Click sounds produced by cod (Gadus morhua)

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(Received 24 September 2003; revised 6 November 2003; accepted 17 November 2003)

Conspicuous sonic click sounds were recorded in the presence of cod (Gadus morhua), together with either harp seals (Pagophilus groenlandicus), hooded seals (Cystophora cristata) or a human diver in a pool. Similar sounds were never recorded in the presence of salmon (Salmo salar) together with either seal species, or from either seal or fish species when kept separately in the pool. It is concluded that cod was the source of these sounds and that the clicks were produced only when cod were approached by a swimming predatorlike body. The analyzed click sounds (n = 377) had the following characteristics (overall averages ± S.D.): peak frequency=5.95±2.22 kHz; peak-to-peak duration=0.70±0.45 ms; sound pressure level (received level)=153.2±7.0 dB re 1 μPa at 1 m. At present the mechanism and purpose of these clicks is not known. However, the circumstances under which they were recorded and some observations on the behavior of the seals both suggest that the clicks could have a predator startling function. © 2004 Acoustical Society of America. [DOI: 10.1121/1.1639106]

PACS numbers: 43.80.Ka, 43.80.n, 43.64.Tk [WA] Pages: 914-919

I. INTRODUCTION

Many fish species are known to produce a variety of sounds, and vocalization among teleost fish has been documented for over 40-50 families, mostly in association with social interactions, and during reproductive periods, in particular (e.g., Brawn, 1961; Myrberg, 1981; Myrberg et al., 1993; Lobel, 1992; Ladich, 1991, 1997; Mann and Lobel, 1998; Nordeide and Kjellsby, 1999). Such fish sounds are usually pulsed, with most of their energy below 3 kHz, and have been characterized as grunts, moans or clicks (e.g., Schneider, 1967; Hawkins and Rasmussen, 1978; Myrberg, 1981). The sounds may be very intense (>130 dB re 1 μ Pa), which may be important in announcing the size or the physical strength of an individual (Ladich et al., 1992; Myrberg et al., 1993; Crawford et al., 1997). Sound production during nonspawning periods commonly occurs during intraspecific and interspecific aggression, or when fish are disturbed or frightened (e.g., Brawn, 1961; Myrberg, 1981; Ladich, 1997). If sounds are used during agonistic encounters they are usually accompanied with visual agonistic displays (Ladich, 1990; Hawkins, 1993; Mann and Lobel, 1998). Such sounds vary from low frequency grunts and drumming sounds (40–1700 Hz) to higher frequency creaking sounds, clicks and stridulation sounds (1–6 kHz) in various species (Ladich, 1997).

Cod (Gadus morhua) have well-developed drumming muscles and are known to produce grunts with their main energy below 1 kHz under a variety of circumstances (McKenzie, 1935; Brawn, 1961; Hawkins and Rasmussen, 1978; Nordeide and Kjellsby, 1999; Midling et al., 2002; Soldal and Totland, 2002). Free-ranging cod have also been found to produce series of knocks with frequencies below 0.6 kHz, in addition to grunts (Midling et al., 2002), but other sounds have, to our knowledge, not been reported for this species.

We recently conducted a bioacoustic study to investigate

the potential use of echolocation and acoustical cues by captive harp and hooded seals in connection with hunting of live fish. In that context we recorded click sounds in the presence of both seals and cod that in subsequent follow-up investigations were found to origin from the cod. Here we describe the nature of these cod sounds and the circumstances under which they were recorded.

II. MATERIALS AND METHODS

A. Experimental design

The study was originally designed to identify potential sound production by seals in connection with locating, chasing, and capturing live prey (fish). The present paper only describes those experiments and results that are pertinent for our discovery of some previously undescribed cod sounds. That part of the study involved five types of experiments.

In the first type of (seal-fish) experiments, three subadult/adult harp seals (Pagophilus groenlandicus) and two sub-adult/adult hooded seals (Cystophora cristata; Table I) were maintained, one or two at the time, in a 40 000 liters seawater pool while cod (Gadus morhua) were introduced into the pool, 1-3 fish at the time. Any sounds produced in the 20 min following cod introduction (or until all cod had been captured and devoured by the seals) were monitored and recorded for later analyses. These experiments were conducted either with the pool room fully lit (from artificial light sources as well as outdoor light penetrating via eight pool room windows), or with all lights turned off and with blinds on all windows. Light intensity was about 180 lux during light conditions, and 0 lux during dark conditions, as determined with a Grosser Panlux Electronic Luxmeter (Germany). The activities of seals and fish could be surveyed without disturbing the animals during light conditions by use of a video camera (CCD Video, CV252 C, Japan) which was mounted in the ceiling above the pool, and connected to a video screen (CCD, Transvoice Screen, Japan) placed in an

TABLE I. Gender, age, and time in captivity before sound recording experiments were started, for the seals used in the present study.

