FEATURE ARTICLE

Ontogenetic and interspecific variation in hearing ability in marine fish larvae

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ABSTRACT: In most demersal marine teleost fishes, larvae develop in the pelagic environment, but must locate appropriate settlement habitats. One potential cue for locating settlement habitats that has received recent interest is acoustic cues from reef habitats. Although it is clear that settlement-stage fish larvae can hear, it is less clear how hearing ability develops during the larval phase, or how auditory abilities vary among species and families. Auditory-evoked potentials were used to investigate hearing in larvae of 5 fishes (*Epinephelus coioides*, *E. fuscoguttatus*, Serranidae; *Eleutheronema tetradactylum*, Polynemidae; *Caranx ignobilis*, Carangidae; and *Macquaria novemaculeata*, Percichthyidae) over a range of sizes (9 to 28 mm). Ontogenetic improvement in hearing of up to 25 dB was found in 4 species. We also assessed hearing ability within and between 4 families (Serranidae, Lutjanidae, Pomacentridae and Carangidae) using larger larvae of 11 species from tropical and warm temperate habitats (the serranids and carangid above plus *Epinephelus malabaricus*, *Plectropomus leopardus*, *Lutjanus carponotatus*, *L. sebae*, *Pomacentrus nagasakiensis*, *P. amboinensis*, *Gnathanodon speciosus* and *Elagatis bipinnulata*). Within pomacentrids, carangids and lutjanids, hearing sensitivity differences among species were found. This high within-family variance results in no difference in hearing ability among the 4 families. A key component of modelling reef connectivity is the estimation of larval attraction distances. The data provided herein clearly demonstrate that attraction varies both ontogenetically and among species. Both developmental stage and species must be taken into account when estimating distances over which sound cues emanating from settlement habitats can be detected.

KEY WORDS: Hearing ability · Larvae · Marine teleost fishes · Ontogeny · Auditory-evoked potentials · Dispersal · Connectivity · Audiogram

Dramatic ontogenetic improvements in hearing may enable fish larvae to find coral reefs for settlement.

Image: J. M. Leis

INTRODUCTION

The majority of demersal teleost fish species have a pelagic larval period during which advection from settlement habitats is potentially very large (Moser et al. 1984, Leis 1991). For modelling purposes, recruitment to suitable habitats has generally been assumed to be a largely passive, physical process, with larvae being at the mercy of currents to bring them close to reefs for settlement (Frank et al. 1993, Roberts 1997, Leis 2006). It is now well established that larval dispersal and settlement are not entirely passive processes. Larvae of some fishes return to their natal reefs to settle (Jones et al. 1999, 2005, Swearer et al. 1999, Almany et al. 2007, Planes et al. 2009), and habitat selection at settlement has been demonstrated at scales

ranging from kilometres to metres (Leis & McCormick 2002). It is also clear that marine teleost larvae have well-developed swimming and orientation abilities early in the larval stage (e.g. for reviews see Leis 2006, Fisher & Leis 2009) and that these abilities are sufficient for larvae to play an active role in settlement location (e.g. Leis & Carson-Ewart 1997, Fisher 2005, Leis 2007). What remains unclear, however, is what sensory cues larvae may employ to direct their swimming movements (Montgomery et al. 2006), and when during the pelagic larval phase can they be detected.

The role of sound in orientation to settlement habitats has been the subject of some discussion in recent literature, with some authors stating larval hearing abilities can be useful in detecting distant reefs (Leis et al. 2003, Simpson et al. 2005, Leis & Lockett 2005, Wright et al. 2005, 2008, 2010), while others have argued that larval hearing is not sensitive enough to detect reefs from much more than a kilometre, and perhaps shorter (Myrberg & Fuiman 2002, Mann et al. 2007). Sorely missing from this debate are data on hearing abilities of the pelagic larval stages of marine fishes, except for a very few species at settlement (Wright et al. 2005, 2008, 2010). It is also unclear how hearing changes ontogenetically in these species, although, from settlement onwards, 4 species in the families Pomacentridae and Sparidae improve in hearing sensitivity with growth over at least some frequencies (Kenyon 1996, Iwashita et al. 1999, Egner & Mann 2005, Wright et al. 2005). Until the auditory abilities of pre- and post-settlement stages of more species are quantified, the potential role of hearing in self-directed larval settlement and subsequent recruitment will remain elusive.

The purpose of the current study was to greatly expand our knowledge of the auditory capabilities of pelagic larval stages of marine fish and to examine how these abilities change through ontogeny at the species level. In addition, to determine if results obtained herein can be generalised to other species, we examined the variation in hearing abilities within 4 families. Studies into the hearing abilities of adults from the same family or genus have produced conflicting results. Different pomacentrid species have similar hearing abilities (Kenyon 1996, Myrberg & Spires 1980) as do 2 members of the genus *Astyanax* (Characidae) that inhabit vastly different environments (Popper 1970). Conversely, the families Holocentridae (Coombs & Popper 1979) and Sciaenidae (Ramcharitar et al. 2004, 2006) contain some species that have high hearing sensitivities and other species with relatively poor hearing sensitivities. No study has compared the auditory ability of species from the same family or genus during the larval stage. By comparing larval hearing ability across species and ontogeny, we hope to provide an estimate of the generality of hearing and to greatly strengthen the data available for assessing the potential attraction distance for larvae that use acoustic cues to locate settlement habitats. Knowledge of when behaviours and sensory abilities such as hearing develop and how sensory sensitivities vary with growth and across species is vital for inclusion into larval dispersal models.

