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Detection and reaction of fish to infrasound

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Hearing in fish has until a few years ago been considered to cover a sound frequency range from 20–30 Hz up to below 1000 Hz in most species. It is now known that the frequency spectrum extends down in the infrasound range (below 20 Hz). For cod, plaice, perch, roach, and salmon, hearing thresholds have been established by a conditioning technique for sound frequencies down to below 1 Hz. Tests on the behavioural reaction to sound in juvenile salmon have been performed in a large tank. Infrasound (10 Hz) produced spontaneous avoidance responses, while no such responses could be seen at 150 Hz. Tests on down-river migrating salmon smolts have also been performed. During a stimulation period of 170 min, only six fish passed the operating 10 Hz sound source, whereas 338 fish passed during a silent period of the same duration. The 150 Hz stimulation had no evident effect on the migration.

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Introduction

The audible sound frequency range of fish has been investigated for a number of species. Roughly speaking, all species perceive sound in the low frequency range up to several hundred Hz, while some, notably the clupeoids and the ostariophysean species, have an upper limit of 4000–7000 Hz. The latter groups have a particular anatomical structure connecting the swimbladder to the inner ear.

All fish audiograms have the lowest threshold below 1000 Hz. Measured as sound pressure, the lowest values are in the 100–200 Hz range in the non-specialized species. An extensive list of fish audiograms has been given by Fay (1988). None of them includes threshold values for frequencies below 20 Hz.

Until a few years ago, little interest was paid to the possible reception of infrasound (below 20 Hz). One reason for this was simply that auditory thresholds increased toward both higher and lower frequencies from a middle range of highest sensitivity. However, this was because the threshold values were plotted as sound pressure, which is not the appropriate stimulus for the auditory hair cells. These cells cannot be stimulated by pressure variations in the propagated sound wave as such, but rather by the kinetic sound component, i.e. particle displacement, particle velocity, or particle acceleration (Fig. 1a). Particle acceleration has been pointed out as a likely candidate for the auditory stimulus for the sensory cells (Enger, 1966), and a study by Sand (1974) clearly supports this proposal. In fish without swimbladders, particle motion must be the only possible stimulus parameter. For a fish with a swimbladder, however, sound pressure also can stimulate the sensory cells because the swimbladder can act as a pressure-to-displacement transformer. For the lowest frequencies, however, the swimbladder seems to play no role in sound perception (Sand and Enger, 1973; Sand and Hawkins, 1973).

Physiological studies on infrasound perception

Replotting fish audiograms as acceleration thresholds reveals a threshold curve that is fairly flat in the low frequency range (Fig. 1b). Accordingly, one might expect that the hearing range in fish could extend far down in the infrasound range.

The first report on infrasound perception was published by Sand and Karlsen (1986), who were able to obtain responses as far down as 0.1 Hz in codfish (*Gadus morhua*). Karlsen has obtained similar results from perch (*Perca fluviatilis*) (1992a) and plaice (*Pleuronectes platessa*) (1992b). The methods used have been described in these papers. Sensitivity to sound was tested

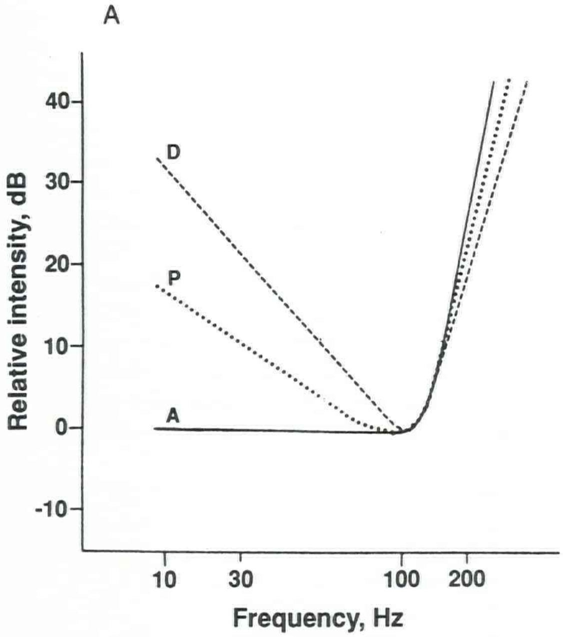

Figure 1. A. Hypothetical fish audiograms related to particle displacement (D), sound pressure (P), or particle acceleration (A). Auditory thresholds have usually been related to particle displacement or sound pressure, leaving the impression that infrasound hearing seems unlikely. By relating thresholds to particle acceleration, the apparent increase in thresholds toward lower frequencies disappears (from Karlsen, 1992c). The relation between particle displacement (d), velocity (v), and acceleration (a) is the following: $v = d(2\pi f)$; $a = d(2\pi f)^2$. Sound pressure is proportional to v.

