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Sound detection by Atlantic cod: An overview

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ABSTRACT:
The Atlantic cod (*Gadus morhua*) is among the commercially most important fish species in the world. Since sound plays such an important role in the lives of Atlantic cod and its related species, understanding of their bioacoustics is of great importance. Moreover, since cod are amenable to studies of hearing, especially in open bodies of water, they have the potential to become a "model species" for investigations of fish hearing. To serve as the basis for future studies, and to bring together what is now known about cod hearing, this paper reviews the literature to date. While there is some discussion of other species in the paper, the focus is upon what is already known about cod hearing, and what now needs to be known. An additional focus is on what knowledge of cod hearing tells about hearing in fishes in general. © *2020 Acoustical Society of America*. https://doi.org/10.1121/10.0002363

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I. INTRODUCTION

The Atlantic cod (*Gadus morhua*), like many other species in the taxonomic group Gadiformes, produces sounds that are used by individual animals to communicate with one another during territorial behavior, courtship, and spawning (reviewed by Hawkins and Picciulin, 2019). Atlantic cod also use sound detection to monitor the soundscape, detect prey, and avoid predators (reviewed by Hawkins and Myrberg, 1983; Hawkins and Picciulin, 2019). Indeed, fishers, resource managers, and researchers are starting use of gadoid sounds as a reliable and non-invasive way of locating spawning sites (e.g., Casaretto *et al.*, 2014), enabling protection of the spawning fish from overfishing or other potentially harmful human-made (anthropogenic) sounds such as those produced during seismic surveys, dredging, and pile driving.

In order to understand the engagement of Atlantic cod with sound, it is first necessary to understand how the species detects and processes sound, and how it behaviorally responds to sound. Thus, this paper is written with several goals in mind. First, a goal is to bring together what is known about hearing by Atlantic cod so that the wealth of information is, for the first time, together in one review. As part of this, we see this paper as serving as the basis for a better understanding of fish hearing in general. Our second goal is to provide a broad overview of the Atlantic cod hearing as well as to provide a gap analysis to help future investigators better understand what we need to know about hearing in Atlantic cod (and other species). Our third goal is to provide a broad review of the literature for regulators, resources managers, fishers, and others who are responsible for this commercially important species group—individuals who are not likely to go to the primary literature but who need to better understand hearing by Atlantic cod in order to better serve the use of the species by humanity.

A. Introducing cod

The Atlantic cod is an abundant and commercially important species of marine fish in the taxonomic family Gadidae (order Gadiformes) that is widely consumed by humans. Other economically important gadoids include the haddock (*Melanogrammus aeglefinus*), whiting (*Merlangius merlangus*), pollack (*Pollachius pollachius*), tadpole fish (*Raniceps raninus*), and a single freshwater species, the burbot (*Lota lota*) (Fig. 1). There are several other species called cod, including the Pacific cod (*Gadus macrocephalus*) and the Greenland cod (*Gadus ogac*). Within this paper, we use "cod" synonymously with Atlantic cod, while we give full common names when we refer to other species.

The Atlantic cod is found in the North Atlantic Ocean and up to the circumpolar part of the Arctic Ocean. It is also found in other cold-water regions off the North Atlantic, as well as in fjords of several countries (Brander, 1994). It lives and feeds close to the seabed, down to depths of 600 meters, where it preys on fishes and invertebrates. The cod also travels and preys in midwater, and occasionally moves near the water surface. Some individual cod have been shown to spend most of their time in shallow water, while others migrate to deeper and colder waters (Pampoulie *et al.*, 2008). Cod fishery catches can be quite large, and it is one of the most heavily fished species in the North Atlantic (Heath *et al.*, 2014).

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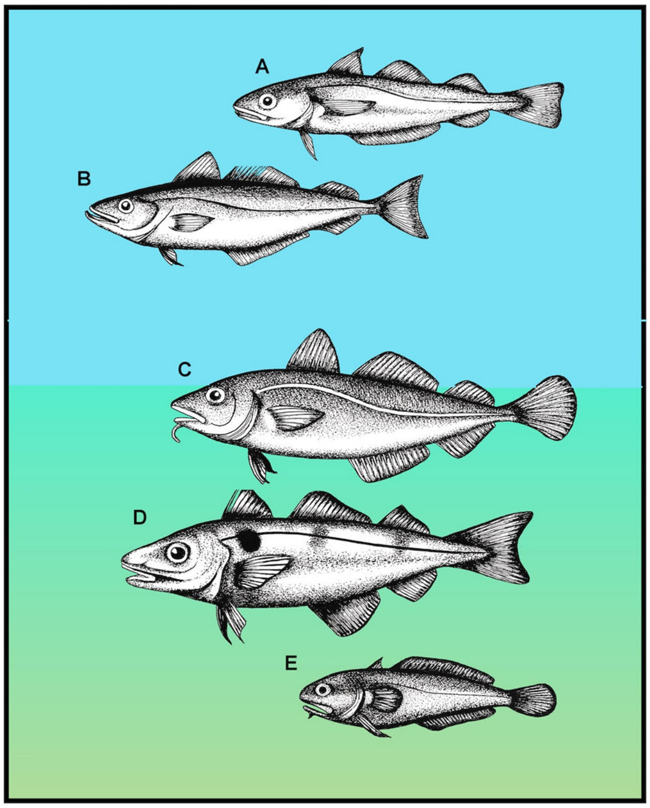

FIG. 1. (Color online) Marine members of the gadoid family. The position of the fish in the figure is indicative of their relative normal depths in the water column. (A) Whiting, (B) pollack, (C) Atlantic cod, (D) haddock, and (E) tadpole fish. (Figure copyright 2020 Anthony D. Hawkins. All rights reserved.)

B. Cod compared with the goldfish and other species

In examining the literature on fish hearing it becomes apparent that most of what we know is in relation to anatomy of the peripheral auditory system, acoustic behavior, hearing sensitivity, and bandwidth (reviewed in Ladich and Fay, 2013; Popper and Hawkins, 2019), though there are also some data on peripheral and central auditory system physiology and central nervous system (CNS) anatomy (reviewed in Walton *et al.*, 2017), but data are limited to very few of the more than 33 000 known extant fish species.

However, it is important to understand that what a fish hears and how it uses sound involves much more than just the range of frequencies it detects (bandwidth) and the lowest sound levels it can hear at a particular frequency (sensitivity)! The really important aspects of hearing (in all vertebrates) include the ability to detect signals in the presence of background noise, discriminate between different sounds (e.g., of friend vs foe), determine the direction of a sound source (e.g., to know the position of a predator or food), analysis of the "acoustic scene," and a number of other complex psychophysical functions that provide animals with considerable information about their acoustic environment (e.g., Fay and Megela Simmons, 1999).

As will be demonstrated in this review, there is a rather extensive body of data on hearing by Atlantic cod as well as on its acoustic behavior (a few of the earlier studies on cod hearing include Buerkle, 1967, 1968, 1969; Chapman and Hawkins, 1973; Schuijf and Siemelink, 1974; Hawkins and Chapman, 1975; Schuijf, 1975). While we know something about hearing in over 120 other species (reviewed in Ladich and Fay, 2013), the only species where there is a larger body of data on hearing capabilities than the cod is the goldfish (*Carassius auratus*) (see Fay and Megela Simmons, 1999; Fay, 2014). However, goldfish are not known to make sounds or to use sound in any behaviors (though they likely use sound to analyze and respond to the acoustic scene).

There is also a lesser body of data on hearing capabilities of two other species, the toadfish (*Opsanus tau*) and the plainfin midshipman (*Porichthys notatus*) (e.g., Edds-Walton and Fay, 2009; Edds-Walton, 2016; Mohr *et al.*, 2018). Both species have well-known acoustic behaviors in relatively shallow water (e.g., Winn, 1972; Zeddies *et al.*, 2012). And since they can be easily studied in the lab, these species have provided a wealth of data about the role of the CNS in both acoustic behavior and hearing. However, both species live in shallow water and close to the bottom, whereas the commercially important cod lives in deep water and often moves up through the water column.