Animal	Gender	Age	Time in captivity	
Harp seals				
G-2	Male	Unknown (subadult->2 yrs)	8 mo	
G-3	Female	Unknown (subadult->2 yrs)	10 mo	
G-5	Female	Unknown (adult->5 yrs)	5 mo	
Hooded seals				
K-1	Female	Unknown (adult->4 yrs)	4 days	
K-66	Male	2.5 yrs	2.5 yrs	

adjacent room. A total of 130 cod were introduced, in combinations as shown in Table II.

The second type of (seal-fish) experiments represented a control situation in which juvenile salmon (*Salmo salar*) were introduced instead of cod, while the pool was filled with freshwater instead of seawater. Otherwise these experiments were conducted in exactly the same way as described for the first experimental series. A total of 114 salmon were introduced, in combinations as shown in Table II.

In the third type of experiments, seven cod were introduced into the pool without seals. They were then chased using a hoop net (lights turned on) for 30 min, while any sounds were recorded (Table II).

In the fourth type of experiments, a human diver was placed in the pool while 10 cod were introduced, and sounds were recorded while the diver approached and followed the cod (lights turned on). Altogether 20 cod were confronted with a diver in two 30 min experiments (Table II).

In a fifth type of experiments, cod and salmon (one species at the time) were introduced into the pool (48 cod and 30 salmon, in total), in the abscence of other animals and disturbances, while sounds were recorded for different periods of time (Table II). Recordings of background noise were also conducted in the pool without animals present during a total of 1.5 hours.

B. Experimental animals

The experimental animals were obtained and maintained between experiments as follows: All seals were captured as weanling pups or adults on pack-ice in the Greenland Sea, in connection with scientific expeditions in 1999/2000 under authorization by the Norwegian Government (Royal Minis-

try of Fisheries). They were brought to the Department of Arctic Biology, University of Tromsø, where they were housed in two 40 000 liters seawater pools under simulated natural light/dark rhythms (corresponding to those at 70° N latitude), and fed a daily ration of fresh-frozen and thawed herring supplemented with a B-vitamin complex, as described by Blix *et al.* (1973). The pool was equipped with a 1.5 m wide wooden ledge along one of its sides which allowed the seals to haul out, and the pool was circulated with seawater at an average temperature of 5 °C, while room air temperature ranged between 8 °C and 10 °C. The age and sex of the seals at the time of the experiments are given in Table I.

A total of 205 cod and 144 salmon were obtained from a marine research station (Kårvika Havbruksstasjon) outside Tromsø, where cod were kept in large net enclosures in the sea, while juvenile salmon were maintained in land-based freshwater tanks, until they were brought to the Department of Arctic Biology for use in the experiments. Upon arrival at the department, they were temporarily maintained in a 500 liters seawater (cod)/freshwater (salmon) tank through which cold (3 °C-5 °C) water was continuously circulated, and oxygenated by pumping air into the water. All cod were juveniles, measuring 20-40 cm in length, except in the experiment with a human diver, in which the cod were somewhat larger, measuring 40-60 cm, while the juvenile salmon measured 20-30 cm in length (Table II). All fish that were transported to the facilities were used in experiments within 2-3 days; hence, feeding of the fish was not needed. All experiments were approved by the Norwegian National Animal Research Authority (NARA).

TABLE II. The number of hours of sound recordings, numbers and size of fish used, and numbers of recorded clicks, with mean peak frequency, under various experimental conditions.

	Recording time (h:min)	Number of fishes	Fish size (cm)	Clicks recorded			
Condition				Light	Dark	Total	$F_{\rm peak}$ (kHz
Cod+harps	13:30	65	20-40	54	83	137	5.99±1.82
Cod+hoods	8:30	65	20-40	88	79	167	6.66 ± 2.48
Salmon + harps	4:50	38	20-30	0	0	0	
Salmon + hoods	16:30	76	20-30	0	0	0	
Cod+hoop net	0:30	7	20-40	0		0	
Cod+human	1:00	20	40-60	73		73	4.26 ± 1.07^{a}
Cod	2:00	48	20-40	0		0	
Salmon	1:00	30	20-30	0		0	

 $^{^{}a}F_{peak}$ significantly different from those recorded in the presence of harp or hooded seals [p < 0.001, Mann-Whitney U = 1995.5 (harps) and 2178.0 (hoods)].