MATERIALS AND METHODS

Study species. The 5 species for which hearing ontogeny was tested in the present study consisted of a pelagic, but coral-reef associated, carangid (*Caranx ignobilis*), a serranid of inshore tropical reefs (*Epinephalus coioides*), a serranid of clear-water coral reefs (*E. fuscoguttatus*), a polynemid of tropical inshore, soft-bottom habitats (*Eleutheronema tetradactulum*) and a percichtyid (*Macquaria novemaculeata*) of warm temperate estuarine and freshwater environments, but whose larvae are found in estuarine and coastal waters. An additional 8 species were tested over a more limited size range near the end of the pelagic larval period for taxonomic comparisons. All the taxonomic-based comparisons were conducted using species that live on coral reefs as adults with the exception of 2 pelagic members of the Carangidae, *Gnathanodon speciosus* and *Elagatis bipinnulata*.

The results presented here on *Pomacentrus nagasakiensis*, *P. amboinensis*, *Plectropomus leopardus*, *Lutjanus carponotatus*, *Gnathanodon speciosus* and *Elagatis bipinnulata* were taken from previously published studies (Wright et al. 2005, 2008, 2010), as a comparison for the data on all other species dealt with in the present study.

Larvae. Larvae used for the present study were obtained from 3 different sources—reared larvae from aquaculture facilities in Australia and Taiwan, as well as wild-caught larvae from the Great Barrier Reef, Australia. Size classes were chosen based on the availability of larvae and kept consistent across species, so a direct comparison could be made.

Larvae of *Epinephelus malabaricus*, *E. coioides*, *E. fuscoguttatus* (Serranidae), *Caranx ignobilis* (Carangidae), *Lutjanus sebae* (Lutjanidae) and *Eleutheronema tetradactylum* (Polynemidae) were from aquaculture facilities near Kaohsiung, southern Taiwan. The larvae were obtained from 3 different pond types—*E. malabaricus* and *E. tetradactylum* from outdoor, concrete ponds; *C. ignobilis* from outdoor, earth ponds; and *E. coioides* and *E. fuscoguttatus* from indoor, concrete ponds. The conditions under which *L. sebae* were reared are unknown. The larvae of *Macquaria novemaculeata* (Percichthyidae) were obtained from Searle

Aquaculture, in northern New South Wales. Larvae were reared in outdoor plastic tanks.

Light traps deployed at night 100 to 200 m seaward of the reefs west of Lizard Island on the Great Barrier Reef, Australia (14° 40′ S, 145° 27′ E) were used to capture settlement-stage larvae of *Pomacentrus nagasakiensis*, *P. amboinensis* (Pomacentridae), *Plectropomus leopardus* (Serranidae), *Lutjanus carponotatus* (Lutjanidae) and similar-sized individuals of the pelagic species *Gnathanodon speciosus* and *Elagatis bipinnulata* (Carangidae). Traps were deployed near the surface over a depth of from 10 to 20 m in December 2003 and January 2004. Larvae were collected from the traps first thing in the morning, and auditory assessment of the larvae was carried out on the day of capture (Wright et al. 2005, 2008, 2010).

The nomenclature of early life-history stages of marine fishes is complex, with many different systems of terminology and no consensus on the most appropriate. Depending on the nomenclature used, the early life-history stages studied here could be labelled with a variety of names. We do not attempt to distinguish between larvae and juveniles, but, for this paper, adopt an ecological perspective that includes individuals that are subject to pelagic dispersal prior to settlement. This would not include the young of pelagic, carangid species, but to avoid awkward phrasing and for simplicity we refer to all the young fish we studied as larvae, but acknowledge that some terminologies might refer to them by other labels.

Auditory-evoked potential. Assessing the auditory abilities of larvae of fishes is made difficult due to their fragile nature, and the fact that larvae grow and develop quickly and then metamorphose into juveniles, so behavioural conditioning is not possible because of the time required to train animals. Auditory-evoked potential (AEP) measures the electrical response to sound stimuli in and around the auditory brainstem (Hall 1992). It provides an instantaneous measurement of hearing ability and is ideal for work with fragile fish larvae. The AEP methodology used in the current study was adapted from Higgs et al. (2003) and followed the protocol described in Wright et al. (2008, 2010). The sound stimuli used for testing were pure tone bursts, 10 ms in duration, gated through a Hanning window with a 2 ms rise–fall time. Frequencies of 100 to 2000 Hz were presented to the fish in random order, covering the expected range of fish hearing (Fay & Megala-Simmons 1999). The 10 ms duration is equal to the period of the 100 Hz tone, so a small distortion may have been evident at this lowest frequency due to the ramp time. At each frequency, sound pressure levels (SPLs) were increased in 5 dB increments, until a stereotypical response was seen, and then increased for at least another 10 dB to ensure the AEP

waveform increased in magnitude as the SPL increased. Averages of 200 responses (100 from stimuli presented at 90° and 100 from stimuli presented at 270° to cancel stimulus artefacts) were taken for each SPL at each frequency. Calibration of acoustic output was done daily using a hydrophone (HighTech Inc. HTI-96 Min Series hydrophone, sensitivity −163.7 dB V/1 μPa) placed in the position of the fish holder, after removal of the holder from the tank. For each frequency, root mean square (RMS) output was measured using an oscilloscope (Tektronix TDS 1002), and BioSig was then used to attenuate to the desired decibel level.

Two stainless steel subdermal electrodes (Rochester Electromedical Inc.) were used to collect AEP responses, with the recording electrode placed dorsally, just posterior to the operculum and the reference electrode positioned dorsally in the nasal region. Each electrode was coated in nail varnish (except for the tip) for insulation and was positioned using a micromanipulator. Auditory thresholds, or the lowest SPL played to the fish that produced a clear response, were determined visually, as visual detection has been shown to produce comparable results to statistical methods (Mann et al. 2001). Controls were run by testing a dead fish, which at no time produced a result that resembled a response waveform (Fig. 1). All physiological testing was carried out under the University of New South Wales, Animal Care and Ethics Permit 03/54.