C. Brief overview of underwater sound

In order to understand fish bioacoustics, including the acoustic behavior of cod, it is first necessary to have a brief background about underwater acoustics. Much more detail about underwater sound as applied to fishes can be found in a number of recent reviews (e.g., Hawkins and Popper, 2016; Nedelec *et al.*, 2016; Popper and Hawkins, 2018; Popper and Hawkins, 2019) as well as the website www.dosits.org.[1]

As sound is generated in water and other media, kinetic energy is imparted to the medium and the component particles of the medium oscillate back and forth, monitored as the particle displacement, velocity, and acceleration. The water is also compressed and rarefied, creating sound pressure. Whereas particle motion is not of great importance for hearing in air, the auditory system of fishes evolved primarily to detect particle motion and special adaptations are required (e.g., a swim bladder) to detect sound pressure (e.g., Popper and Hawkins, 2018; Schulz-Mirbach *et al.*, 2020). Thus, in order to investigate fish hearing, it is necessary to understand that particle motion is critical for their hearing, and to examine the detection of both particle motion and sound pressure.

D. Caveats to fish hearing studies

Most studies of fish hearing have been done in tanks (reviewed in Ladich and Fay, 2013; Fay, 2014; Popper and Hawkins, 2019). However, it is now understood that the acoustic environment of most tanks is far from ideal for studies of fish hearing since the sound field, including its particle motion components, may be very different than those that a fish would encounter in the wild (e.g., Duncan *et al.*, 2016; Rogers *et al.*, 2016). One related problem is that while invesigators may measure particle motion, they do not always do so on three axes. Also, while some invesigators give pressure and particle motion levels, they have no way of knowing if the fish is responding to one or the other (or both) and this means that few particle motion "thresholds" are provided. Thus, it is important to monitor and determine the level and direction of particle motion in tanks, but differentiation between detection of sound pressure and particle motion can only be done where the sound field can be manipulated such as in highly specialized tanks or in the field, as has been done for the cod (Hawkins, 2014).

While it is clear that field studies are logistically complex, they have a number of real advantages over tank work. For example, the effects of reflecting boundaries (e.g., tank walls) can largely be eliminated. Moreover, it is possible to vary the distance of the fish from the sound source, and thus the sound pressure to particle motion ratio can be varied. Sounds can also be generated by sound projectors at different directional positions and distances.

Much of the work we discuss on cod has been done in the field (e.g., Enger and Andersen, 1967; Chapman, 1973; Chapman and Hawkins, 1973; Hawkins and Chapman, 1975; Hawkins and Sand, 1977). These studies, therefore, provide unique opportunities to understand fish hearing from the perspective of "wild animals," without the limitations imposed in some other studies.

There is an additional concern regarding how hearing is measured. While many of the earlier studies used conditioning paradigms where fishes had to perform some task when they detected sound, such as avoid a shock, change heart rate, or go to a feeder (e.g., Tavolga and Wodinsky, 1963; Chapman and Hawkins, 1973; Sand and Hawkins, 1974), there has been a recent trend to use physiological methods with electrodes in or near the ear, auditory nerve, or brainstem (reviewed in Ladich and Fay, 2013). However, as discussed in detail by Popper *et al.* (2019), such studies do not actually measure the ability of the animal to hear and respond to sound since the auditory system of the brain is also involved in signal analysis to enable the response of the animal (also see Sisneros *et al.*, 2016). Instead, these electrophysiological studies only measure the detection responses of the ear and lower part of the auditory brainstem and so cannot be defined as overall measures of hearing sensitivity or bandwidth.

II. HEARING ABILITIES OF COD

In the earliest studies on cod hearing, Buerkle (1967) determined hearing bandwidth and sensitivity using classical conditioning of their heart rate in a tank. Buerkle found that cod had good sensitivity to sounds up to 283 Hz, while at 400 Hz hearing sensitivity was relatively poor [Fig. 2(A)]. However, levels of background noise in the experimental tank were high enough to influence the thresholds and so the lowest level of detection (often called the absolute threshold) could not be determined. Buerkle (1968) went on to confirm that the thresholds varied directly with the background noise, with the signal to noise ratios remaining the same at all background levels for each frequency [Fig. 2(A)]. Masking was most pronounced when the noise and signal frequencies coincided (Buerkle, 1969).

Buerkle's studies were in tanks, but subsequently, Chapman and Hawkins (Chapman, 1973; Chapman and Hawkins, 1973; Hawkins and Chapman, 1975; Hawkins and Sand, 1977) avoided tank problems and provided better control of the sound field by working at Loch Torridon, on the west coast of Scotland, a large and deep fjord, that is open to the sea (Hawkins and Chapman, 2020). The cod was placed in a small cage at the top of a tower that was mounted on the seabed (Fig. 3). The sound projectors in midwater at different distances from the fish enabled the ratio of particle motion to sound pressure to be changed and also enabled sounds to be presented to the cod from different directions. A behavioral approach using classical conditioning of heart rate was used to determine the auditory thresholds, resulting in the audiograms shown in Fig. 2(B). However, the thresholds were influenced by natural variations in the levels of ambient noise in the sea loch [Fig. 2(C)].

By generating sounds at different distances, it was possible to vary the ratio of particle motion to sound pressure, thereby measuring hearing sensitivity to both sound pressure [Fig. 2(B)] and particle motion [Fig. 2(D)] independently, something that cannot be done in a tank (Chapman and Hawkins, 1973). The cod sound pressure thresholds at all frequencies between 50 and 500 Hz (the highest audible frequency), were independent of the sound source distance (from 1.7 to 50 m), confirming that the cod were sensitive to the sound pressure. However, at frequencies below 50 Hz, the sound pressure thresholds fell when the sound source was closer, showing that the cod were responding to the particle motion at these low frequencies [Fig. 2(D)].

A. Amplitude discrimination

Going beyond the detection of tones, Chapman and Johnstone (1974) showed that cod could discriminate between pure tone pulses that differed in sound pressure amplitude. By reducing the amplitude difference in 1 dB steps, the cod were shown to be able to discriminate two sounds that were different by 1.3 dB at 50 Hz. This just noticeable difference (JND) varied between 3.7 and 6.7 Hz from 110 to 250 Hz and increased to about 9.5 dB at 380 Hz.

B. Masking and the critical band

A critical function of hearing is the ability to detect on signal in the presence of other sounds. Hawkins and Chapman (1975) measured masking in cod by investigating the detection of pure tones in the presence of other masking sounds. The ambient noise levels in Loch Torridon were much lower than in most aquarium tanks, including those used by Buerkle (1968, 1969). However, small changes in the ambient noise levels took place within the sea, as wind and weather conditions changed, resulting in variations in

