (***)	$b = 0.5$ $d = 0.4$	$z = -0.31$ $P = 0.76$ (NS)
Depth	Water column depth each minute (measured from tank bottom)	$b = 1.4$ $d = 1.6$	$z = -1.6$ $P = 0.12$ (NS)	$b = 1.6$ $d = 1.0$	$z = -3.29$ $P = 0.001$ (***)	$b = 1.5$ $d = 1.1$	$z = -2.97$ $P < 0.005$ (***)	$b = 1.5$ $d = 1.7$	$z = -1.60$ $P = 0.11$ (NS)

Note: Before and during exposure values were compared using the Wilcoxon test for matched pairs. The variables b and d represent median values before and during exposures, tb and td represent total numbers of reversals before and during, respectively. NS, not significant; **, significant at a 99% confidence level.

change in depth similar to the decreasing amplitude exposures.

The pinger had no demonstrable impact on the number of schools the fish formed, the proportion of time spent on either the with- or without-pinger sides of the tank, the frequency with which fish changed from clockwise to counter-clockwise swimming, their swimming speed, or the depth they chose (Table 2; Figs. 5*h* and 6*h*).

Experiment 3: repetition of experiment 2 in a free-field environment

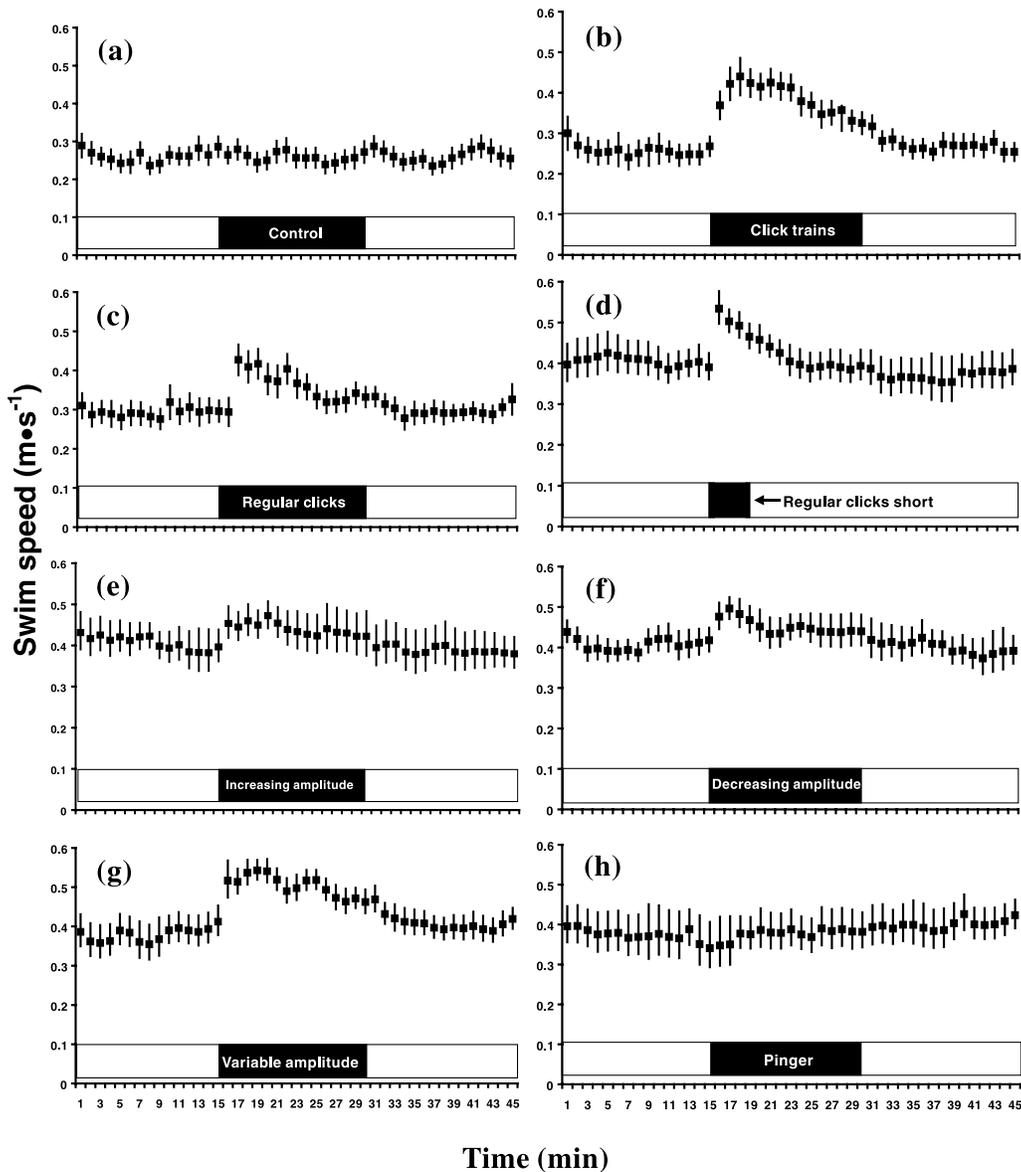
Ten groups with 10 fish in each were exposed to either click trains ($n = 3$) or regular click trials ($n = 7$) in the tethered net pen during the summer of 2000. As with the indoor tank experiments, fish swam significantly faster during the 3-min exposures than during the 3 min preceding the tests (median before = 0.16; median during = 0.22 $m \cdot s^{-1}$ (an increase of 1.36 \times), Wilcoxon test for matched pairs $z = -2.803$, $P < 0.005$, $n = 10$) and positioned themselves significantly deeper in the net pen ($z = -2.80$, $P < 0.01$). Again, no fast-start startle responses or bubble releases were observed. No tendencies to avoid the side of the pen nearest the speaker were apparent to the observer at the time or on reviewing the videotapes.