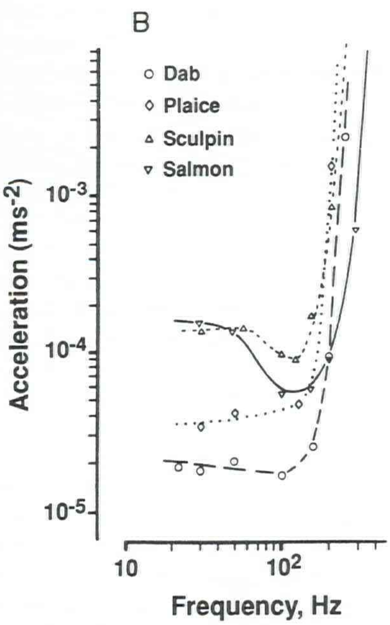

Figure 1. B. Auditory particle acceleration thresholds for four species. Data have been replotted from Chapman and Sand (1974), Hawkins and Johnstone (1978), and Pettersen (1980) (from Karlsen, 1992c).

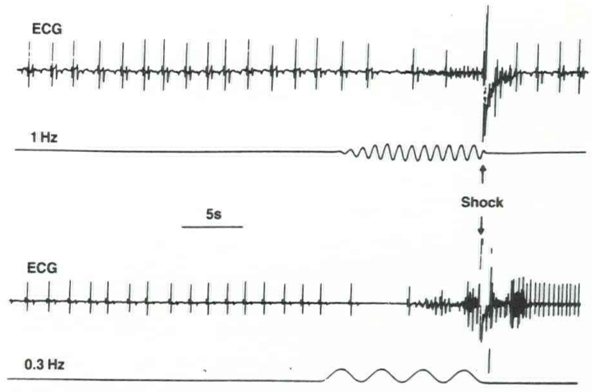

Figure 2. Record of electrocardiogram (ECG) in perch placed in the acoustic tube. A conditioned slowing of the heart rate (bradycardia) is seen in response to 1 Hz and 0.3 Hz infrasound stimulation, shown in the lower trace of each example. An electric shock was given at the end of each stimulus (from Karlsen 1992a).

by a cardiac conditioning technique (Chapman and Hawkins, 1973). An example is shown in Figure 2 for the perch, and the infrasound audiogram for plaice is given in Figure 3. Indirect evidence makes it probable that sole (*Solea solea*) can be included in the list of fish perceiving infrasound (Lagardère and Villotte, 1990).

An important question was whether infrasound reception really is hearing – in the sense that the inner ear is the sensory organ involved – or whether the receptors reside in the lateral line organ. It is now documented that the latter possibility can be ruled out (Karlsen and Sand, 1987; Karlsen, 1992a). The lateral line organ is certainly sensitive to low-frequency oscillatory water

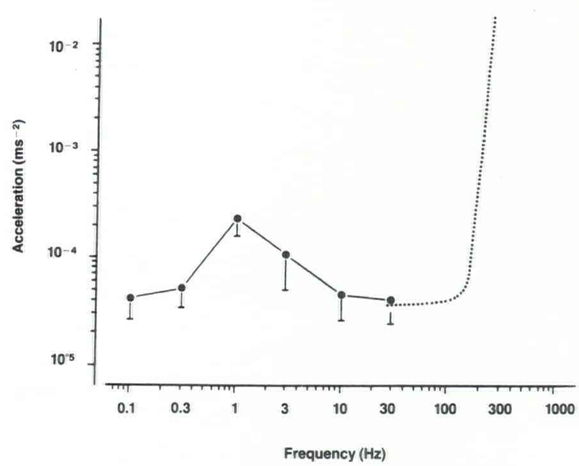

Figure 3. Auditory thresholds for frequencies 0.1–30 Hz in plaice. Points are mean values, vertical bars show one standard deviation. Dotted curve for frequencies 30–300 Hz gives replotted acceleration thresholds for plaice (from Chapman and Sand, 1974) (from Karlsen, 1992b).

motion. The point is that this organ senses hydrodynamic flow or oscillatory movements of the water relative to the fish surface. Such relative water motions are only generated when the sound source is in the immediate vicinity of the fish, i.e. less than a fish length away (Sand, 1981; Enger *et al.*, 1989). At a greater sound source distance, when the fish and surrounding water move in the same way, only the acceleration-detecting inner ear is stimulated.