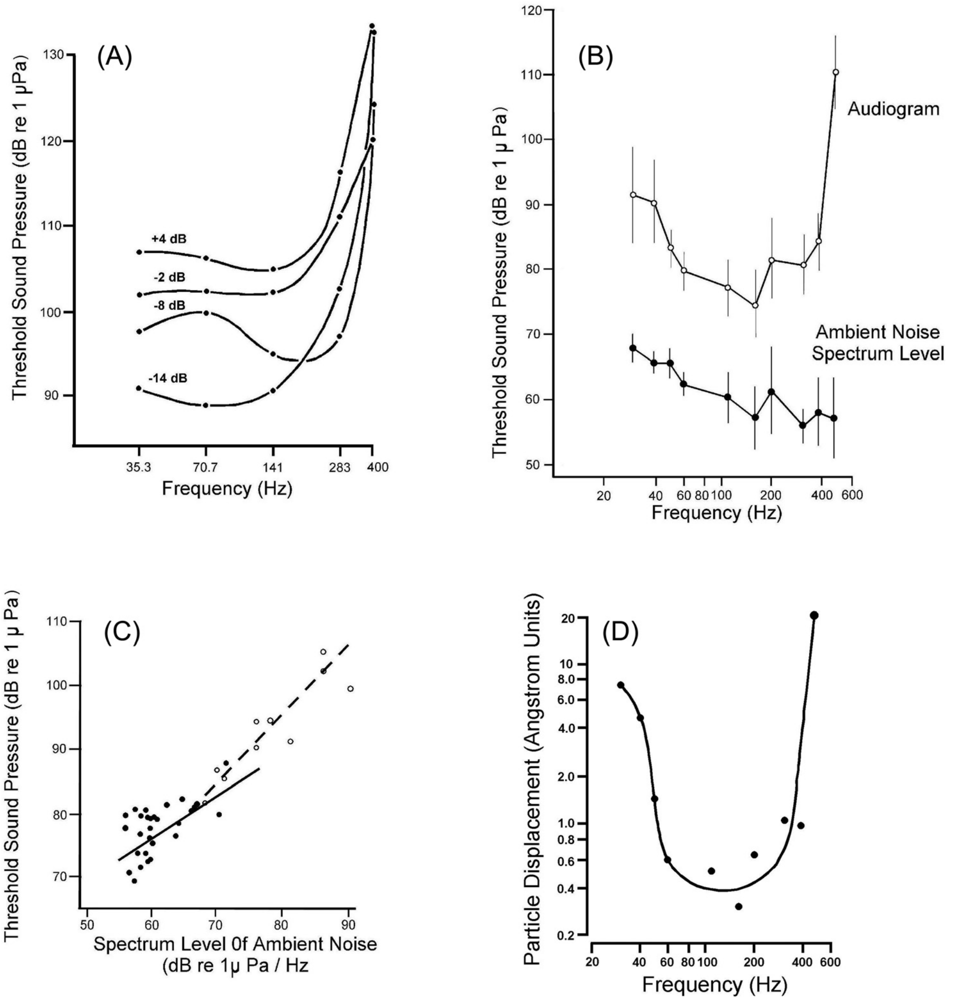

FIG. 2. (A) Mean thresholds for cod derived by Buerkle (1968) in a laboratory tank at four levels of man-made background noise. (Redrawn, with permission, Canadian Science Publishers). (B) Audiogram of the cod derived in the sea loch, shown as sound pressure thresholds, with the background levels of ambient noise also shown. (C) Changes in the thresholds at 110 Hz resulting from changes in the ambient noise level, with the natural changes shown with filled in dots and higher man-made levels shown with open dots. (D) Particle displacement thresholds. The data in (B), (C), and (D) are derived from Chapman and Hawkins (1973).

the auditory thresholds [Fig. 2(C)]. The results demonstrated that the detection of sounds by the cod was masked by the ambient sea noise (Hawkins and Chapman, 1975), and the pure tone threshold sound levels were raised in the presence of the noise. Masking was negligible under calm sea conditions (sea state 0), but at higher sea states, masking took place because of the increased background noise levels. It is therefore evident that the sound sensitivity of cod is matched to ambient noise levels in the marine environment, and cod may therefore be adversely affected by anthropogenic noise.

With mammals, pure tone signals are masked most heavily by noise frequency components at the same and similar frequencies, and the term "critical band" is applied to the range of frequencies that is effective in masking a particular signal (e.g., Greenwood, 1961). At Loch Torridon, Hawkins and Chapman (1975) investigated whether critical bands exist in the cod. Two different techniques were used. First, noise bands of different frequency width were generated and detection thresholds for a pure tone stimulus were measured as the band was made narrower and narrower. At some narrow bandwidths, the signal-to-noise ratio declined. This demonstrated that it was the frequencies in the noise band that were close to the pure tone that were responsible for the masking.

Second, determination was made of pure tone thresholds during the playback of various narrow bands of noise (10 Hz wide) that were centered at different frequencies. Masking was greatest when the center frequency of the noise band coincided with the frequency of the pure tone sound signal (Fig. 4). These experiments demonstrated the presence of a critical band for masking in the cod and suggested that cod are able to discriminate between sounds that differ in frequency.

Chapman (1973) found that the masking effect of noise on the cod became reduced when the noise was transmitted from loudspeakers that were spatially separated from the pure tone sound projector (Fig. 5). Chapman and Johnstone (1974) then did experiments using four sound projectors in the horizontal plane, allowing a wider range of spatial separation between the signal and masking noise. There was a significant decrease in the mean threshold-to-noise ratio for angles greater than 10°. Subsequent experiments conditioned cod to a short period of switching a pulsed tone from one sound projector to another at different angles of azimuth. The cod readily learned to respond to the switching when the loudspeakers were separated by 20° or more. Later experiments showed that the cod could discriminate between sound projectors at different angles in the median

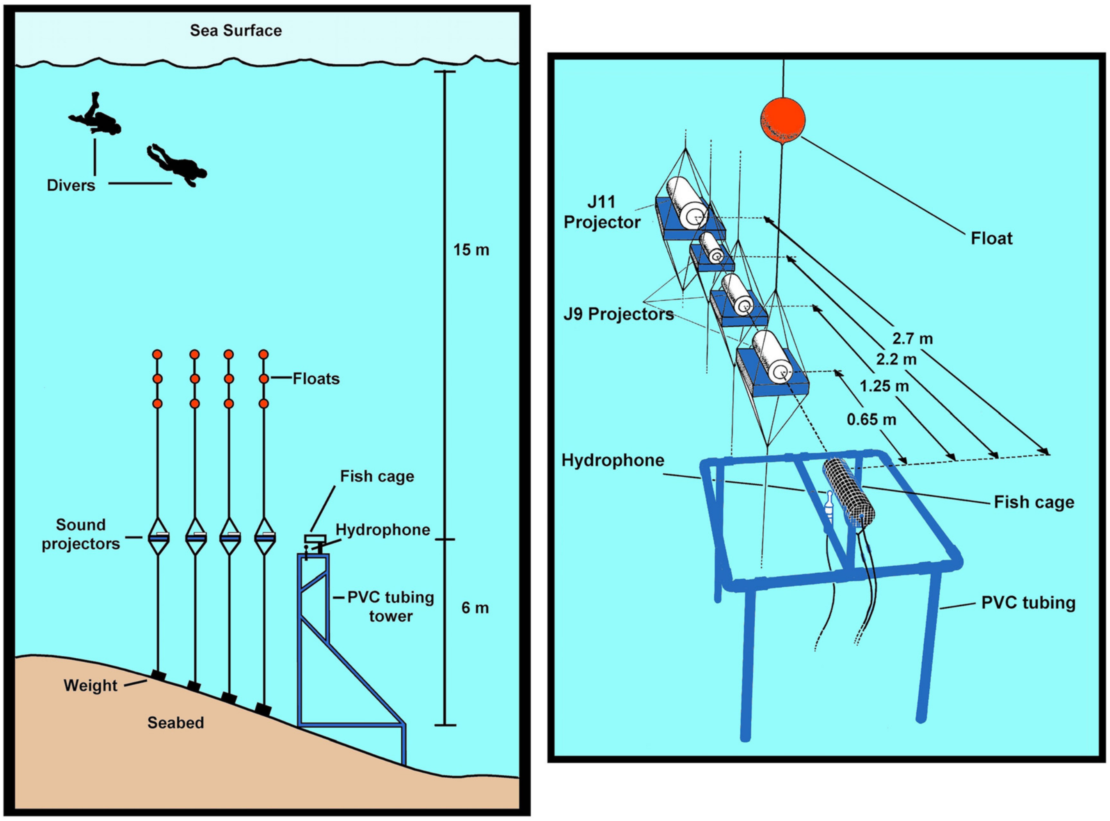

FIG. 3. (Color online) The acoustic setup at Loch Torridon. (Left) Tower on the seabed. (Right) Cage containing the cod, with cables connected to the shore carrying the heartbeat signals from the cod and conveying electric shocks to the conditioning system. Sound projectors were initially placed at different distances, and later also at different angles in the horizontal and vertical planes. (Figure copyright 2020 Anthony D. Hawkins. All rights reserved.)

vertical plane (Hawkins and Sand, 1977). It was also shown by Schuijf and Hawkins (1983) that cod could discriminate between pure tones alternately emitted from two sound projectors that were located at different distances from the cod.

C. Directional hearing

Schuijf and his colleagues had carried out experiments on directional hearing by fishes, including the cod, in a Norwegian fjord (Schuijf, 1976b,a). In his first study, Schuijf (1975) used a food reward to train cod to orientate towards a sound source and found that they could discriminate between two sound sources at opposite corners of a cage. However, after surgically removing the saccule and lagena of one ear from a single cod, it could no longer discriminate between the two sources, even though the fish were still able to detect the sound. It was apparent that the brain needs input from hair cells oriented in different directions to determine the location accurately.

It was proposed by Schuijf (1975) that the cod determined sound direction by monitoring the particle motion of the sound field, presumably employing the directional orientation of the inner ear sensory cells (Dale, 1976). However, Schuijf (1975) also concluded that the detection of only particle motion may be insufficient to determine the direction of a sound source. Because the particle motion alternates as being from and away from the source, a particle motion detector has a 180° ambiguity in the response detector. This leads to the likelihood that fishes cannot discriminate between sound sources that are 180° apart. Despite this suggestion, it was shown that cod, indeed, could discriminate between signals coming towards the head as compared to those coming towards the tail (Schuijf and Buwalda, 1975).