Discussion

These experiments have shown that Pacific herring do respond to broadband echolocation-type click sounds. The responses observed were both simple and overall relatively subtle. Feeding fish ceased striking at prey and took up more typical schooling behaviour, whereas already schooling fish increased both their swimming speed and their depth. The fish showed the ability to alter the magnitude of their response depending on the nature of the sound exposure. For example, clicks of variable amplitude produced a greater overall change in swim speed than the same clicks played in either increasing or decreasing amplitude order. Changes in swim speed for all trials typically represented an increase of between 130 and 170% compared with pre-exposure speeds. All swimming speeds, both before and during exposures, were cruising speeds sustainable over considerable periods for herring of this size (Blaxter and Dickson 1959). The durations of the speed elevations and depth increases were also variable and related to the duration of the exposure. The increase in swim speed and increase in depth resulting from the 3-min exposures lasted longer than the exposures themselves, but the swim speeds were not sustained throughout the 15-min exposures. However, the decay of elevated swimming speeds during the longer exposures does not appear to have signified exhaustion. Their close relationship with the types of exposure received rather than any particular duration or distance swum suggests a behavioural rather than energetic cause. Furthermore, the changes in depth were unlikely to require significant energetic expenditure but still returned to more normal levels during longer exposures suggesting either habituation or gradual abandonment of the response despite continued stimulation.

Although the feeding fish left the food patch during exposures, no avoidance of the speaker or its vicinity in either the indoor tank or net pen was observed. In the net pen, the predominant signal received by the fish would have been in the

Fig. 5. Swim speeds of nonfeeding fish before (open bar), during (solid bar), and after (open bar) exposures. The sound type is indicated in the solid bar. Mean \pm 1 SE bars shown, $n = 16$ for each.