Auditory thresholds were also assessed in terms of particle acceleration to better characterise all relevant stimuli for teleost hearing. To estimate particle acceleration, 2 underwater hydrophones were used to obtain pressure differences at all decibel levels and frequencies (adapted from Mann et al. 2006). Tones (duration 3 s) were played, and the output from the hydrophones was sent to a spectrum analyser (Model SR760, Stanford Research Systems). The V_{rms} for the entire response was averaged and divided by the hydrophone calibration (174.5 VμPa^{-1}). The corrected pressure difference between the 2 hydrophones was divided by the distance between the hydrophones. This number was then divided by the density of seawater (used in the experimental tank). Particle acceleration was calculated for the X, Y and Z planes, and the acceleration magnitude [calculated by $\sqrt{(X^2 + Y^2 + Z^2)}$] is reported in the current study. Although both pressure and particle motion audiograms are reported on the same figure, the 2 measures are not directly comparable.

Statistical analyses. Generalised linear modelling (GLM) was used to statistically assess differences in hearing ability between different size classes of the same species or between different species of the same genus or family, due to the unbalanced nature of the datasets. Significant differences in hearing ability among families were identified using GLM, with each
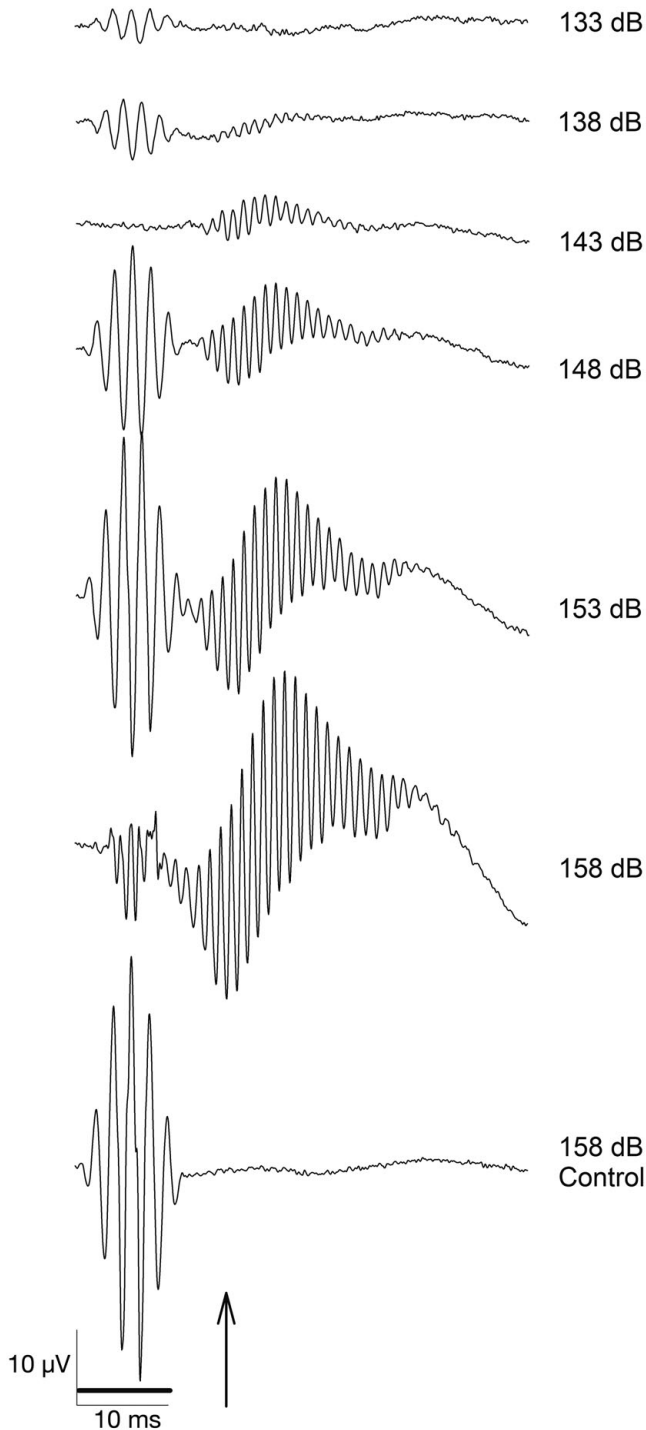
Fig. 1. *Macquaria novemaculeata*. Example response wave-form for a larva to a 600 Hz tone burst. The stimulus duration was 10 ms, as indicated by the thick black bar under the traces, and this portion of the response is an artefact of the stimulus. The arrow indicates the position of the response. Auditory threshold, or the lowest sound pressure level to show a response in the example waveforms, occurred at 138 dB re 1 μPa as a characteristic dip followed by a rise, which increased in amplitude as the sound intensity increased. Response waveforms for all frequencies were similar, except at 100 and 200 Hz, which had more peaks

species nested within the appropriate family. Some fishes showed no response at some frequencies, so comparisons of hearing ability between size class or species were done using only the frequencies for which all size classes or species involved had responded. Where significant differences were found between groups, Bonferroni post hoc tests were conducted. For all tests, α = 0.05 was considered significant. All analyses were conducting using the software package SYSTAT Version 9 (SYSTAT Software International).

RESULTS

Waveforms produced in response to frequencies >200 Hz were typical of an AEP—at the cessation of the stimulus, the response waveform showed a drop in microvolt output from the stable background, followed by a sharp rise back to background levels (Fig. 1). For the frequencies of 100 and 200 Hz, the response waveform had several waves at the cessation of the sound stimuli. For all frequencies, responses increased in magnitude as the SPL was increased.