Schuijf (1976a) ultimately proposed that directional hearing might involve both comparing the responses of hair cells oriented in different directions (e.g., determination of the axis of particle motion by vector weighing), and also analysis of the phase relationship between the sound pressure and particle motion to eliminate any remaining 180° ambiguities. To test this phase model in three-dimensional space, experiments were done under a raft at Loch Torridon (Buwalda *et al.*, 1983). The results demonstrated that cod were able to discriminate between two low-frequency sound sources that were positioned opposite one another along the median vertical plane. This discrimination was possible for all stimulus directions, thus suggesting that cod (and possibly other species), can directionalize sound in three-dimensions. The studies also confirmed the idea that detection of sound propagation direction by the cod is based on vector weighing and also detection of the phase relationship between the particle motion and sound pressure. For more detailed discussions of sound source localization by fishes see Sand and Bleckmann (2008) and Hawkins and Popper (2018a).

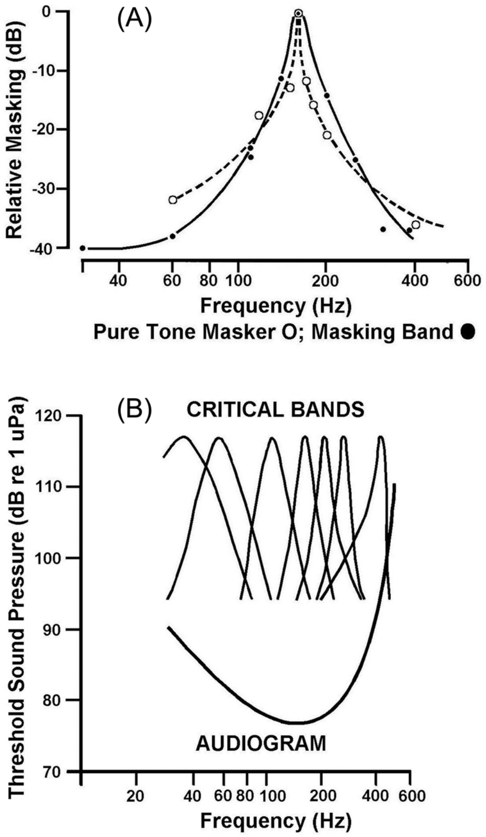

FIG. 4. (A) Masking of a pure tone at 160 Hz by 10 Hz wide noise bands and pure tones at different frequencies. Masking brings about a rise in the pure tone hearing thresholds in the presence of the other sounds. Masking is most pronounced when the center frequency of the noise band or pure tone coincides with the stimulus frequency (shown as 0 in the masking axis). The relative masking axis shows the reduction in masking, as the frequencies of the other sounds are changed, resulting in a critical band curve. (B) Critical band curves of the cod are shown at different frequencies, using 10 Hz wide noise bands. At the lower pure tone frequencies, the masking curves are symmetrical, whereas at higher frequencies, the curves are asymmetrical, with a steeper decline in masking on the high frequency side. (Figures redrawn from Hawkins and Chapman, 1975, with permission.)

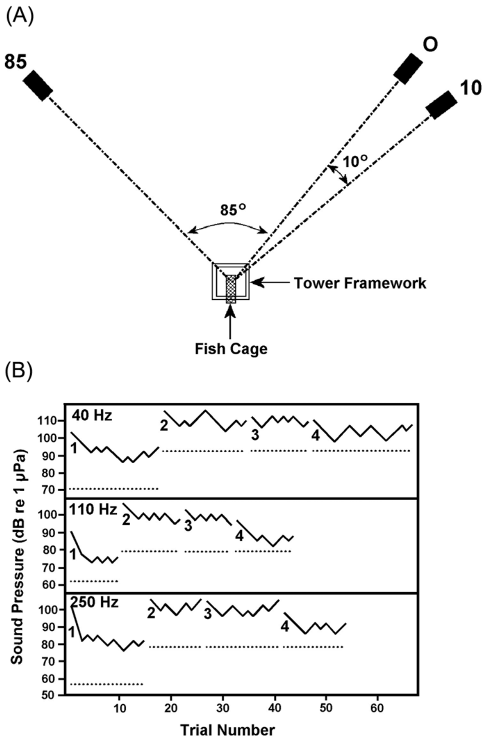

FIG. 5. Changes in the masking of pure tones by white noise transmitted from different sound projectors. (A) The positioning of the sound projectors in a horizontal plane in the sea. O is the sound projector producing the pure tone signal, and 10 and 85 are the sound projectors separated from it by 10° and 85°. Reproduced with permission from Chapman and Johnstone (1974). (B) Testing was done using the staircase method (see Tavolga and Wodinsky, 1963) where the sound level is successively raised and lowered by several dB in each trial to bracket the 50% sound threshold level for different directions of the masking noise. (1) Masking by ambient sea noise; (2) masking by white noise from the same projector as the pure tone; (3) masking from a projector separated by 10°; (4) masking from a projector separated by 85°. Experiments were done at three frequencies: 40, 110, and 250 Hz. The spectrum levels of noise at the tone frequencies are shown by the dotted lines (from Chapman, 1973, with permission).

III. STRUCTURE OF THE COD EAR

Hearing in the cod, as in other fishes and vertebrates, is mediated by the inner ear, an organ that is morphologically similar among bony fishes (reviewed in Hawkins and Popper, 2018a; Schulz-Mirbach *et al.*, 2020). The inner ear of fishes is an accelerometer-like system for the detection of particle motion, but the cod also has an ancillary structure, the swim bladder, that enhances hearing by enabling the detection of sound pressure in addition to particle motion. The role of the gas-filled swim bladder is discussed below.

A detailed description of the structure of the cod ear was provided by Dale (1976), as redrawn in Fig. 6. The semicircular canals lie in three orthogonal planes and are filled with perilymph. Each canal terminates in an enlarged ampulla which contains a sensory patch of typical vertebrate sensory hair cells overlain by a gelatinous cupula. As the head turns, the resulting angular acceleration results in movement of the fluid in the canal and motion of the cupula, thereby bending the cilia of the hair cells which then releases a neurotransmitter and stimulates innervating vestibular neurons of the eighth cranial nerve (Platt, 1983).

The ear also has three sac-like otolith organs, each containing a single calcareous otolith. As shown in Fig. 7, the otolith lies close to one wall of its sac in close proximity to the sensory epithelium (also called the macula). The chambers of the otolith organs are filled with endolymph. The three sacs are connected to one another, with, in cod (and most non-otophysan fishes), the saccule being the largest. The lagena lies at the caudal end. A wall of each sac is lined with a sensory epithelium that contains sensory hair cells and supporting cells (Fig. 7). Ciliary bundles on the apical end of each hair cell project into the lumen of the otolith organ and is surrounded by a gelatinous otolithic membrane. As shown in Fig. 6, the otolith is in contact with the otolithic membrane which holds it in place near the sensory epithelium.

The head tissues of the fish are similar in density to the surrounding water and tend to move in a similar pattern to the water itself. However, the otoliths are very dense and tend not to move to the same extent, resulting in the sensory

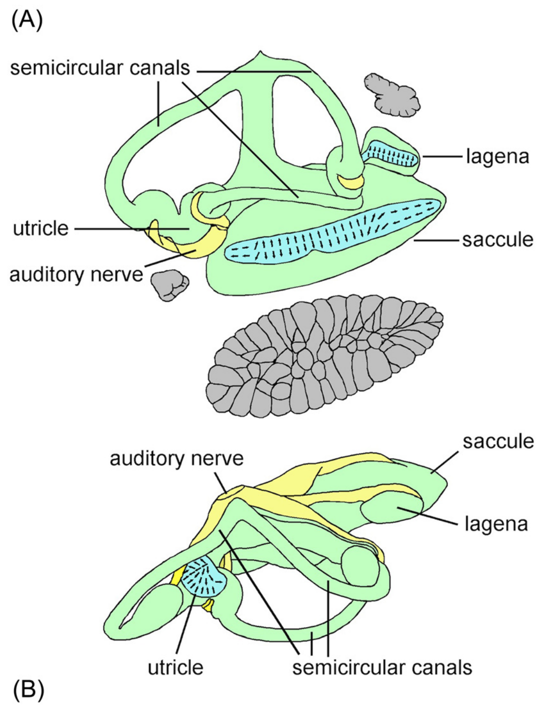

FIG. 6. (Color online) (A) The left ear of the cod viewed laterally, showing the otoliths (gray) removed from the maculae and the orientation of hair cells within the maculae of the saccule and lagena. (B) The ear viewed dorsally showing the orientation of the hair cells in the macula of the utricle. Anterior is to the left in both figures. (Figure copyright 2020 Anthony D. Hawkins. All rights reserved).

hair cells being stimulated by this difference between the motion of the otolith and the macula. Since the sensory hair cells in cod, like in the ears of all vertebrates, are morphologically and physiologically polarized, bending of the ciliary bundle in different directions results in different levels of stimulation of fibers of the eighth cranial nerve (e.g., Wersäll and Flock, 1965). The morphological polarization, as seen for cod in Fig. 6, is based on the organization of the ciliary bundle of each hair cell where the one true cilium, the kinocilium, is at one end with a graded series of stereocilia behind it.