C. Sound recordings

The 40 000 liters experimentation pool (measuring 5.8 m in length by 5.6 m in width and with water depth ranging between 1.2 and 1.4 m) was made out of plywood, covered with fiberglass and a polyester-based topcoat. All pool machinery (pumps supplying new and recirculated water and water filtering machines) was turned off during experiments. An omnidirectional Brüel and Kjær Type 8103 hydrophone [frequency range 0.1-180 kHz flat ($\pm 2 \text{ dB}$) up to 100 kHz, and sensitivity -211.7 ± 0.25 dB re 1 V μ Pa⁻¹; Brüel and Kjær, Denmark] was suspended from the ceiling of the pool room into the center of the pool at a water depth of approximately 65 cm (i.e., midway between bottom and surface). The hydrophone and cable were protected by a wire mesh (wire, $\emptyset = 1$ mm) to avoid mauling by the seals. The hydrophone cable was connected to a Nexus Type 2692 amplifier (Brüel and Kjær, Denmark) in the adjacent surveillance room, which in turn sent signals to a loudspeaker, an oscilloscope (Type HM205-3 Hameg, Germany), and a Racal Store 4DS analog instrumentation tape recorder (Hardley Industrial Estate, England), respectively. The recorder was operated at a tape speed of 30 inches per second, enabling flat recordings from 0.2 to 150 kHz (±3 dB), with a signal-tonoise ratio of 40 dB. It was calibrated using a Wavetek sound generator (Wavetek 182, Wavetek Corp., IN, USA).

Sound recordings were started in connection with fish introduction and were continued until all fish had been devoured (in the seal-fish experiments) or until the experiment was terminated 20 min after the introduction of fish. Live fish were kept in a dark room for at least 30 min prior to the darkness experiments, assuming that this would provide the fish with sufficient time to adapt to dark conditions.

D. Sound analyses

All recorded sounds of possible animal origin were identified from the recorded tapes by replaying them at various tape speeds, both via a loudspeaker and an oscilloscope. Identified sounds were then digitalized and analyzed on a personal computer with a sound card, using analysis software programs (Bat Sound Pro, Petterson Electronics 1996, Sweden, or MATLAB, The MathWorks Inc. 1984–1999, MA, USA).

Minimum ($F_{\rm min}$), maximum ($F_{\rm max}$), and peak ($F_{\rm peak}$) frequencies were determined, either using the energy distribution area of the spectrograms, or by using a power spectrum analysis. Short-duration sounds were also described by their peak-to-peak duration ($t_{\rm peak}$), centroid frequency ($F_{\rm cent}$), and the root-mean-square bandwidth (BW_{rms}). These measurements were made using a program constructed on MATLAB. Received sound pressure levels (SPL, in dB re 1 μ Pa) were estimated based on the voltage output (as determined by use of the oscilloscope), taking the hydrophone and amplifier sensitivities into account.

E. Statistics

Sound characteristics are presented as arithmetic means with standard deviations, or as medians. Between-experiment comparisons of sound characteristics were made

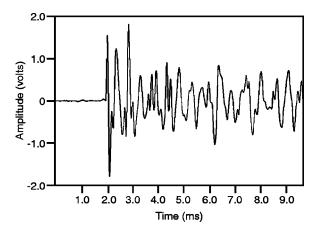


FIG. 1. Short waveform of a single click recorded in the presence of cod and a male harp seal. Duration (t_{peak}) , ca. 0.3 ms.

using nonparametric tests (Kruskal-Wallis and Mann-Whitney), using SPSS for Windows, version 11.0 (SPSS Inc., IL, USA), with differences considered significant at a level of p < 0.05.