Hearing thresholds established by the conditioning technique are far below the intensities necessary to alert or to frighten a fish. We have observed changes (bradycardia) in the heart rate in salmon smolts in response to high sound intensities (Knudsen *et al.*, 1992). Such an unconditioned bradycardia can be considered as an alerting response and was obtained for frequencies of 5, 10, 60, and 150 Hz, with a marked increase in threshold with increasing frequency. At 60 Hz, the spontaneous bradycardia or alerting response was obtained at some 50 dB above the hearing threshold established by Hawkins and Johnstone (1978), and at 150 Hz, more than 70 dB above threshold (Fig. 4). Particularly striking was the more pronounced bradycardia (i.e. longer heartbeat interval) occurring during low-frequency stimulation.

Behavioural studies

Among the many studies on the reactions of fish to sound, few deal with infrasound. In most cases the lower limit is 30 Hz, but from some studies one can extract data

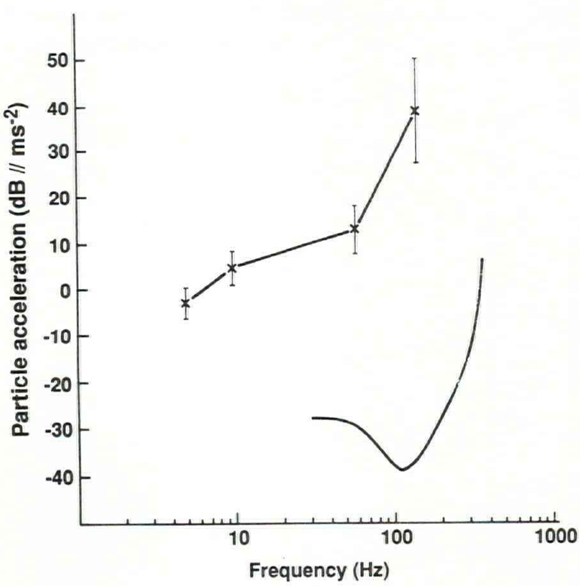

Figure 4. Thresholds for spontaneous changes in heart rate (bradycardia) in juvenile Atlantic salmon, compared with particle acceleration audiogram (lower curve). The audiogram is based on data from Hawkins and Johnstone (1978) for frequencies above 30 Hz (from Knudsen *et al.*, 1992).

comprising also part of the infrasound range. Myrberg and co-workers (1976) attracted sharks to a low-frequency sound source. The sound signals were modulated noise bands of 10–20, 20–40, and 40–80 Hz. The two lower noise bands were the most effective in attracting silky sharks (*Carcharinus falciformis*) in the Florida Strait, while the whitetip shark (*C. longimanus*) was attracted equally well to all three noise bands. These tests clearly indicate a sensitivity to low-frequency sound, even in the infrasound range in sharks.

Behavioural studies on the reaction to infrasound in bony fishes are scarce. Olsen (1979) reported an avoidance reaction of herring stimulated with noise bands of 50–100 and 3–10 Hz. To our knowledge, this is the earliest report in which an infrasound source has been used.

In fisheries research, there has been great interest in studying the reaction of fish to fishing vessels and fishing gear, particularly in connection with acoustic methods of population assessment (e.g. Olsen, 1979; Olsen *et al.*, 1983; Ona, 1988; Ona and Godø, 1990; Misund, 1990). From observations on cod, haddock, herring, and polar cod, these species all seem to react to a passing vessel, particularly to the propeller noise. The low-frequency components in vessel and gear noise are very strong, extending into the infrasound range. Whether the infrasound components in the noise play any role in the fish's reaction to the trawl is another matter.

In the studies mentioned above, a reaction to low-frequency noise was demonstrated by swimming away from the sound source. However, there are also examples of an attractive effect of low-frequency stimulation. Chapman (1976) found that cod, saithe, and lythe avoided a low-frequency, narrow-band sound source (down to 30 Hz) in experiments performed during one year, whereas they were attracted to the same sound source the following year. Low-frequency, pure-tone stimulation, on the other hand, always attracted fish.

In experiments in which recordings of vessel and trawl sound were played back to cod and herring in a pen, Engås *et al.* (1992) found clear behavioural reactions to the unfiltered sounds and also to filtered sound in the 60–300 Hz range. Filtered noise in the 300–3000 Hz range evoked a strong reaction in herring, but not in cod. The low-frequency band of 20–60 Hz did not evoke a convincing response in either species. Unfortunately, infrasound stimulation was not included in these experiments, but from these results there seems to be no reason to believe that infrasound would be important for fishing operations.