Dale (1976), using scanning electron microscopy, found that the saccular macula is divided into three regions based on the orientation of the sensory hair cells (Fig. 6). The forward (or rostral) region of the saccular macula has hair cells oriented in the fish's rostro-caudal direction and the same pattern is found at the caudal end of the macula. The middle macula region has hair cells oriented in a vertical direction, facing dorsally and ventrally.

Dale also found that the utricular macula, like that of all vertebrates, has hair cells in two groups, but due to the curvature of the epithelium the cells, are actually oriented along a wide range of axes. He also showed that the lagena is divided into two longitudinal strips, with the dorsal strip polarized ventrally and the ventral strip polarized dorsally, so that the polarization is near vertical along the length of the macula. Each macula within the ear is connected to several nerve rami of the eighth cranial nerve.

Importantly, as pointed out by Dale, even though the hair cells in each epithelial region appear to be oriented in the same direction, this is actually not quite the case since the epithelia bend along their length, thereby changing the exact plane on which hair cells even within the same region sit (also see Schulz-Mirbach *et al.*, 2020). This means that within the six otolith organs, the cod (as in most other fishes) has hair cells oriented in a very wide range of directions, presumably resulting in hair cells in different areas of the maculae detecting sounds from all the different directions around the fish. This complex series of input from different directions is focal to vector weighting in directional analysis.

In general, the hair cell orientation patterns found in cod are also found in other gadoid species including the freshwater burbot (Popper, 1981) and the hake (*Merluccius merluccius*) (Lombarte and Popper, 1994). They are also generally similar to patterns found in many other teleost species (e.g., Popper and Coombs, 1982; Schulz-Mirbach *et al.*, 2014).

IV. ENHANCING HEARING WITH THE SWIM BLADDER

A. Hearing and the swim bladder

Cod, like the majority of bony fish species, have a gas-filled swim bladder located in the abdominal cavity. The swim bladder probably first evolved for buoyancy control, allowing fishes to maintain a position in the water column without constantly exerting energy (reviewed by Alexander, 1966). However, in many fishes, including the cod, the swim bladder has taken on additional roles—most notably sound production (Brawn, 1961; Hawkins and Picciulin, 2019) and hearing (e.g., Sand and Enger, 1973). The role in hearing arises since the gas in the swim bladder is more compressible than the water. Thus, the gas bubbles pulsate when subjected to sound pressure, generating peripheral particle motion levels that exceed the particle motion levels within the water. This particle motion is re-radiated to the ear. If the swim bladder is close enough to the ear, or directly connected to it, the signal reaching the ear is sufficiently strong to be detected, thereby increasing the frequency range of hearing and the lowest sound levels detectable (Alexander, 1966). If the swim bladder is far away from the ear, it may not provide acoustic information.

The relationship between the swim bladder and ear can be intermediate, as in the cod and other species that detect both sound pressure and particle motion. In cod, the anterior end of the swim bladder projects rostrally and ends quite close to the ears. Indeed, the anterior projections from the cod swim bladder extend into the cavity behind the cranium. The cod swim bladder increases in its size and volume with age, and the projections increase in length.

The first studies to determine the role of the swim bladder in cod hearing were by Enger and Andersen (1967). Their field studies recording microphonic potentials from the ear led them to suggest that the swim bladder served to make the cod sensitive to sound pressure in the upper range

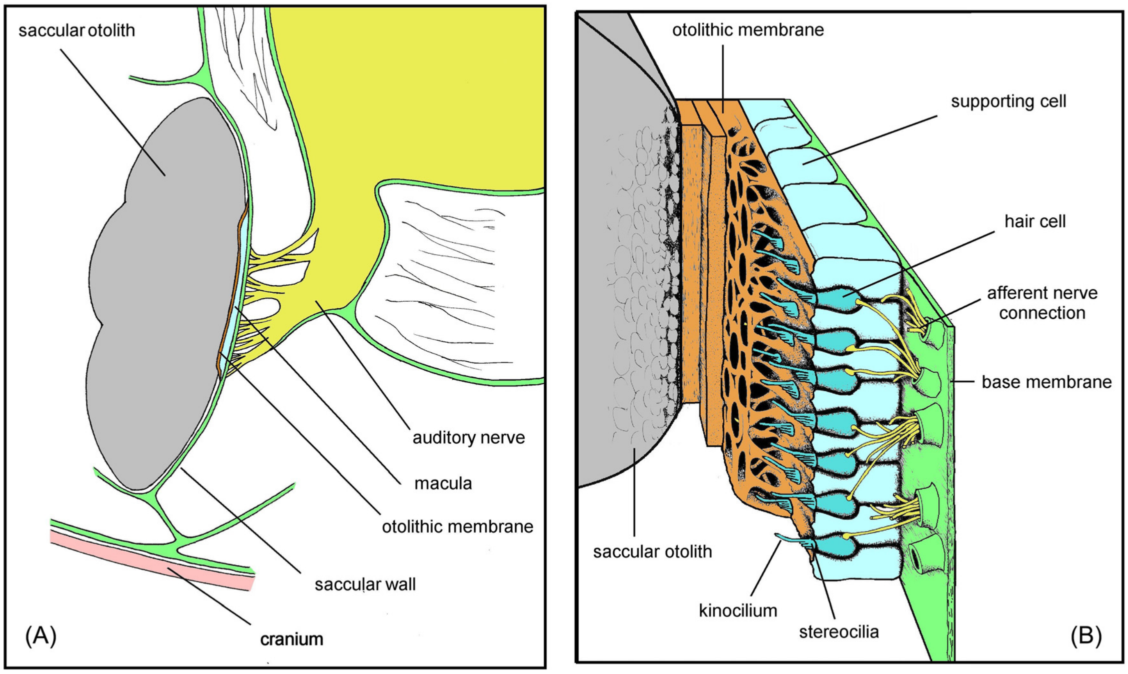

FIG. 7. (Color online) (A) Cross section of the head and saccule showing the position of the saccular otolith of the cod next to the sensory macula. (The yellow structures are the nerves and the brain.) The ears and the brain are contained within the cranium, the skull of the fish that is made of bone. The membranes, which are shown in green, surround the brain and the otolith organs. (B) The saccular macula, showing the sensory hair cells, connected to afferent nerve fibers, overlain by the fibrous otolithic membrane that is connected to the otolith. (Figure copyright 2020 Anthony D. Hawkins. All rights reserved.)

of its audible frequencies. Their suggestion was later supported by the hearing experiments on the cod (Chapman and Hawkins, 1973) and other gadoid species (Chapman, 1973).

The role of the swim bladder in cod was also examined by Sand and Enger (1973) who recorded microphonic potentials from the ear with and without gas in the swim bladder (Fig. 8). When the swim bladder had little or no gas, there was a decrease in the highest detectable frequency, and hearing sensitivity was reduced by more than 20 dB in the optimal frequency range (200–300 Hz). However, the sensitivity was not altered at frequencies below 100 Hz. This confirmed that the swim bladder served to transform sound pressure to particle motion and that the labyrinth itself was detecting particle motion.

B. The acoustic properties of the cod swim bladder

The acoustic properties of the cod swim bladder were examined by Sand and Hawkins (1973) with intact living fish at different depths in the center of a 60 m deep flooded quarry. This enabled analysis of the resonance frequency and damping of the swim bladder. This was done first in a free-field and then with the source close to a fish. The cod was placed within a cage, inside a large, ring-shaped, piezoelectric sound transducer, and the cage and equipment were lowered and raised to different depths for tests (Fig. 9).

Results showed that the resonance frequency and damping changed with rapid changes in depth (Fig. 10). However, the cod adjusted the resonance frequency when it stayed at a particular depth. This adjustment took but a few minutes, often reaching a steady new frequency within 30 min. In each case, the adjusted resonance frequency was always well above the highest frequency the fish could hear, and higher than that predicted for a gas bubble of similar volume. The resonance was also heavily damped by the tissues surrounding the swim bladder. The gain provided by a swim bladder is frequency dependent. Below a certain frequency, which depends on both the swim bladder volume and depth, the swim bladder provides no auditory gain.