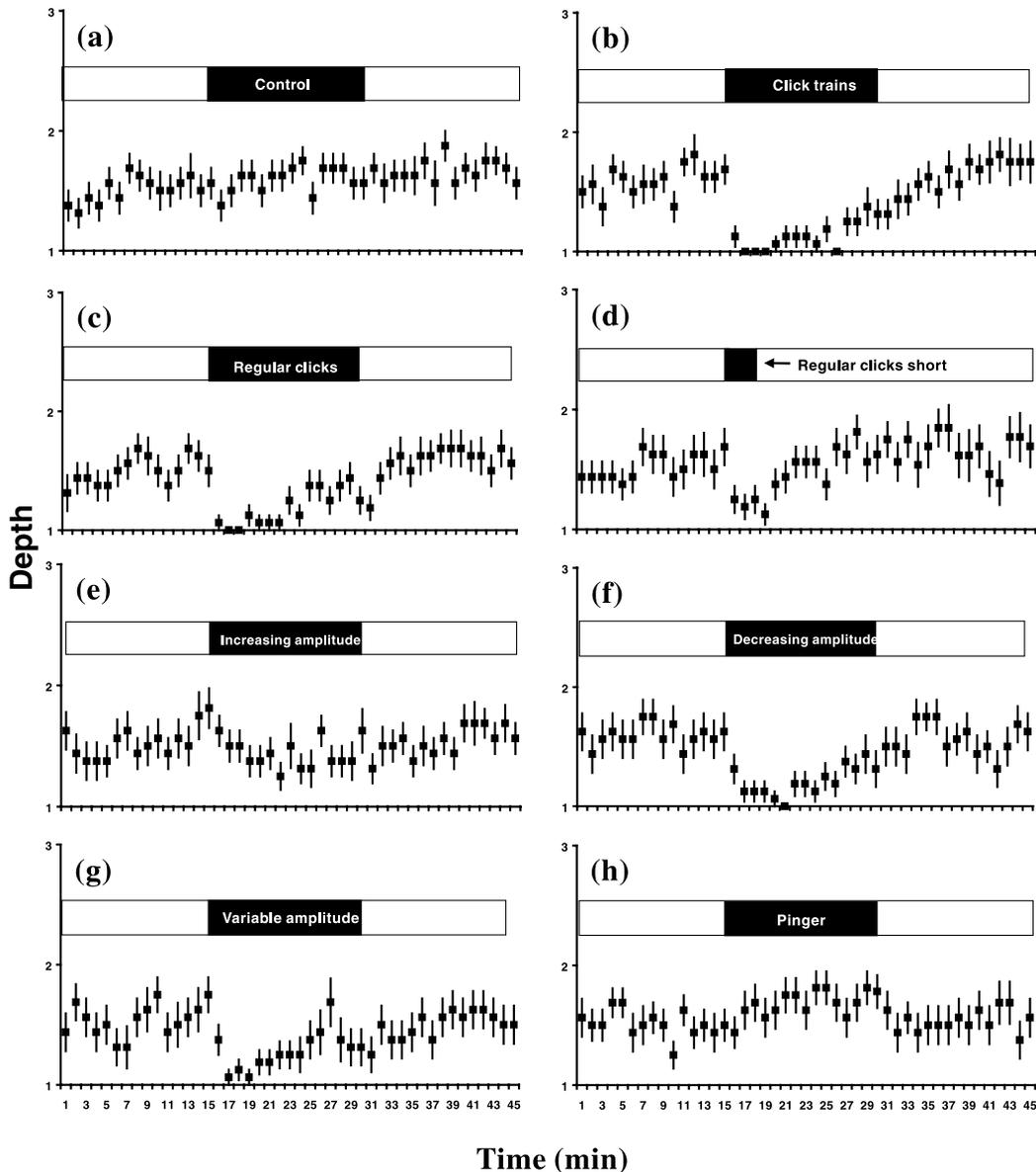
far-field and therefore potentially given them little directional information, however the absence of some spatial response in the indoor tank is somewhat surprising. On circuiting, fish would pass within at least 2.5 m of the speaker, usually nearer, and therefore potentially gain near-field stimulation with consequent directional information. However, their consistent swim speeds on the with- and without-speaker sides of the tank and their lack of increased turning suggests that they used a tactic of simply increasing speed. Furthermore, the similarity of results between the net pen and indoor tank suggests that near field and amplitude gradients were not essential components to elicit the responses observed.

The behavioural changes detected with exposures to odontocete-type echolocation sounds bear similarities with those found for anthropogenic sounds in other herring studies. Downward movements are reported almost universally

both in enclosure and at-sea studies. Reported descent rates are generally rapid (up to $0.7\text{--}1\text{ m}\cdot\text{s}^{-1}$), decrease with increasing depth, and can take fish from surface waters to as deep as 150 m (Olsen et al. 1983; Misund and Aglen 1992; Pitcher et al. 1996). However, Pitcher et al. (1996) noted that a downward movement in herring schools was not a response to all threats. Individual attacking cod and haddock did not elicit downward flight, whereas an approaching research vessel and a suspected school of saithe did.