Even if the infrasound component in ship and gear noise is of little or no importance for the orientating ability of the fish, however, we feel convinced that infrasound is important to fish under other circumstances and for other purposes. For example, it has been postulated that infrasound perception may play a role in long-range navigation (Sand and Karlsen, 1986).

There is reason to believe that there are species differences with respect to the possible reaction or response that a fish may show towards an infrasound source. In the following we present observations on salmon during infrasound stimulation.

Behavioural response to infrasound of salmon in a tank

Freely swimming salmon smolts have been observed with a video camera in a 4 × 5 m, 2.5 m deep, concrete basin during sound stimulation. The basin was supplied with an adjustable tarpaulin bottom, making it possible to make a depth gradient of 0.5–1.5 m in the tank. The deepest spot could be positioned at various places with respect to the sound source.

Only two sound frequencies were tested, 10 and 150 Hz. Pure tone 150 Hz was produced by a J9 underwater loudspeaker (lower frequency limit about 30 Hz). The underwater infrasound source consisted of an aluminium tube 1.2 m in length, with a 16 cm piston at one end and an electric motor at the other. By means of eccentric coupling to the motor, the piston was driven back and forth at 10 Hz with a peak-to-peak amplitude of 4 cm (for details, see Knudsen *et al.*, 1992).

A small school of 10–20 fish could be observed swimming placidly around in the basin before the sound was turned on, but at the onset of the 10 Hz sound the reaction was immediate. Fish close to the source showed a flight reaction, swimming away from the source. By analysing videotapes, the critical distance at which the flight response occurred was found to be about 1 m, corresponding to a sound level (measured as particle acceleration) some 10 dB above the level for unconditioned bradycardia. By repeating the stimulation, even up to 20 times over a 3–4 h period, the flight reaction was maintained.

Two groups of salmon were tested in this experiment; one group was caught in the wild a few days before the experiment, the other consisted of farmed fish. An interesting difference between the two could be observed. When the "wild" fish were stimulated with 10 Hz, they immediately escaped to the deepest part of the tank, even if this point was directly under the sound source. The domesticated salmon, on the other hand, swam as far away from the source as possible.

The observations made during 150 Hz stimulation were in striking contrast to the reactions seen in response to the 10 Hz stimulation. No visible reaction to intense 150 Hz stimulation could be observed, even when the fish were only a few centimetres from the loudspeaker membrane.

Observation on salmon smolts in the wild

In the river Sandvikselven near Oslo, we have made some field observations on seaward-migrating salmon smolts. At a particular spot in the river, the water flows in two parallel runs. At the end of one of them, a trap is placed so that the number of smolts passing can be counted. The same two sound sources described above were placed close to the trap. The sound stimulation periods lasted from 10 to 40 min, and were followed by silent periods of the same duration.

Intense sound of 150 Hz had no visible effect on the migrating smolts, as measured by the numbers passing downstream, but the effect of 10 Hz stimulation was dramatic. In nine periods with 10 Hz sound, only 6 salmon passed, compared with 338 salmon passing during nine silent periods of the same duration.

Concluding remarks

Infrasound perception in fish now seems well documented. Among the rather few species for which we have behavioural data, there is a clear distinction between sharks and teleosts. Large sharks are attracted to an infrasound source and will even attack it, whereas the fairly small teleosts investigated are scared by infrasound. The behavioural repertoire may be vastly different in various species. One might easily imagine that the response, i.e. attraction or avoidance, depends on whether the species is a natural predator or prey. It is also possible that small specimens may show a fright reaction, whereas in larger adult fish this may change to attraction. The possible importance of infrasound to fishing operations is as yet uncertain.

References

Chapman, C. J. 1976. Some observations on the reaction of fish to sound. *In* Sound reception in fish, pp. 241–255. Ed. by A. Schuijf and A. D. Hawkins. Elsevier, Amsterdam. 287 pp.

Chapman, C. J., and Hawkins, A. D. 1973. A field study of hearing in the cod, *Gadus morhua* L. J. Comp. Physiol., 85: 147–167.

Chapman, C. J., and Sand, O. 1974. Field studies of hearing in two species of flatfish *Pleuronectes platessa* (L.) and *Limanda limanda* (L.) (Family Pleuronectidae). Comp. Biochem. Physiol., 47A: 371–385.