As the swim bladder changes in volume, with the cod changing its depth, it might be thought that the hearing ability of the fish would change as it moved to different depths, and that hearing ability would also change with fish size. However, Sand and Hawkins (1973) concluded that by the fish maintaining a resonance frequency that is higher than a comparable bubble and well above its the upper frequency range of hearing, the changes in hearing with fish size and depth would be minimized. They suggested that for fishes such as cod that often change their depth, it is important to have a stable hearing capability, regardless of the size of the fish and the depth at which it swims.

V. ELECTROPHYSIOLOGICAL STUDIES OF THE COD EAR

Understanding about cod hearing also comes from physiological recordings from the inner ear and the eighth cranial nerve. The first such studies were by Enger and his colleagues (e.g., Enger, 1963; Enger and Andersen, 1967; Andersen and Enger, 1968; Horner *et al.*, 1980). In this section, we review these studies and include some data from an unpublished dissertation (King, 1985) on responses of cod

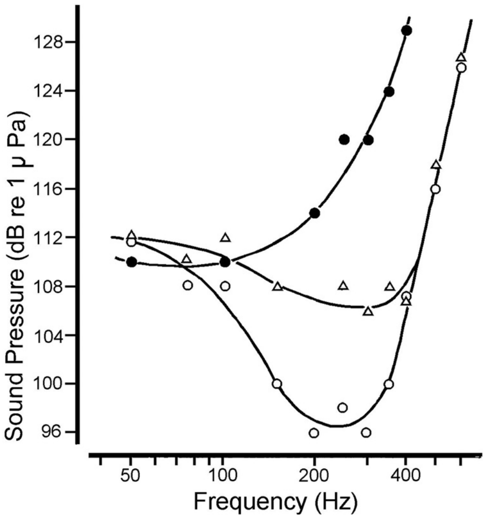

FIG. 8. Cod audiograms prepared by Sand and Enger (1973) showing the sound pressures evoking microphonic potentials at different frequencies, varying with the volume of gas in the swim bladder. Open circle, full swim bladder; open triangle, half full; filled circle, empty. The existence of gas in the swim bladder has a positive effect on sensitivity to sound pressure. Reproduced with permission.

primary afferent fibers to pure tones that is relevant to understanding cod hearing, as well as fish hearing in general (copies of the dissertation can be obtained from the first author).

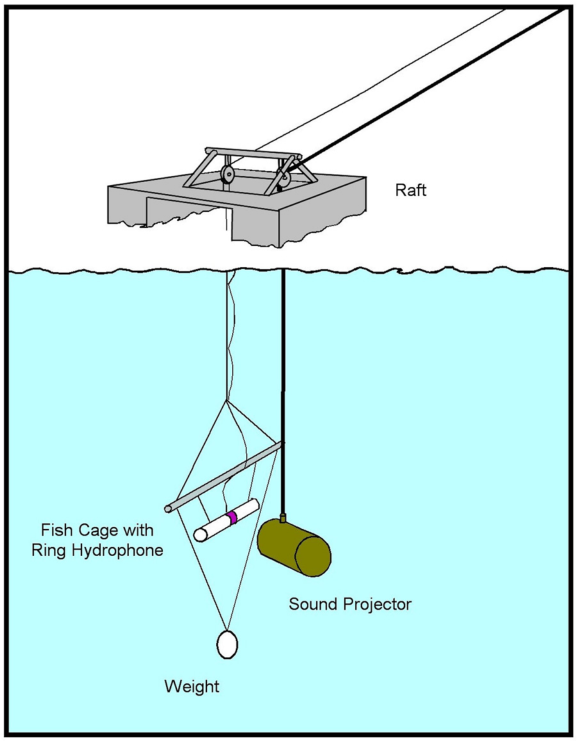

FIG. 9. (Color online) The experimental equipment used to examine the acoustic properties of the cod swim bladder. The living cod was lowered and raised from a raft, together with a sound projector, and a ring hydrophone that was used to monitor the resonance response of the swim bladder. (Figure copyright 2020 Anthony D. Hawkins. All rights reserved.)

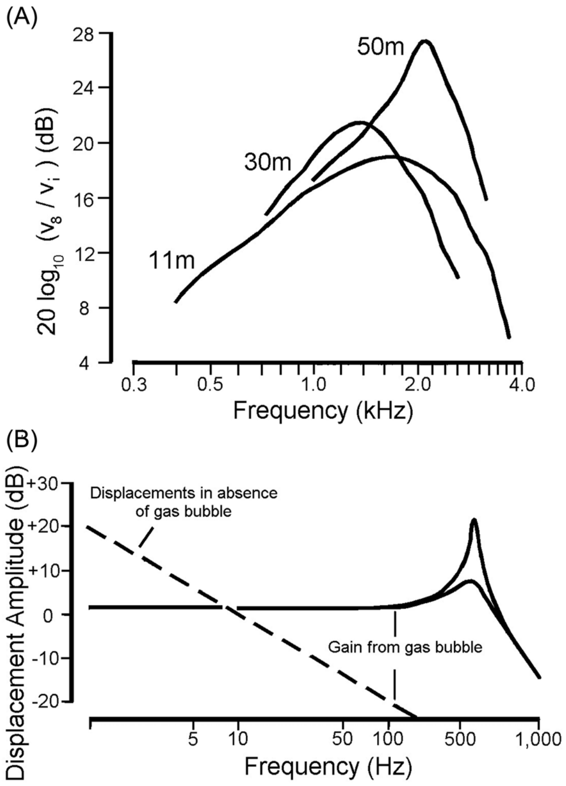

FIG. 10. (A) Resonance curves for a 16 cm cod at three different rapidly changed depths. The fish was adapted to 11 m and then moved to two greater depths. Both the resonance frequency and the damping changed with depth but stabilized when the cod remained at a particular depth for 30 min or more. (B) Curves illustrating the radial pulsation of a damped bubble (*Q* values of 10 and 2 are indicated) in a sound field. Bubble radius is 1–5 cm and the depth 20 m. The sound pressure is kept constant at 1 dyn/cm^2. The water displacements accompanying this sound pressure for a propagated plane wave in the free field are shown by the broken line. (Reproduced with permission from Sand and Hawkins, 1973.)

A. Sound quality analysis

Typically, nerve fibers in goldfish show responses tuned to a narrow band of frequencies, with their spikes phase-locked to each frequency. Changes in stimulus intensity at a given frequency are usually accompanied by changes in both the degree of phase locking and the number of spikes per second (Furukawa and Ishii, 1967; Fay, 1978). In contrast, King (1985) found that the tuning of the auditory nerve fibers in the cod is rather broader. At high stimulus levels, in addition to phase locking, the number of spikes per second is close to the frequency of the stimulus. There was no indication of peripheral frequency analysis within the cod ear, although the presence of auditory filtering within the cod auditory system has been demonstrated (Hawkins and Chapman, 1975). The location of frequency discrimination may take place within the CNS of the cod.

In his study, King (1985) vibrated the fish and also generated sound pressure within the swim bladder. Electrical potentials were recorded from the left labyrinths of a cod placed within a fish-holder that was mounted on a table (Fig. 11) that could be vibrated in different directions at different amplitudes and different frequencies. It was possible

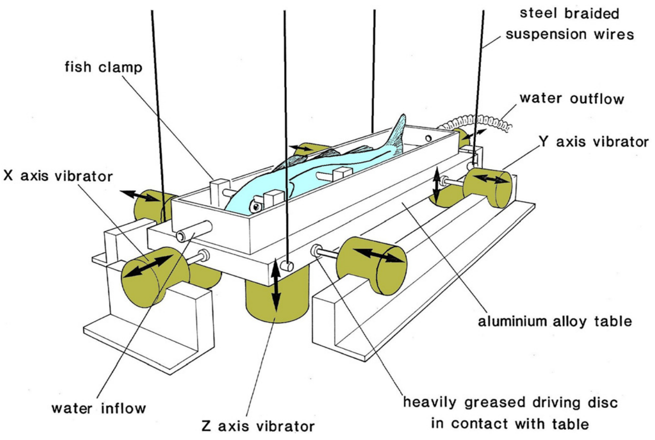

FIG. 11. (Color online) The cod vibration set-up. The upright body of the cod was held within a water-bath mounted on an aluminum base. The responses of auditory nerve fibers from the otolith organs were monitored using extra-cellular micro-electrodes placed within the head of the cod. The fish-holder and its aluminum base were suspended from a rectangular steel frame using four braided steel wires. Vibrations in different horizontal and vertical directions were achieved, as each of the three axes could be driven independently, to enable the fish-holder to be vibrated in specific directions. Its movement was monitored using three seismic velocity sensors. (Figure copyright 2020 Anthony D. Hawkins. All rights reserved.)

to make high amplitude clicks as well as pure tones. To stimulate via the swim bladder, a plastic tube ending in a large hypodermic needle was inserted directly into it, and pressure variation within the organ was generated by a J-9 sound projector connected to the plastic tube, and it was monitored within the swim bladder using a needle and tube connected to a calibrated microphone.