Ontogeny of hearing in 5 species

Caranx ignobilis

Of the 3 size classes tested (9–13, 14–18 and 19–23 mm), there was no significant difference between the 2 smallest size classes, with auditory thresholds increasing (decreasing sensitivity) from 100 to 400 Hz and then fluctuating for frequencies of 500 Hz and above (Fig. 2a). Across all frequencies, the auditory detection of the 19–23 mm size class was significantly more sensitive than that of the 2 smaller size classes (GLM, $F_{2,181}$ = 65.0, p < 0.001). The auditory thresholds of the 19–23 mm size class increased between 100 and 300 Hz, before decreasing between 400 and 700 Hz and then rising again at 800 Hz. In terms of individual frequencies, at 100 Hz, the threshold of the 19–23 mm size class was significantly lower than that of the 14–18 mm size class (but not the 9–13 mm size class) (Bonferroni, p < 0.01), and, at 200 Hz, there was no significant difference between the detection ability of the 3 groups. For all other frequencies, the 19–23 mm size class was more sensitive by 10 to 15 dB than the other 2 size classes. When expressed in terms of particle acceleration, there was a significant effect of size on threshold (GLM, $F_{2,181}$ = 47.6, p < 0.001): the largest size class (19–23 mm) was more sensitive than the other 2 size classes (Fig. 2a).
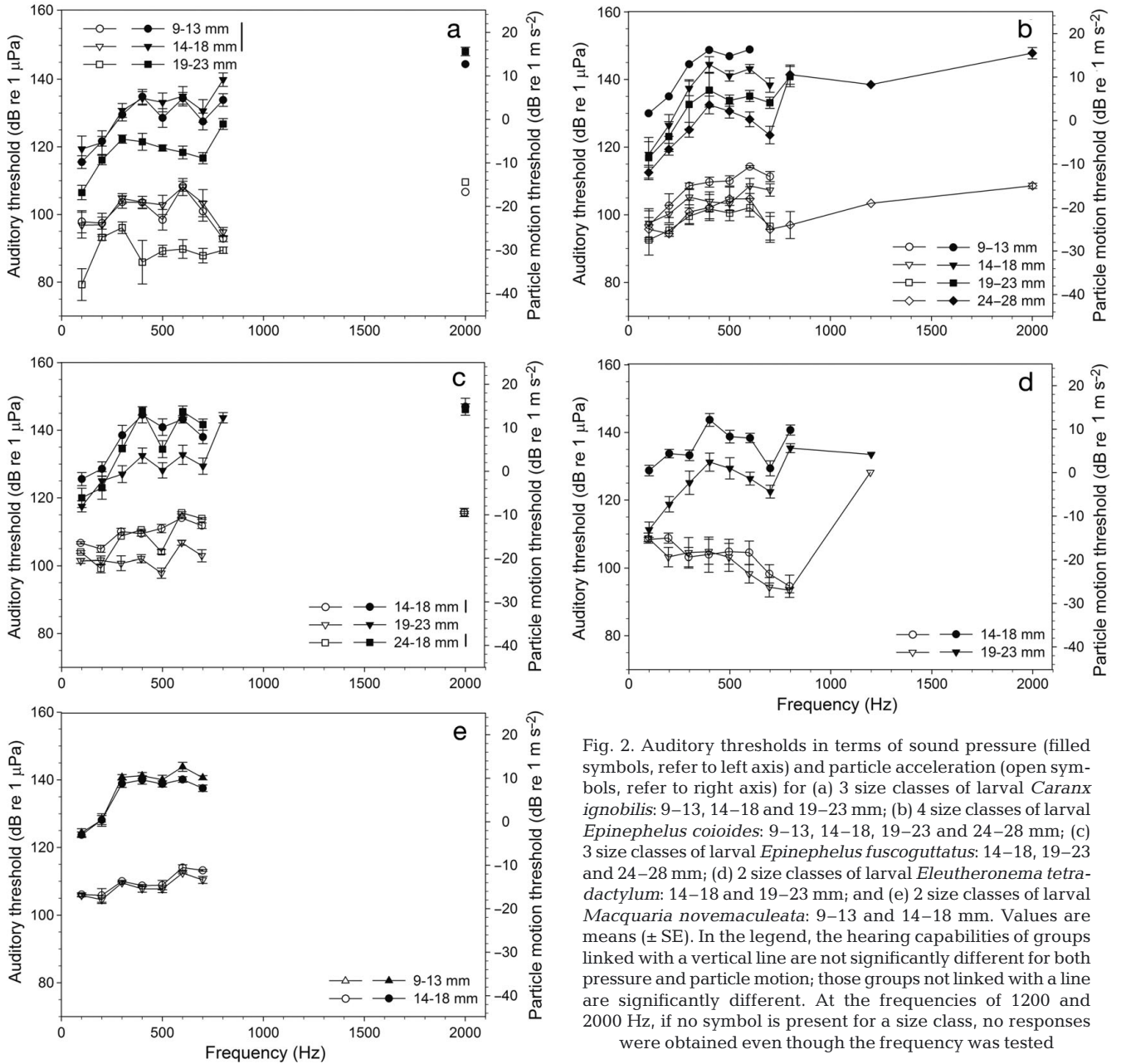
Fig. 2. Auditory thresholds in terms of sound pressure (filled symbols, refer to left axis) and particle acceleration (open symbols, refer to right axis) for (a) 3 size classes of larval *Caranx ignobilis*: 9–13, 14–18 and 19–23 mm; (b) 4 size classes of larval *Epinephelus coioides*: 9–13, 14–18, 19–23 and 24–28 mm; (c) 3 size classes of larval *Epinephelus fuscoguttatus*: 14–18, 19–23 and 24–28 mm; (d) 2 size classes of larval *Eleutheronema tetradactylum*: 14–18 and 19–23 mm; and (e) 2 size classes of larval *Macquaria novemaculeata*: 9–13 and 14–18 mm. Values are means (± SE). In the legend, the hearing capabilities of groups linked with a vertical line are not significantly different for both pressure and particle motion; those groups not linked with a line are significantly different. At the frequencies of 1200 and 2000 Hz, if no symbol is present for a size class, no responses were obtained even though the frequency was tested

Epinephelus coioides

Four size classes were tested (9–13, 14–18, 19–23 and 24–28 mm). The audiograms for *Epinephelus coioides* for all size classes were of similar shape, and all had 100 and 200 Hz as the most sensitive frequencies in terms of both pressure and particle acceleration (Fig. 2b). The detectable frequency range varied according to size class, with a maximum detectable frequency of 700 Hz for the 14–18 mm size class and of 800 Hz for the 19–23 mm size class, whereas the 24–28 mm size class detected all tested frequencies. The pressure detection threshold decreased with size in *E. coioides*. The pres-

sure detection thresholds across all frequencies of the other 3 size groups were significantly different (GLM, $F_{2,137} = 33.8$, p < 0.001), with the 24–28 mm size class being the most sensitive across all frequencies except 800 Hz. There was also a significant effect of size on particle motion (GLM, $F_{2,137} = 29.4$, p < 0.001): sensitivity improved as larval size increased (Fig. 2b).