III. RESULTS

A total of 377 sonic clicks of similar characteristics were analyzed during the course of the study. The clicks either occurred as singular clicks (n=163, Figs. 1 and 2), clicks preceded by a pre-click (n=80, Fig. 3) or double/triplet

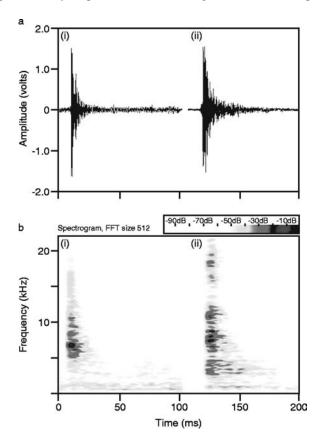


FIG. 2. (a) Oscillogram of a single click recorded in the presence of cod and (i) a human diver (SPL, 153 dB re 1 μ Pa at 1 m), and (ii) a male harp seal (SPL, 154 dB re 1 μ Pa at 1 m). (b) Spectrogram (Hanning window) of a single click recorded in the presence of cod and (i) a human diver (frequency range, 4.6–11.2 kHz; $F_{\rm peak}$, 6.7 kHz), and (ii) a male harp seal (frequency range, 2.7–18.7 kHz; $F_{\rm peak}$, 7.6 kHz).

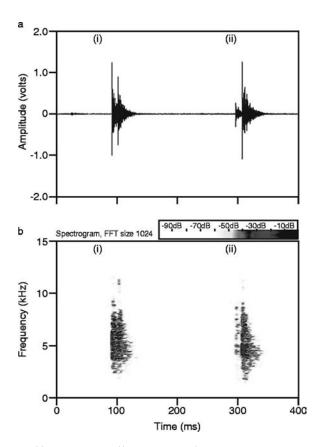


FIG. 3. (a) Oscillogram of (i) a double click (SPL of clicks, 152 dB/150 dB re 1 μ Pa at 1 m; interval between clicks, 19.2 ms) and (ii) a click with a preclick (SPL of preclick and click, 142 and 152 dB re 1 μ Pa at 1 m, respectively; interval between preclick and click, 22 ms), as recorded in the presence of cod and a male harp seal. Durations ($t_{\rm peak}$), 0.3–2 ms. (b) Spectrogram (Hanning window) of a double click (i), and a click with a preclick (ii), as recorded in the presence of cod and a male harp seal. Frequency range, 3.6–8.3 kHz; $F_{\rm peak}$, ca. 5 kHz.

clicks (n=134, Fig. 3), all having a very sudden onset and similar frequency characteristics (Table III). The overall average $F_{\rm cent}$ and BW_{rms} were $7.06\pm3.79~\rm kHz$ and $4.15\pm2.77~\rm kHz$, respectively, while the average SPL was estimated to be $153.2\pm7.0~\rm dB$ re 1 μ Pa at 1 m, ranging between $139.2\pm7.0~\rm and$ $163.2\pm7.0~\rm dB$ re 1 μ Pa at distances of 0.2 m and 3 m, respectively (based on $n=184~\rm analyzed$ clicks).

In the type 1 experiments (cod with seals), 304 analyzable clicks were recorded, distributed with n = 167 clicks in the presence of cod and hooded seals, and n = 137 clicks in the presence of cod and harp seals (Table II). In contrast, no similar clicks were recorded in any of the type 2 experiments (salmon with seals), in the type 3 experiments with cod and a hoop net, or in the control experiments (type 5) with either

cod or salmon alone in the pool. However, when cod were introduced into the pool with a human diver (type 4 experiments), a total of 73 analyzable clicks were recorded. The characteristics of clicks recorded under various experimental conditions differed in that clicks recorded in the presence of a human diver were of significantly lower frequencies than those recorded in the presence of seals [p<0.001, Mann-Whitney U=1995.5 (harp seals) and 2178.0 (hooded seals); Table II]. However, the average $F_{\rm peak}$ of clicks recorded in the presence of cod and harp seals did not differ significantly from that of clicks recorded in the presence of cod and hooded seals (p=0.075, Mann-Whitney U=10086.0). Cod showed a strong avoidance behavior both when approached by the human diver and by the seals.

In addition to clicks, 2 grunts were also recorded when cod were confronted with a human diver. These grunts had a $t_{\rm peak}$ of 190 ms and $F_{\rm peak}$ between 0.50 and 0.73 kHz. The average SPL was estimated to be 133 \pm 3.0 dB re 1 μ Pa at 1 m, ranging between 116 and 146 dB re 1 μ Pa, at distances of 0.2 and 3 m, respectively.