Engås, A., Misund, O. A., Soldal, Aud, V., Horvei, B., and Solstad, A. 1992. Fish behaviour and vessel noise: catch data analysis, and play-back experiments. Can. J. Fish. aquat. Sci. (in press).

Enger, P. S. 1966. Acoustic threshold in goldfish and its relation to the sound source distance. Comp. Biochem. Physiol., 18: 859–868.

Enger, P. S., Kalmijn, A. J., and Sand, O. 1989. Behavioral investigations on the functions of the lateral line and inner ear in predation. *In* The mechanosensory lateral line: neurobiology and evolution, pp. 575–587. Ed by S. Coombs, P. Görner and H. Münz. Springer-Verlag, New York.

Fay, R. R. 1988. Hearing in vertebrates: a psychophysics databook. Hill-Fay Associates, Winnetka, Illinois. 621 pp.

Hawkins, A. D., and Johnstone, A. D. F. 1978. The hearing of the Atlantic salmon, *Salmo salar*. J. Fish Biol., 13: 655–673.

Karlsen, H. E. 1992a. The inner ear is responsible for detection of infrasound in the perch. (*Perca fluviatilis*). J. Exp. Biol. (in press).

Karlsen, H. E. 1992b. Infrasound sensitivity in the plaice (*Pleuronectes platessa*). J. Exp. Biol. (in press).

Karlsen, H. E. 1992c. Infrasound detection in fish. PhD thesis, University of Oslo.

Karlsen, H. E., and Sand, O. 1987. Selective and reversible blocking of the lateral line in freshwater fish. J. Exp. Biol., 133: 249–262.

Knudsen, F. R., Enger, P. S., and Sand, O. 1992. Awareness reactions and avoidance responses to sound in juvenile Atlantic salmon, *Salmo salar* L. J. Fish Biol., 40: 523–534.

Lagardère, J. P. et Villotte, J. P. 1990. Performance particulière d'un poisson plat (*Solea solea* L.) en écoute basse fréquence. 1er Congrès Français d'Acoustique. Colloque C2: 631–634.

Misund, O. A. 1990. Sonar observations of schooling herring: school dimensions, swimming behaviour, and avoidance of vessel and purse seine. Rapp. P.-v. Réun. Cons. int. Explor. Mer, 189: 135–146.

Myrberg, A., Gordon, C. R., and Klimley, A. P. 1976. Attraction of free ranging sharks by low frequency sound, with comments on its biological significance. *In* Sound reception in fish, pp. 205–228. Ed. by A. Schuijf and A. D. Hawkins, Elsevier, Amsterdam. 287 pp.

Olsen, K. 1979. Observed avoidance behaviour in herring in relation to passage of an echo survey vessel. ICES Fishing Tech. Comm. CM 1979/B: 18.

Olsen, K., Angell, J., Pettersen, L., and Løvik, A. 1983. Observed fish reactions to a surveying vessel with special reference to herring, cod, capelin and polar cod. ICES/FAO Symposium on Fisheries Acoustics. Bergen, Norway, June 1982. FAO Fish. Rep., 300: 131–138.

Ona, E. 1988. Observations of cod reaction to trawling noise. ICES Fisheries Acoustics, Science and Technology Working Group, Oostende, April 1988. 10 pp.

Ona, E., and Godø, O. R. 1990. Fish reaction to trawling noise: the significance for trawl sampling. Rapp. P.-v. Réun. Cons. int. Explor. Mer, 189: 159–166.

Pettersen, L. 1980. Frekvensdiskriminering hos ulke (*Cottus scorpius*), en fisk uten svømmeblære. Master's thesis. University of Oslo. 64 pp. (in Norwegian).

Sand, O. 1974. Directional sensitivity of microphonic potentials from the perch ear. J. Exp. Biol., 60: 881–899.

Sand, O. 1981. The lateral-line and sound reception. *In* Hearing and sound communication in fishes, pp. 459–478. Ed. by W. N. Tavolga, A. N. Popper, and R. R. Fay. Springer-Verlag. New York.

Sand, O., and Enger, P. S. 1973. Evidence for an auditory function of the swimbladder in the cod. J. Exp. Biol., 59: 405–414.

Sand, O., and Hawkins, A. D. 1973. Acoustic properties of the cod swimbladder. J. Exp. Biol., 58: 797–820.

Sand, O., and Karlsen, H. E. 1986. Detection of infrasound by the Atlantic cod. J. Exp. Biol., 125: 449–460.