The responses of the primary afferent nerve fibers in the cod to pure tone vibrations were examined at different frequencies in both the vertical and horizontal planes. Phase locking to one half or the other half of the stimulus cycle was observed from all the sound sensitive units, with the phase locking changing with frequency in a manner previously seen in goldfish (Furukawa and Ishii, 1967; Fay and Olsho, 1979). This indicated that all the primary afferent fibers investigated in the cod were associated with hair cells of a particular polarization. Nonspontaneous units showed good phase locking and spontaneous units often showed synchronization before a change in the spike rate. The functional significance of this synchrony is not clear, but it may aid the transfer of spectral information to the CNS. Phase detection has also been demonstrated to be important in cod hearing, especially in relation to directional hearing (Buwalda *et al.*, 1983), as discussed earlier. Schuijf and Hawkins (1983) also proposed that phase discrimination is important for distance discrimination in the cod.

The frequency ranges over which most units from all parts of the ear were sensitive were broad, especially in relation to the critical bands presented for the cod by Hawkins and Chapman (1975), although each of the individual fibers was tuned to a rather narrower band of frequencies than the cod audiogram (Fig. 12). However, there were increases in the rate of spike production associated with the stimulus level for most units. The dynamic range of the cod afferent fibers was 20–40 dB. As well as the spike rate, the intensity responses could also be characterized in terms of the synchronization of the spike discharges to individual cycles of the pure tone, measured by an index of synchrony. A high level of phase locking was attainable at all frequencies, up to 480 Hz, the upper frequency limit of the cod. The degree of synchrony, and the relatively broad frequency response range of the individual fibers may suggest that there is a transfer of spectral information to the CNS in the cod.

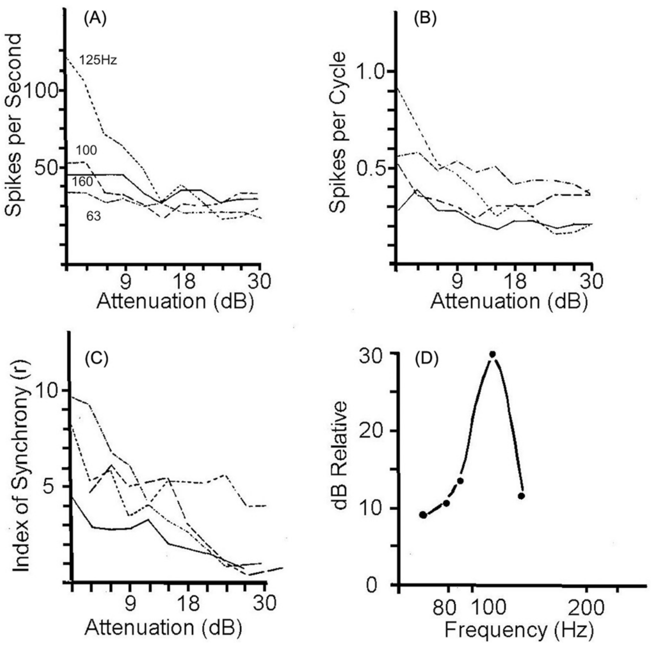

FIG. 12. Frequency response characteristics of a spontaneously active nerve unit. (A) Spikes per second at different levels of sound attenuation for several frequencies with the frequencies shown for the different lines. (B) Spikes per cycle. (C) Degree of synchrony with the stimulus waveform, decreasing as the sound level was attenuated. (D) Relative frequency curve for the nerve unit, based on the number of spikes per second occurring at a fixed stimulus level for each frequency tested (from Horner, 1980, with permission).

It was also possible to record the responses of some anterior saccular nerve units under sound pressure stimulation within the swim bladder (King, 1985). The anterior and mid-saccular units were more sensitive to the particle velocity radiated from the swim bladder than to the far-field particle velocity, while posterior saccular units were very insensitive to particle velocity radiated from the response of the swim bladder to sound pressure. This difference between the anterior and posterior saccule was also supported by microphonic measurements by Buwalda and van der Steen (1979). That study demonstrated that sound pressure and particle motion channels in the nerves to the brain are likely to be separate in the cod. It is likely that some parts of the cod maculae are sensitive to the particle motion re-radiated by the swim bladder, while others are not.

B. Sound localization

Nerve fiber activities and microphonic measurements have also been used extensively for determining the directional characteristics of the otolith organs. The first directional experiment on sound localization was carried out on the haddock, a close relative of the cod (Enger *et al.*, 1973). In this study, Enger and his colleagues measured microphonic potentials from the saccule as the fish was subjected to vibration from different directions.

Later, it was shown by Buwalda and van der Steen (1979) that the level of microphonics from the saccule of the cod depended on the direction of the sound. The microphonic levels showed a cosine dependence upon sound direction, indicating that the left and right saccules responded to different directions, the directions of the two saccules separated by 73°. Then, Horner *et al.* (1980) and Hawkins and Horner (1981) showed directional responses by the primary afferent neurons in the cod (Fig. 13). In these studies, vibration at different angles in the horizontal and vertical planes produced response changes in individual auditory neurons. In addition, these action potentials correlated with a particular phase of the received sound. Their results corresponded to the expected directional patterns, based on the hair cell orientations, with no obvious variation of directivity at different sound frequencies.

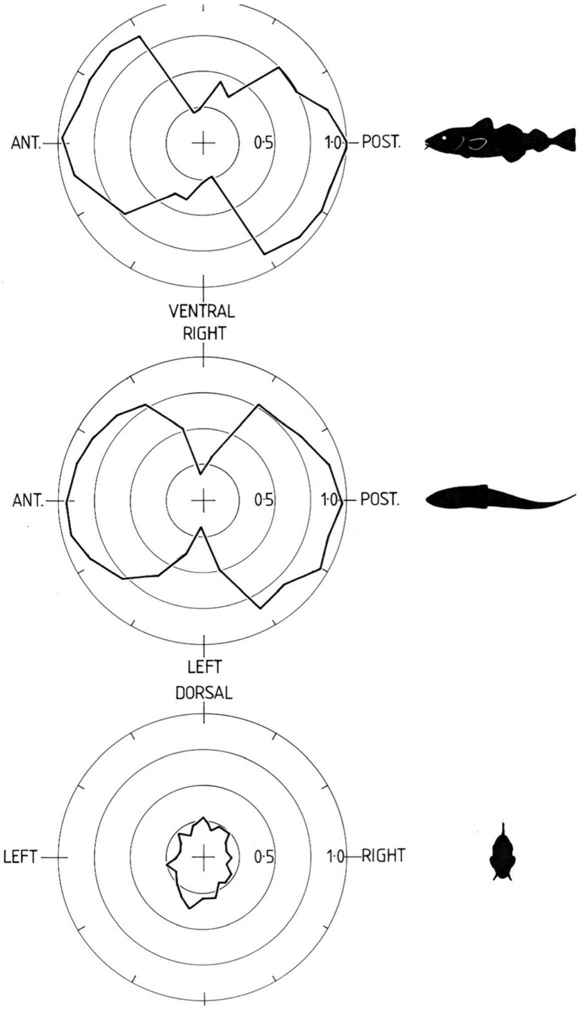

FIG. 13. Responses of a nerve unit from the anterior saccular ramus of the left auditory nerve of the cod to vibration at 360-degree angles in three orthogonal planes, to a pure tone at 160 Hz, using a vibration table. The radial axes show the number of spikes per cycle at the different angles within each plane. The response is highly directional (the data were taken from Hawkins and Horner, 1981).

King (1985) carried out more detailed experiments on the directional response patterns of the otolith organs of the cod, using the fish vibration system shown in Fig. 11. Microphonic potentials and primary afferent fiber activity levels were measured from the utricle, saccule, and lagena in response to vibration of the cod along three orthogonal axes, and also during presentation of a pressure stimulus using the gas tube passing directly into the swim bladder. The hair cells and the individual nerve fibers showed a cosine response, and their directionality generally matched the hair cell orientations. Different parts of the inner ear were sensitive to vibration from different directions, as shown by the differences in the number of spikes per cycle generated by stimulation at different angles. Saccular units were found to be most sensitive within the sagittal plane, with the best response angle of the units differing within this plane. The best angles of response in the utricular units were much more spread than in the saccule, and a significant vertical component was seen in most of the recordings

The directional response experiments demonstrated that the cod inner ear is effectively a three-dimensional detector of the direction of particle motion. Units from different locations within the otolith organs show different directional responses. There are nerve fibers with distinct directional preferences in all of the three-dimensional directions and these responses follow the hair cell orientations (King, 1985).