Epinephelus fuscoguttatus

The frequency range over which *Epinephelus fuscoguttatus* responses were detected also varied between

the 3 size classes tested (14–18, 19–23 and 24–28 mm) in terms of pressure (Fig. 2c). The 14–18 and 24–28 mm size classes responded to frequencies of 100 to 700 and 2000 Hz, but showed no response to either 800 or 1200 Hz. In contrast, the 19–23 mm size class detected frequencies of 100 to 1200 Hz, but not 2000 Hz. No clear ontogenetic trend in threshold was found for the 3 size classes of *E. fuscoguttatus* (Fig. 2c). The 14–18 and 24–28 mm size classes had similar detection abilities, whereas the 19 to 23 mm larvae had significantly lower sensitivities overall (GLM, $F_{2,108}$ = 33.1, p < 0.001). In terms of particle acceleration, fish were again most sensitive to low frequencies, and there was a significant effect of size on threshold (GLM, $F_{2,108}$ = 26.2, p < 0.001), but there were no consistent differences among size classes (Fig. 2c).

Eleutheronema tetradactylum

Audiograms of the 2 size classes (14–18 and 19–23 mm) were of similar shape, with auditory thresholds increasing from 100 to 400 Hz, then decreasing between 400 and 700 Hz, before rising again at 800 Hz (Fig. 2d). The 19–23 mm size class heard over a wider frequency range, detecting 1200 Hz, whereas the 14–18 mm size class never responded at >800 Hz. For the 14–18 mm size class, 100, 200, 300 and 700 Hz were the most sensitive frequencies, whereas for the 19–23 mm size class, 100, 200 and 700 Hz were the most sensitive. The pressure detection threshold decreased by 5 to 20 dB with increased size (GLM, $F_{1,112}$ = 106.3, p < 0.001), with larger differences at lower frequencies (Fig. 2d). There was also a significant difference (GLM, $F_{1,112}$ = 21.3, p = 0.002) between these size classes in terms of particle acceleration: the 19–23 mm size class had more sensitive particle motion detection (Fig. 2d).

Macquaria novemaculeata

The audiograms of the 2 size classes (9–13 and 14–18 mm) tested were nearly identical in shape in terms of both pressure and particle acceleration (Fig. 2e), with increased sensitivity at 100 and 200 Hz. Overall, the pressure sensitivities of the 2 size classes of *Macquaria novemaculeata* were statistically different (GLM, $F_{1,98}$ = 7.9, p < 0.01), with significantly lower thresholds in the 14–18 mm size class, although the differences were slight (Fig. 2e). Post hoc comparisons showed that the frequencies most responsible for this overall significant pressure difference were 600 and 700 Hz (Bonferroni, both p < 0.05). The particle acceleration sensitivities of the 2 size classes did not differ (GLM, $F_{1,98}$ = 3.0, p = 0.09).

Taxonomic differences

Interspecific differences in hearing ability were found in 3 of the 4 families tested for pressure detection and particle acceleration detection. The 3 carangid species had significantly different pressure detection thresholds across all frequencies (GLM, $F_{2,107}$ = 111.4, p < 0.001), as well as significantly different particle acceleration thresholds (GLM, $F_{2,107}$ = 82.3, p < 0.001) (Fig. 3a). The auditory thresholds for *Caranx ignobilis* were significantly lower (sensitivity greater) than those for both *Elagatis bipinnulata* (Bonferroni, p < 0.001, all frequencies) and *Gnathanodon speciosus* (Bonferroni, p < 0.001, frequencies >200 Hz). The thresholds of *E. bipinnulata* and *G. speciosus* were also significantly different from each other (Bonferroni, p < 0.01), due to an increased sensitivity of *G. speciosus* at 600 Hz. The shape of the audiograms of *C. ignobilis* and *G. speciosus* were similar, with *C. ignobilis* having its most sensitive hearing at 100 Hz and a second peak in sensitivity at 700 Hz, whereas the other 2 species had no statistically significant 'best' frequency, rather a range of frequencies over which the hearing sensitivities were the equivalent (*G. speciosus*: 100, 200, 300, 500, 600 and 700 Hz; *E. bipinnulata*: all frequencies to 800 Hz).

A significant difference in pressure detection abilities across all frequencies was also found between the 2 lutjanid species (GLM, $F_{1,74}$ = 38.7, p < 0.001) (Fig. 3b). *Lutjanus carponotatus* had more sensitive hearing at all frequencies, except 100, 200 and 800 Hz, and detected 1200 Hz, which *L. sebae* did not. The audiograms of the 2 species were different: *L. carponotatus* had no clear best frequency, whilst *L. sebae* had more sensitive hearing at 100 and 200 Hz relative to higher frequencies. There was also a significant difference (GLM, $F_{1,74}$ = 51.7, p < 0.001) in particle acceleration thresholds between these 2 species (Fig. 3b).

The 2 pomacentrid species had significantly different hearing sensitivities (GLM, $F_{1,88}$ = 7.2, p < 0.01) in terms of both pressure and particle acceleration (GLM, $F_{1,88}$ = 5.6, p = 0.02) (Fig. 3c): *Pomacentrus nagasakiensis* had more sensitive hearing than *P. amboinensis*, due mainly to the difference in response to 700 Hz, although the differences were not large (Fig. 3c). In both species, hearing was most sensitive over a range of frequencies—*P. nagasakiensis* 100, 200 and 300 Hz and *P. amboinensis* from 100 to 300 and from 600 to 800 Hz—and both species had identical hearing bandwidths (100 to 2000 Hz).