IV. DISCUSSION

Sound recordings in a small pool are associated with obvious problems, primarily caused by reverberations. During the present study echoes disturbed signals by often overlapping the second signal. Also, the reported clicks were unexpectedly loud, and some signals therefore tended to overload the sound recording system. Both these factors made analyses of sounds sometimes difficult and reduced the number of clicks being successfully analyzed. We were nevertheless able to record and analyze conspicuous and characteristic sonic clicks in the presence of cod and seals (both harp seals and hooded seals), and in the presence of cod and a human diver. However, we were unable to record similar clicks in the presence of salmon and seals, or while salmon or cod were alone in the pool, either undisturbed or when being chased with a hoop net (cod). Also, clicks were not recorded while seals were alone in the pool, or while no animals were present at all. These findings strongly suggest (1) that the recorded clicks originated from cod and (2) that the sounds were produced by cod when approached by a predator/predatorlike body. To our knowledge, this is the first published documentation of the production of this type of click sounds by cod.

Cod have previously been documented to produce mainly low-frequency sounds under a variety of circumstances, grunts being particularly common in connection with aggression or when the fish is frightened, during, as

TABLE III. Frequency characteristics of different categories of clicks recorded in the presence of cod.

Click type	Number	$F_{\rm peak} \\ ({\rm kHz})$	$F_{\rm min}$ (kHz)	F _{max} (kHz)	F _{cent} (kHz)	BW _{rms} (kHz)	t _{peak} (ms)	interval median (ms)
Single clicks	163	6.17 ± 2.11	3.57 ± 1.92	11.70 ± 4.47	$7.38 \pm 3.72 (n = 83)$	$4.16 \pm 2.55 (n = 83)$	$0.81 \pm 0.51 \ (n = 148)$	
Preclicks	40	6.60 ± 2.66	3.26 ± 2.24	11.92 ± 5.78	$8.55 \pm 5.65 (n=8)$	$4.41 \pm 2.94 (n=8)$	$0.45 \pm 0.39 (n = 39)$	24
Clicks after preclick	40	5.72 ± 2.47	2.69 ± 2.04	11.14 ± 5.11	$8.05 \pm 3.03 (n=8)$	$3.51 \pm 2.13 (n=8)$	$0.60 \pm 0.40 (n = 32)$	
Double/triplets	134	5.55 ± 2.07	3.07 ± 2.12	10.44 ± 6.47	$5.35 \pm 1.26 (n = 10)$	$1.44 \pm 0.28 \ (n = 10)$	$0.67 \pm 0.34 \ (n = 112)$	22
Total	377	5.95 ± 2.22	3.26 ± 2.05	11.23 ± 5.48	$7.06 \pm 3.79 \ (n = 109)$	$4.15 \pm 2.77 \ (n = 109)$	$0.70 \pm 0.45 \ (n = 331)$	

well as outside, the spawning season (e.g., Brawn, 1961; Hawkins and Rasmussen, 1978; Soldal and Totland, 2002). Such grunts have their main energy below 1 kHz, durations of 60–200 ms and source levels of 120–133 dB re 1 μ Pa at 1 m (Brawn, 1961; Hawkins and Rasmussen, 1978; Midling et al., 2002; Nordeide and Kjellsby, 1999), thus, being similar to the two grunts recorded in the present study. It should be noted, in this context, that the recording equipment was not set to record sounds below 200 Hz and that background low-frequency noise caused by swimming movements of the animals may have disguised some lower-frequency grunts (<500 Hz) in the present study. Moreover, Brawn (1961) reported that only cod with body lengths of >37 cm produced grunt sounds, and the fact that most cod used in the present study were smaller than this might contribute to explain the sparse occurrence of grunts. Series of lowfrequency knocks (below 0.6 kHz) have also been recorded from free-ranging cod (Midling et al., 2002), but no report on medium-frequency clicks similar to those reported in the present study seems to exist. This may be related to the fact that the clicks apparently were produced only when cod were confronted with, and approached by, a predatorlike body, like a seal or a human diver, while no clicks were recorded when cod were chased with a hoop net. Brawn (1961) reported that cod that were confronted with a conger eel (Conger oceanicus) produced low-frequency grunts with a peak frequency of about 50 Hz, but no mention was made of any click sounds. However, the production of intense click sounds is known from other species of fish, such as Pollimyrus isidori during social interaction (Crawford et al., 1997), Botia horae during juvenile agonistic encounters (Valinsky and Rigley, 1981), and during the defense of territory in Lagodon rhomboides (Caldwell and Caldwell, 1967).