The central processing of the directional information provided by the hair cells and their nerve fibers remains to be examined, but it is clear that the cod is able to separate the sound pressure and particle motion inputs in order to determine the direction and distance of sound sources.

Directional hearing in most terrestrial vertebrates is based on difference in sound pressure levels, phase, and time of arrival at the two ears and comparisons of such signals within the CNS (see papers in Popper and Fay, 2005). The mechanism of directional hearing in fishes involves comparison of the response of differently aligned particle motion vector detectors within the two ears (Horner *et al.*, 1980; Hawkins and Popper, 2018a), and comparison within the CNS of the signals received from the different vector detectors would appear to be responsible for sound localization (reviewed in Walton *et al.*, 2017).

Horner *et al.* (1980) also demonstrated that some binaural interaction occurs within the cod brain. Recordings of CNS responses to sounds were made in the medulla oblongata close to the acoustical lobes at the level of the eighth nerve root. Single units in the acoustical lobes usually displayed irregular spontaneous activity, and the sound responses of the units were phase locked to the stimuli. Some of these units received peripheral input from the contralateral side and did not show evidence of binaural input, although some of the units within the acoustical lobes and the torus semicircularis did receive input from both ears, providing some evidence of binaural input.

VI. SOUNDS MADE BY THE COD

Though this review focuses on hearing, it is important to also understand that cod, like other gadoids, produce sounds and use them in a variety of behaviors (e.g., Hawkins and Myrberg, 1983; Hawkins and Picciulin, 2019). Their calls consist of grunts, made up of rapidly repeated low frequency sound pulses. Most of the energy is at frequencies below 1 kHz, with a peak at around 95 Hz. Like many other gadoid species, they use the sounds for communication, including mating and territorial behaviors, as recently reviewed by Hawkins and Picciulin (2019). Very briefly, cod make sounds using striated drumming muscles that attach to the swim bladder. Both male and female cod produce similar grunts during aggressive interactions. The grunts are made singly, or in a short series, and are produced over the year by females and males, but during spawning mainly by the males (Rowe and Hutchings, 2006).

VII. THE EFFECTS OF NOISE ON COD

To this point, we have focused on discussing what is currently known about cod hearing. Indeed, the importance of understanding fish hearing in general, and cod hearing in particular, has become increasingly important as concerns grow on the potential adverse effects of anthropogenic (man-made) sound on fishes (reviewed by Hawkins and Popper, 2018b; Popper and Hawkins, 2019; Soudijn *et al.*, 2020).

Since sound is highly important to many fish species, including the cod, for communication and for learning about their acoustic environment, any interference with their ability to detect sounds (e.g., masking, damage to hearing capabilities) may affect their behavior, fitness, and survival of individuals and/or populations. In addition, highly intense sounds may also have physiological and physical effects on the fish that can result in reduced fitness and may also lead to their death. Thus, it is increasingly important that we know a good deal more about cod (and fish hearing) if we want to protect fish, and mitigate the impact of sounds on them (Popper *et al.*, 2020).

There are many sources of anthropogenic sounds, with very different acoustical characteristics (reviewed in Popper *et al.*, 2014; Popper and Hawkins, 2019). One of the major concerns with regard to anthropogenic sound and cod (and other commercially important species) are the underwater sounds produced by ships (Stanley *et al.*, 2017; Ivanova *et al.*, 2020), and by fishing vessels and their gears (Chapman and Hawkins, 1969). There are also concerns about the potential effects of pile driving and seismic air guns (e.g., Engås *et al.*, 1996; Davidsen *et al.*, 2019; Hubert *et al.*, 2020; Soudijn *et al.*, 2020).

For example, Stanley *et al.* (2017) found that the detection of natural sounds by the cod and haddock is adversely affected by the high levels of ambient noise generated by shipping vessels in the sea. It has also been shown by Ivanova *et al.* (2020) that the presence and movement of vessels can induce a horizontal shift in the home ranges of the Arctic cod (*Boreogadus saida*). It is clear that gadoid species regard ship and trawl noise as a threat, and they can respond by moving away and decreasing their exploratory activities (Chapman and Hawkins, 1969).

There is also potential concern with regard to the sounds produced during fishing. For example, Chapman and Hawkins (1969) found that the noise from the fishing vessel dominated until the trawl moved very close to the hydrophone, when the trawl noise dominated. Comparison with the hearing abilities of cod revealed that they would be able to detect ships and trawls at considerable distances.

The sounds made by ships and fishing gears are likely to be especially important in influencing the behavior of cod at night, when vision is less possible. Ona and Godø (1990) examined the effects of noise from pelagic trawling upon haddock and showed that the vessel noise during trawling can cause avoidance reactions in demersal fish. Other work carried out on the functioning of fishing gears has been reviewed by MacLennan (2017). It is important to understand cod acoustics in order to consider ways of minimizing the effects of trawls and other devices upon cod communication.

Chapman (1975) undertook a series of experiments on the reactions of wild gadoid fishes to sound stimuli using a high-resolution sector-scanning sonar system, accompanied by an underwater TV camera. The fishes showed consistent avoidance reactions to low frequency narrow band noise stimuli, but as the bandwidth was reduced, the avoidance was less marked and when low frequency pure tones were transmitted, there was a reversal in response, and fish were actually attracted to the stimuli. As the tone transmission was switched between sound projectors, the fish gathered at the active sound source, confirming that cod are able to orientate towards particular sound sources.

There are very few data on the mortality of fishes as a result of sound exposure (considered by Hawkins and Popper, 2018b). Deaths can potentially occur when fishes are very close to impulsive sources such as pile-driving sources and explosions (Popper and Hastings 2009), although this has yet to be quantified in any way for cod.

It is evident that the behavior and survival of cod may be especially susceptible to disturbance by any human activities that generate sounds. Moreover, future studies need to consider not only the effects of sound on individual animals but also at the population level, as considered for the cod by Soudijn *et al.* (2020).

VIII. CONCLUSIONS

Much is known about the hearing abilities of cod from studies conducted under natural conditions in midwater well away from reflecting boundaries. In these studies, the free-field conditions allowed the particle motion to be properly monitored and sounds to be transmitted from different directions and distances. This is in contrast to studies for most other species, where work has been done in lab tanks where the acoustic environment is quite different than that normally encountered by fishes. At the same time, while cod have taught us a good deal, we know far less other aspects of hearing in cod than we do for goldfish and various species of toadfish.

Considering the commercial importance of cod, and its contribution with other gadoids to critical parts of the human diet, further understanding of cod hearing and cod acoustic behavior will be critical for future exploitation and management of this resource in a way that is both supportive of cod populations for the future and allows more effective use of them as food. Moreover, a major reason for understanding cod acoustics is to help design ways to avoid or minimize the effects of anthropogenic sources of sound interfering with cod communication and behavior.

At the same time, and in order to fully understand cod hearing capabilities and mechanisms and their reactions to sounds, additional studies are required. In particular, it is necessary to examine the sound processing by cod, as much as has been done for the goldfish by Fay 1978; 2014. While we have argued that many hearing studies need to be done in the field, a number of the studies needed for cod focus on sound processing, and these studies are not impacted by the nature of the sound (pressure vs particle motion) that the fish detects.

In addition, there is a great need to understand the biomechanics of hearing in the cod ear, including the functional relationship between sound, the otolith, and the sensory epithelia. In addition, we know very little about the sensory cells of the ear in cod, or how they are innervated, and almost nothing is known about what happens to sound in the cod CNS and how the sound is processed.

Clearly, from every perspective, cod have not only been the basis for providing immense insight into fish hearing, but they are also of such importance to humans that they should serve as an exceptional model for future studies of fish hearing. Of course, this is not to say that work should not be done on other species—indeed, species such as goldfish provide a much more manageable system in the lab for some studies where there is less concern about the sound field, while toadfish species provide a much more malleable system for studies of the brain and behavior. And, of course, the zebrafish (*Danio rerio*), while a species without any known acoustic behavior (like the goldfish), is a far better species for studies of the genetics of hearing and the ear than cod or any other species.

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