Changes in swim speeds may be more common than reported. Avoidance responses are often described whereby fish appear to leave an area on commencement or approach of a stimulus. However, such a response need not actually require active avoidance. Hering (1969), for example, reported that escaping herring chose a direction to swim in and then kept it even if the heading took them directly toward the aversive stimulus. Thus, simply by increasing swim

Fig. 6. Swimming depths of nonfeeding fish before (open bar), during (solid bar), and after (open bar) exposures. The sound type is indicated in the solid bar. Mean \pm 1 SE bars shown, $n = 16$ for each. Fish depth was recorded on each circuit and ascribed to bins (bottom, bottom–middle, middle, etc.). 1 represents the tank bottom and 3 represents the surface.



speeds and maintaining a straight trajectory, schools of fish receiving an acoustic stimulus would move horizontally and thus frequently appear to avoid a fixed or moving sound source. The increase in swim speed as a result of the 15-min variable amplitude click sound exposure in this study, for example, would have taken the average school of fish horizontally an extra 140 m. The duration of interactions and their consequent flight distances are likely to be shorter. In real fisheries interactions, a straight horizontal flight along random headings by ensounded fish would reduce the numbers occurring directly in the path of a net or sonar beam. A simple mechanism such as this could explain many of the “avoidance” responses that have been documented (Misund et al. 1996; Suuronen et al. 1997). Frequently, these events have been detected using ultrasonic echosounders. The recently discovered high-frequency hearing capabilities of clu-

peoids and their potential responses to transient sounds containing high frequencies could imply that the impacts of the echosounders themselves (rather than just the low frequencies produced by engines, warps, etc.) need to be considered. In a recent case where herring avoidance of a survey vessel was thought to have been disproven (Fernandes et al. 2000), the presence of the same echosounders (producing 38-kHz signals) on both the ship and the control appears to have been overlooked.

The absence of fast-start escape responses (Blaxter and Hoss 1981), fountain effects (Hall et al. 1986), or bubble emissions (Nøttestad 1998) in any of the experiments performed in this study suggest that the sound stimuli were not perceived as a sign of imminent danger (Astrup 1999). This raises the question of what evolutionary force could have driven the development of the subtler, potentially long-range

responses observed. No matter how appropriate, these behaviours have clearly not evolved in response to human-related fishing activities (MacLennan and Simmonds 1992). Their being a tactic to avoid predation from echolocating odontocetes has historically been excluded as a possibility (Bone and Marshall 1982), but has more recently gained interest and credibility (Mann et al. 1997; Astrup 1999). Odontocete echolocation systems bear similarities with man-made ship mounted sonar systems. Their sounds are predominantly high in frequency (ship, 0.4–500 kHz; cetacean 0.3–325 kHz), short in duration (ship, 1 μ s to 1 s; cetacean 40 μ s to 0.6 ms), and loud (ship, 180–230+ dB; cetacean, 135–230 dB re 1 μ Pa at 1 m; Richardson et al. 1995). Sonar beams from ships may be directed forward, downward or to the side, whereas odontocete biosonar sounds are directed forward.

For odontocetes hunting relatively small prey a tiny portion of their outgoing sounds return as echoes. The discrepancy between the intensity of the outgoing sound and the returning echoes produces a potential zone ahead of the hunting cetacean where prey sensitive to the appropriate frequencies can hear the echolocation sounds, but if their own acoustic reflectivity is small enough, will not provide echoes loud enough to be detectable to the odontocete (Astrup 1999). The nature of this zone is dependent on the hearing sensitivities of both the prey and the odontocete and the prey target strength. The existence of this spatio-temporal window may offer the opportunity for prey to escape before being perceived by the predator. We suggest that the avoidance responses observed in this and previous studies of clupeoid behaviour may represent just such an adaptation. The cessation of feeding, adoption of polarised schooling, and increases in swim-speed coupled with a lack of turning would help fish overtaken by the outer fringes of a hunting odontocete's sonar beam to move away before entering the zone where their own echoes would be detectable to the echolocator. Clearly, directional hearing capabilities would help fish take an optimal path of escape. However, even without accurate information on the bearing of the sound source, simply increasing speed in any direction would potentially help many schools dodge the relatively narrow sonar beam (<50°, Au 1993) operated by odontocete cetaceans. Similarly, changes in depth (either ascending or descending) could take fish out of the equally narrow vertical beam. Upward avoidance movements appear rare in clupeoids but downward trajectories are common and would be especially beneficial against air-breathing predators, such as odontocetes. By diving down, the fish would effectively increase the energetic costs of foraging for their predators and therefore encourage them to switch to shallower schools or other prey items (Boyd 1997). Furthermore, by descending, the increased pressure would reduce the fishes' swimbladder cross-sectional area and so reduce their own target strength (Ona 1990) thereby increasing their window of opportunity for undetected escape.

