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Introduction

Concern has been expressed as to whether juvenile fish, and in particular salmon smolts, may be more sensitive to sound than adults. If this were the case, it might imply that the effects of noise on them during wind farm construction could have a proportionally greater effect than on adult fish.

The purpose of this report is to consider the available information relating to the effects of life stage on fish sensitivity to sound and to consider whether immature individuals are at more risk of its effects.

From the scientific studies of ontogenetic development in animals, several have been conducted on fish, and in one instance, crustaceans (see Lovell *et al.,* 2006). Overall, the fish species that have been investigated are divided into two main groups, those that are hearing specialists (responding to the pressure component of underwater sound), and those that are hearing generalists (only responding to the velocity of water particles). From the hearing specialists, the otophysan carps (Cypriniformes spp.) and especially the zebrafish (*Danio rerio*) along with the catfish (Siluriformes spp.) have received much of the scientific attention. From the hearing generalist fish, the orders Perciformes (the most prolific fish order) and Batrachoididae (Toadfishes) have, to date, been the main subjects of such investigations.

Hearing specialist fish

Higgs *et al.* (2003) used the Auditory Brainstem Response (ABR) and morphological techniques to investigate the development of auditory form and function in zebrafish (*D. rerio*) ranging in size from 10 to 45 mm total length. The authors found no difference in auditory sensitivity, latency, or amplitude with development, but did note that the maximum detectable frequency increased from 200 Hz at 10 mm to 4000 Hz at 45 mm TL. The extension of the audible frequency range coincided with the development of Weberian ossicles in *D. rerio*, and the authors conclude that auditory development in otophysan fish is comparable to middle ear development in mammals. Zeddies & Fay (2005) investigated ontogenetic development of acoustically evoked behavioural response in *D. rerio* to pure tones. Fish were placed in small wells that could be driven vertically at defined frequencies and velocities. Video images were used to determine the intensity and frequency at which the fish responded to the stimulus tones. *D. rerio* up to 4 days post fertilization did not respond to the stimulus tones, whereas fish from 5 days to adult were found to respond; however, unlike Higgs *et al.* (2003), the frequency bandwidth and threshold of the stimulus sound required to elicit behavioural responses did not change with age. Similarly, Popper (1971) reported no change in auditory sensitivity with growth from juvenile and adult goldfish (*Carassius auratus*) using a heart rate conditioning paradigm.

Lechner & Ladich, (2008) studied how diversity in swim-bladder and Weberian ossicle dimensions affects hearing in catfishes; the authors conclude that larger swim bladder volumes along with an increase in ossicle dimensions and numbers, improves hearing ability at higher frequencies in catfishes. Following this, Lechner *et al.* (2010) studied ontogenetic development of hearing and sound production in the otophysine mochokid catfish (*Synodontis schoutedeni*). The smallest juveniles showed the poorest hearing abilities of all size groups tested at frequencies between 50 Hz and 1,000 Hz and the highest hearing sensitivities between 5 and 6 kHz.

Hearing generalist fish

Iwashita *et al.* (1999) studied ontogenetic development in 0 to 2 year-old red sea bream (*Pagrus major*). The authors used a heart conditioning paradigm to obtain hearing thresholds. The most sensitive frequencies were 300 Hz for the year 0 and 1 cohort fish, and 200 Hz for the 2 year olds. The minimum detectable thresholds were 92.4 dB, 83.0 dB and 71.3 dB for the 0, 1 and 2 year old fish respectively. The authors report that as the fish grew, thresholds at the lower frequencies between 100 to 200 Hz significantly decreased. It is considered that hearing sensitivity of red sea bream improves as they grow from juvenile to adult. Similarly, Wysocki & Ladich (2001) studied ontogenetic development in the vocalizing anabantoid fish (*Trichopsis vittata*) again from the perciform order. Hearing thresholds were measured in six size groups using the Auditory Brainstem Response (ABR) technique. Results were compared to sound pressure levels and spectra of sounds recorded during fighting. Auditory evoked potentials were present in all size groups and complete audiograms were obtained from 0.18 to 0.30 g juveniles. Auditory sensitivity during development increased between 0.8 kHz and 3.0 kHz. The most sensitive frequency within this range shifted from 2.5 kHz to 1.5 kHz, whereas thresholds decreased by 14 dB. These results indicate that the frequency bandwidth of auditory thresholds decreases with age whilst hearing sensitivity improves.

Kenyon (1996) conducted psychophysical experiments demonstrating that the hearing abilities of two damselfish species (again from the Perciform order) change during ontogeny. Auditory thresholds from four size-groups of juvenile bicolor damselfish (*Pomacentrus partitus*), and *P. variablis*, were determined through classical conditioning experiments conducted in a standing wave tube. Young juveniles (10 to 27 days post-metamorphosis) exhibited poor hearing, with detection thresholds ranging from 54 dB (at 300 Hz) to 15 dB (at 1500 Hz) higher than known adult thresholds. Thresholds decreased exponentially with increasing age, while rapidly approaching adult levels. Sisneros & Bass (2005) investigated saccular afferent neurons from the midshipman fish (*Porichthys notatus*) from 4 to 12 months of age. Comparisons with adult fish show that auditory sensitivity increased with age and size, while temporal encoding of frequency did not show any significant shifts.