At a size of 17–23 mm, the 3 serranids tested (*Epinephelus coioides*, *E. fuscoguttatus* and *Plectropomus leopardus*) had similar auditory thresholds across all frequencies in terms of both pressure and particle acceleration (Fig. 3d). The frequencies at which hearing was most sensitive did, however, differ among the
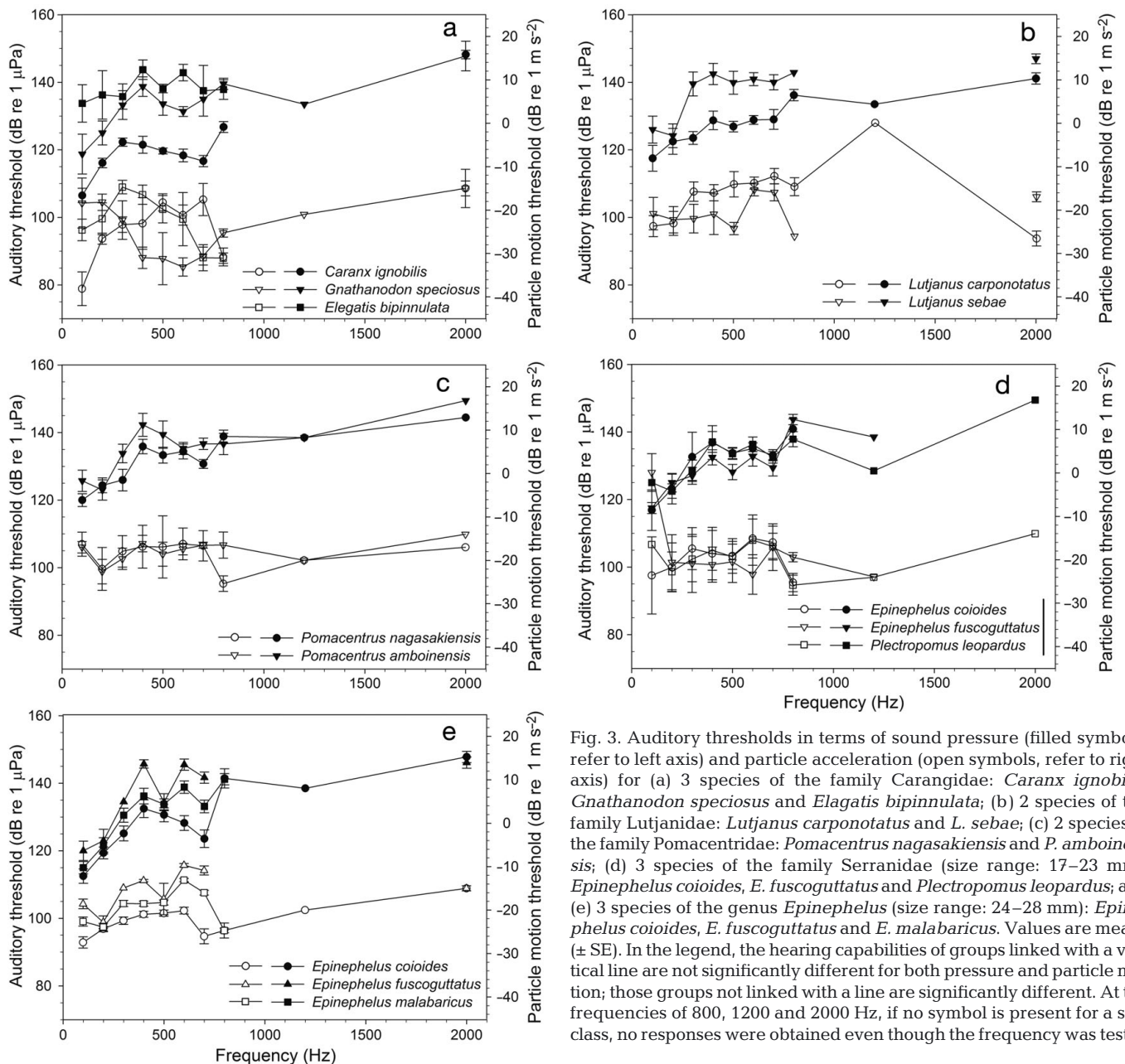
Fig. 3. Auditory thresholds in terms of sound pressure (filled symbols, refer to left axis) and particle acceleration (open symbols, refer to right axis) for (a) 3 species of the family Carangidae: *Caranx ignobilis*, *Gnathanodon speciosus* and *Elagatis bipinnulata*; (b) 2 species of the family Lutjanidae: *Lutjanus carponotatus* and *L. sebae*; (c) 2 species of the family Pomacentridae: *Pomacentrus nagasakiensis* and *P. amboinensis*; (d) 3 species of the family Serranidae (size range: 17–23 mm): *Epinephelus coioides*, *E. fuscoguttatus* and *Plectropomus leopardus*; and (e) 3 species of the genus *Epinephelus* (size range: 24–28 mm): *Epinephelus coioides*, *E. fuscoguttatus* and *E. malabaricus*. Values are means (± SE). In the legend, the hearing capabilities of groups linked with a vertical line are not significantly different for both pressure and particle motion; those groups not linked with a line are significantly different. At the frequencies of 800, 1200 and 2000 Hz, if no symbol is present for a size class, no responses were obtained even though the frequency was tested

3 species. *E. coioides* heard best at 100 and 200 Hz, whereas the other 2 species had a slightly broader range of frequencies over which they heard well—*E. fuscoguttatus* at 100, 200 and 300 Hz and *P. leopardus* at from 100 to 300, 500 and 700 Hz.