A situation where the active detection systems of the predator potentially provide information and possibilities of escape to prey is not unique. A similar but better-understood interaction occurs between echolocating bats and nocturnal insects, notably moths. As with other longstanding predator-prey dynamics, both parties appear to have engaged in an arms race with the evolution of a diverse array of tactics and counter-tactics (e.g.,

Fenton et al. 1998). A similar dynamic might have shaped the behaviour we observe today of both the fish and odontocetes. As with bats, different odontocete species produce echolocation clicks with different characteristics. Small delphinids from the genus *Cephalorhynchus* as well as the phocoenids (porpoises) produce convergent narrowband, high-frequency echolocation clicks centred between 110 and 140 kHz (Au 1993). It may prove fruitful in trying to understand why such narrow-band characteristics have been selected to specifically investigate what impact such precise sounds (in comparison to the broadband sounds used in this study) have on their preferred prey (often clupeoid fish). In addition to the characteristics of the echolocation sounds themselves, foraging behaviour in odontocetes is diverse and potentially reflective of the capabilities of their prey. For example, killer whales (*Orcinus orca*) hunting salmon echolocate for significantly more time than those feeding on marine mammals, probably because of the differing auditory abilities of salmonids and mammals (Barrett-Lennard et al. 1996). As clupeoid fish appear more similar to the latter in auditory ability, we might predict that whales searching for clupeoids use their echolocation more sparingly or differently than they do with other fish species. In any case, it is clear from the literature that the behaviour of prey has too frequently been ignored when trying to understand the foraging patterns and capabilities of cetaceans. Further, by understanding what strategies odontocetes might use to detect fish capable of detecting their own sounds, we may gain insight into methods to improve our own techniques to estimate abundance and to capture acoustically sensitive fish species.

The absence of a measurable response to the acoustic deterrent device (pinger) used in this study is interesting. Firstly, it suggests that not all noises produce the behavioural responses observed for the clicks. Secondly, it makes the significant (at the $P < 0.01$ level) reduction of herring catch in fishing nets equipped with similar pingers in the Kraus et al. (1997) sea trial even more curious. In attempting to explain the absence of a repeatable result during a similar trial in an adjacent sea area, Trippel et al. (1999) suggested that the longer deployment of pingers in the Kraus et al. (1997) study might have drained the batteries. This could have led to pingers that produced lower than normal frequency sounds and hence pushed the frequency away from a null in the clupeoid bimodal hearing range. Although feasible and relatively testable, it seems unlikely however that increased soak time and consequent gradual battery decline could lead to the 85% reduction in catch. Another possibility is that ambient noise levels could have differed between studies and thus raised or lowered the pinger signals either side of background. The ambient noise levels in the indoor tank in the current study proved too low to measure effectively, but were likely to be lower or at worst comparable with those experienced at sea. Furthermore, the proximity of the fish to the pinger (always less than 7 m) makes it unlikely that the pingers were less audible to the fish in this study than in the Kraus et al.'s (1997) sea trial. Therefore, the differences between these studies remain unexplained; however, because our detailed knowledge of the high-frequency hearing abilities of clupeoids are currently limited to just one species (the American shad; Mann et al. 1997), a better understanding of the auditory abilities of other members of the suborder, particularly the commercially and eco-

nominally important Atlantic and Pacific herring, would be extremely valuable. Among many other applications, such information coupled with behavioural studies would aid design of marine mammal acoustic deterrent devices for fishing nets that do not impact catches of clupeoids. Alternatively, if these fish were not the target, such information could aid the design of devices that both reduced unwanted bycatch of marine mammals and clupeoids.

Acknowledgements

The authors are indebted to Alex Fraser, Tom Greenacre (Dukane Corporation), Kristina Swerhun, Lisa Walker, Nathan Webb, Darren Witt, the crew of the *Ocean Provider* and the Bamfield Volunteer Fire Department for their skilled assistance with tanks, fish, and loan of equipment. We thank Carl Schilt, Sonam Bennett-Vasseux, Tara Law, and two anonymous reviewers for comments on the text. This work was carried out with the financial assistance of the U.K.'s Leverhulme Trust, the Natural Sciences and Engineering Research Council (NSERC Canada grant A6869 to L.M.D.) and a Bamfield Marine Sciences Centre Research Associate Award. Herring were caught under licence issued to the BMSC pursuant to the Canadian Fisheries Act RSC-1985 and held according to Canadian Council of Animal Care rules, under permit SFU 541B.

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