We have no data to suggest a possible mechanism for click production in cod, but the frequency range of clicks (>1.5 kHz) suggests that it represents some form of stridulation (Kaatz, 2002), rather than resulting from the contraction of the striated drumming muscles surrounding the swimbladder wall, which is the known mechanism by which cod produce grunts (Brawn, 1961). It may be speculated that the stridulation mechanism involves a sudden movement of skeletal parts against each other, possibly as the cod makes an escape movement when a predator approaches the fish. In fact, Brawn (1961) suggested that sudden movements accomplished sound production in cod. Yet another possibility is the production of distinct pressure pulses generated by rapid swim movements, as reported in schooling fish by Gray and Denton (1991). However, the sound was absent when the cod swam away from the hoop net, and, thus, appears to be actively produced only in particularly threatening situations. In contrast, salmon apparently produced no sounds while escaping the seals, and this also seems to have been the case with regard to Antarctic cod (Dissostichus mawsoni), which were reported to remain silent upon escape from a Weddell seal, Leptonychotes weddellii (Davis et al., 1999). It should be noted, also, that no click or other sound was recorded in the present study after the cod had been seized by the seal, which is in accordance with observations made by Brawn (1961). The click sounds that were recorded from cod in the presence of a human diver were somewhat, but nevertheless significantly, lower in frequency than those recorded in the presence of seals. This may be related to the fact that the cod used in the former experiments were larger in size than those used in the latter (Table II), for reasons beyond our control. This hypothesis presumes that the frequency of produced sounds is size-related, as shown to be the case for other sound producing mechanisms in fish (e.g., Connaughton *et al.*, 2002).

The function of the clicks is also open for speculation. The fact that they only occurred in connection with the approach of a predatorlike body is suggestive of some warning or protective function. The use of intense sounds in similar situations is well known from studies of other fish species (e.g., after disturbance by a competitor or a predator; for review see Myrberg, 1981; Ladich, 1997; Mann and Lobel, 1998), including cod (Brawn, 1961). The presently reported click sounds are outside the optimal frequency range for auditory sensitivity reported for cod (60–310 Hz, Chapman and Hawkins, 1973), making it less likely that they act as warning signals for conspecifics, but audiogram tests have not been conducted at frequencies above 1 kHz. Moreover, Astrup and Møhl (1993) reported that cod are able to detect ultrasound (38 kHz), at least at high intensities (194.4 dB re 1 μ Pa). It therefore cannot be excluded that the presently reported click sounds could be detected by the cod.

An alternative option, however, would be that the sounds are used as a predator deterrent or startling mechanism, along the lines suggested by Mahajan (1963), Pfeiffer and Eisenberg (1965), and Myrberg (1981), and as demonstrated for some insects in their interaction with echolocating predator bats (e.g., Møhl and Miller, 1976; Miller and Surlykke, 2001). The cod clicks had their main energy within the best hearing range of harp seals (Terhune and Ronald, 1972) and of several other marine mammals as well (see review by Richardson et al., 1996), and were therefore probably readily detected by the seals. Circumstantial evidence for a startling/deterrent effect were actually obtained in the present study: Even though the hooded seals appeared unaffected by the clicks, the harp seals were, in fact, observed to abort their approach towards clicking cod on several occasions and also captured a significantly lower proportion of (clicking) cod compared to the similar sized, though nonclicking, salmon (Vester et al., 2001; Vester, 2003). This observation might explain why cod, which are very common in the Barents Sea where their distribution overlaps with that of harp seals, are not found in any abundance in harp seal stomachs, which are instead rich in capelin, herring, and invertebrates (e.g., Nilssen, 1995) that are also readily available in the area.

In conclusion, the present study has demonstrated that cod are capable of producing intense sonic clicks not previously described. The sound production only occurred when cod were confronted with large predatorlike bodies (seals and a human diver) and may act as a predator deterrent.

ACKNOWLEDGMENTS

We are grateful to Rolf Rødven for his kind assistance in connection with the experiments with a human diver, and to

- Magnus Wahlberg at Department of Zoophysiology, Institute of Biological Sciences, University of Aarhus, for help and advice in connection with the sound analyses. This study was financed in part by contributions from the Roald Amundsen Center for Arctic Research, University of Tromsø.
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