In a larger size class (24–28 mm), the 3 *Epinephelus* species had significant pressure threshold differences (GLM, $F_{2,124}$ = 26.4, p < 0.001) and particle acceleration threshold differences (GLM, $F_{2,124}$ = 17.0, p < 0.001) (Fig. 3e). *E. coioides* had more sensitive hearing than *E. malabaricus* at frequencies >500 Hz. Both species had more sensitive hearing than *E. fuscoguttatus*. The

frequencies that *E. coioides* detected best (100 and 200 Hz) were the same for both the 17–23 and 24–28 mm size classes, whilst the range over which *E. fuscoguttatus* heard best expanded to include 500 Hz (therefore, 100 to 300 and 500 Hz). *E. malabaricus* also heard best at the frequencies of 100 and 200 Hz.

There was a large amount of overlap in the audiograms of the 4 families, especially at frequencies of 100 to 400 Hz (Fig. 4). No significant difference in hearing sensitivity was found among the 4 family groups, due in large part to the variance among species within families in hearing sensitivity.
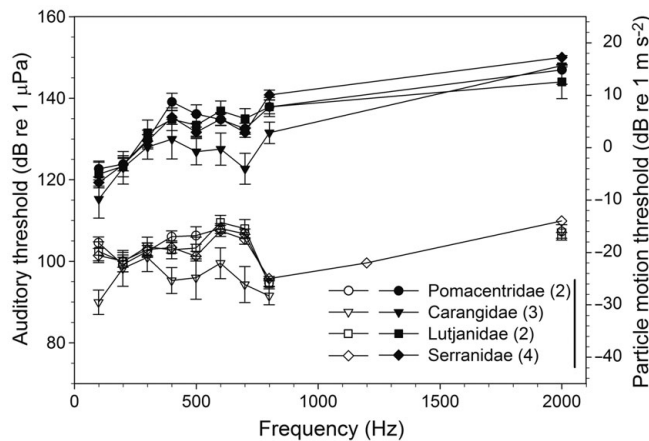
Fig. 4. Auditory thresholds in terms of sound pressure (filled symbols, refer to left axis) and particle acceleration (open symbols, refer to right axis) for 4 families: Pomacentridae (*Pomacentrus nagasakiensis* and *P. amboinensis*), Carangidae (*Caranx ignobilis*, *Gnathanodon speciosus* and *Elagatis bipinnulata*), Lutjanidae (*Lutjanus carponotatus* and *L. sebae*) and Serranidae (*Epinephelus coioides*, *E. fuscoguttatus*, *E. malabaricus* and *Plectropomus leopardus*). Values are means (±SE). In the legend, the hearing capabilities of groups linked with a vertical line are not significantly different for both pressure and particle motion

DISCUSSION

In the ocean, sound emanating from reefs or other sources should be dominated by pressure waves more than a few tens of metres from the sound source (Rogers & Cox 1988). Therefore, for the purposes of orientation, fish larvae should be able to detect sound pressure waves. Clearly, they can do this, as shown by several field experiments (e.g. Simpson et al. 2004, Tolimieri et al. 2004, Leis & Lockett 2005), but it is unclear how this is done, as it is generally assumed that otoliths and their associated hair cells only respond to particle motion, unless pressure waves can be transformed to movement by a swim bladder filled with gas. All the larvae we studied did have inflated swim bladders, so this mode of hearing is presumably available to them. This perspective is, however, based primarily on theory and has not been demonstrated in larval stages, for example, by experiments involving deflating the swim bladder. Other means by which fish larvae may detect sound pressure waves cannot be ruled out.

Our measurements of hearing sensitivity based on particle motion are within the range of those reported for adult sciaenids by Horodysky et al. (2008), but the values reported in the latter study range much more widely than those in the current study. As might be expected, particle motion plays a greater role at lower frequencies (that is, the larvae in the test tank are in the nearfield for particle motion for lower frequency sounds, but not for higher frequencies), but the audio-

gram shape for particle motion differs from that for pressure. Although both particle motion and pressure audiograms have the lowest thresholds at 100 Hz, all particle motion audiograms have a drop in hearing thresholds at 500 Hz; such a drop is lacking in the sound pressure audiograms. We found similar ontogenetic differences in hearing ability whether we expressed our results in terms of pressure detection or particle motion detection. The possibility remains, however, that the pressure sensitivity levels reported here are somewhat lower than they would be in the field (i.e. we have overestimated hearing sensitivity) because of a contribution of particle motion detection to hearing in the laboratory tank. Because of the comparative nature of the current study, however, any overestimations in sensitivity would be equal across taxa, which means the comparisons among taxa or stages would remain valid. We have followed recent recommendations (Horodysky et al. 2008, Popper & Fay 2010) to report hearing thresholds in terms of both particle motion and pressure. The goal of reporting particle motion values is to give some indication of the magnitude of particle motion detection in the laboratory, but there is no straightforward way to subtract this effect from pressure values (see discussion in Popper & Fay 2010). We note, in addition, that all such laboratory measurements are, to some extent, compromised by the fact that no one has devised a means of measuring fish hearing thresholds due to particle motion or pressure in the laboratory without the simultaneous influence of the other. As pointed out by Popper & Fay (2010), this can be done for pressure in the field, but, at present, such measurements could only be accomplished with juveniles or adults (not larvae) and by means of behavioural experiments (not AEP).

Ontogeny

An ontogenetic improvement in pressure detection ability was found for 4 out of the 5 species tested. For 3 of the species (*Epinephelus coioides*, *Eleutheronema tetradactylum* and *Macquaria novemaculeata*), auditory thresholds improved with an increase in size, although in the case of *E. tetradactylum* and *M. novemaculeata* only 2 size classes could be studied. The 2 smallest size classes of *Caranx ignobilis* had similar auditory thresholds, whereas the largest size class (19–23 mm) had improved hearing. Only in *E. fuscoguttatus* was there no ontogenetic improvement in auditory ability; however, this was probably due to insufficient numbers of fish tested in the 24–28 mm size class and the resulting low statistical power (e.g. at the frequencies of 100, 300, 500, 700, 800, 1200 and 2000 Hz only 2 or 3 larvae were available to be tested).