Vasconcelos & Ladich (2008) studied ontogenetic development in the Lusitanian toadfish (*Halobatrachus didactylus*) in five different size classes, ranging from 3 to 32 cm. Hearing thresholds were obtained using the ABR technique, with best sensitivity below 300 Hz in all groups. Lower hearing sensitivity was found in the smallest juveniles at 100 Hz as well as at higher frequencies (800 and 1000 Hz). Egner & Mann (2005) used the ABR technique to measure ontogenetic development of hearing in sergeant major damselfish (*Abudefduf saxatilis*). Audiograms were measured from fish ranging in size from 11 mm to 121 mm. Low frequency thresholds (between 100 and 200 Hz) increased with an increase in size (see Figure 1). All fish were most sensitive to frequencies from 100 Hz to 400 Hz though fish over 50 mm were more likely to respond to higher frequencies up to 1000 to 1600 Hz.

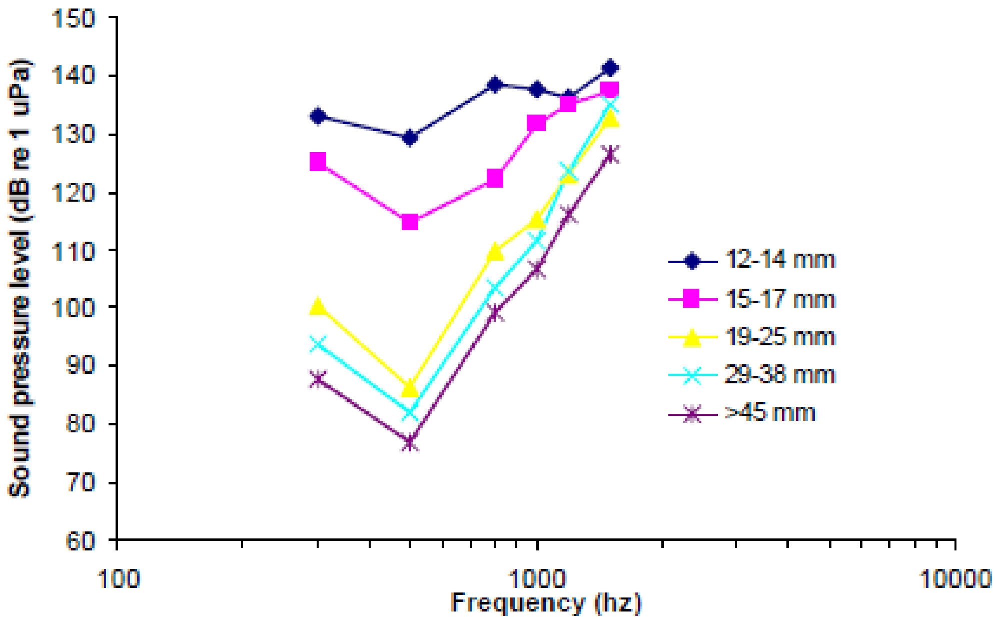

Figure 1. ABR audiograms from sergeant major damselfish (Abudefduf saxatilis), ranging in size from 11 mm to 121 mm (Egner & Mann, 2005).

Discussion

Of interest, Zeddies & Fay (2005) found that deflation of the swim-bladder in adult *Danio rerio* eliminated behavioural responses, though in larval fish it was not observed to affect thresholds; thus indicating velocity sensitivity at a young age that changes to pressure sensitivity as the fish grows. However, it is of interest that the detectable frequency bandwidth reported by Zeddies & Fay (2005) did not change with age, unlike the results reported by Higgs *et al.* (2003) for *D. rerio* and Lechner & Ladich, (2008) on catfish. Corwin (1983) showed that hearing thresholds in the ray (*Raja clavata*) decrease with age, and suggests that this is due to an increase in the number of sensory hair cells in the ear and is comparable to ontogenetic changes in bony vertebrates. In support of this hypothesis, Lombarte & Popper (1994) report that bony fish add sensory hair cells to the saccule and lagena of the ear for several years after hatching. Conversely, Lovell et al. (2006) found that all size classes of the crustacean prawn (*Palaemon serratus*) will respond equally to a 500 Hz tone, though ontogenetic development of the statocyst (the equivalent to the vertebrate ear) is considerably different, with far fewer receptor cell additions with growth. Most importantly, Iwashita et al. (1999), Kenyon (1996) and Wysocki & Ladich (2001) show that in generalist fish, the most sensitive of the audible frequencies become lower, whilst thresholds improve with age; indicating that salmon parr may not share the same hearing thresholds as adult fish.

In summary, the experimental evidence points towards the juveniles of marine species of fish being no more sensitive to sound than the adults of the species. In some cases it appears there is a degree of insensitivity to sound of juveniles when compared with adults, implying some protection from the adverse effects of noise.

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