Several studies have examined (using different techniques) changes in fish hearing sensitivity during juvenile and adult phases, with conflicting results. A dramatic improvement in auditory ability from juveniles to adults was found in 2 species of pomacentrid, *Stegastes partitus* and *S. variablis* (Kenyon 1996). Three studies also reported a frequency-dependent improvement in auditory ability from juveniles to adults (Iwashita et al. 1999, Wysocki & Ladich 2001, Egner & Mann 2005). The hearing ability of 2 marine fishes, the sparid *Pagrus major* (Iwashita et al. 1999) and the pomacentrid *Abudefduf saxatilis* (Egner & Mann 2005), improved with an increase in size, but only at the frequencies of 100 and 200 Hz. A vocalising species, the freshwater characid *Trichopsis vittata* showed a significant improvement in auditory ability only between 800 and 2500 Hz (Wysocki & Ladich 2001). Conversely, no improvement in hearing ability was found from larvae to adults of the freshwater cyprinid *Danio rerio* (Higgs et al. 2003).

Examination of ontogenetic changes to the morphology of the ear and associated nerves were not conducted in the present study, so the morphological reasons for an improvement in auditory ability with size are not known. The addition of new sensory hair cells is one possible mechanism behind an increase in hearing sensitivity. Sensory hair cells continue to be added to the inner ear of fishes throughout their life (Corwin 1981, 1983, Popper & Hoxter 1984, Lombarte & Popper 1994, Higgs et al. 2002). The addition of sensory hair cells correlates with increased hearing sensitivity in elasmobranchs (Corwin 1983), but not in zebrafish (Higgs 2002). Another possibility may be that, as the fish increases in size, so does the otolith, allowing it to act as a better inertial mass and, thus, increasing hearing sensitivity (Gauldie 1988). But, because the mechanisms of hearing in teleosts fishes are not clearly understood, it is difficult to attribute increases in hearing sensitivity to changes in morphology.

Changes in sensitivity were not the only ontogenetic changes in hearing documented in the present study. Two of the species, *Epinephelus coioides* and *Eleutheronema tetradactylum*, also showed an ontogenetic expansion in the frequency bandwidth they were able to detect, at least at the levels we were able to provide with our apparatus. Expansion of the frequency bandwidth with an increase in size has also been demonstrated for *Abudefduf saxatilis* (Egner & Mann 2005), *Trichopsis vittata* (Wysocki & Ladich 2001) and *Danio rerio* (Higgs et al. 2003). For the species with known morphological hearing specialisations, *D. rerio* and *T. vittata*, expansion in the frequency bandwidth coincides with the development of specialised auditory accessories—the Weberian ossicles of *D. rerio* (Higgs et al. 2003), and the suprabranchial chamber of *T. vit-*

tata (Wysocki & Ladich 2001). Serranids are not known to have peripheral auditory structures, and the audiogram of adult *Epinephelus guttatus* (Tavolga & Wodinsky 1963) is in the range expected for a fish without morphological auditory specialisations. One possibility for the hearing improvement seen in both *E. coioides* and *E. tetradactylum* is that, as the swim bladder increases in size, it is brought closer to the ear, aiding in frequency detection and increasing the bandwidth that can be detected (Kenyon 1996). Presumably, however, this would also apply to the other species tested that also possess a swim bladder, but did not have an ontogenetic increase in bandwidth. Conversely, Egner & Mann (2005) found that, in *A. saxatilis*, the smallest size class had more sensitive hearing than larger fish and speculated this may have been due to the closer proximity of the swim bladder to the inner ear in the smallest individuals. As in the present study, neither Kenyon (1996) nor Egner & Mann (2005) investigated the morphology behind these theories, so the true morphological mechanisms behind changes in auditory sensitivity remain unclear.

Taxonomic differences

We found differences in auditory abilities among confamilials in 3 of the 4 families tested. Hearing ability varied among species of carangids, lutjanids and pomacentrids (Fig. 3a,b,c). In contrast, all 3 serranid species of similar size had similar hearing abilities (Fig. 3d). Little, if any, difference in hearing abilities has been found among confamilial adults in previous work. Myrberg & Spires (1980) concluded that, although variations existed between the auditory abilities of adults of 7 pomacentrid species, overall the 7 species were remarkably similar. Kenyon (1996) found the hearing of the 2 juvenile congeneric pomacentrids, *Stegastes partitus* and *S. variablis*, to be similar. However, neither of these studies statistically tested the auditory thresholds of the species involved, so the evaluations of similarity were subjective.

Auditory differences between adult confamilials have been found in cases where one species had known morphological hearing specialisations, while the other species did not. Adults of 2 holocentrid species had very different hearing sensitivities—*Myripristis kuntee* had very sensitive hearing, whilst *Adioryx xantherythrus* had relatively poor hearing (Coombs & Popper 1979). These 2 species have differences in their peripheral auditory structures, which were thought to be responsible for the difference in auditory ability— species from the subfamily Myripristinae have a direct connection between the swim bladder and the auditory bulla, whilst species from the genus *Adioryx* lack

such connections (Coombs & Popper 1979). Similarly, among adults of sciaenid species, there are a range of auditory specialisations, and, consequently, different species have very different auditory capabilities (Ramcharitar et al. 2001, 2006). One sciaenid species, *Bairdiella chrysoura*, can detect sounds of up to 4000 Hz, and this ability is suspected to be due to morphological specialisations of the inner ear and swim bladder (Ramcharitar et al. 2004). The sciaenid *Cynoscion regalis*, which has projections from the swim bladder to the inner ear, can hear up to 2000 Hz (Ramcharitar et al. 2006). Conversely, *Leiostomus xanthurus* has no swim bladder appendages and cannot hear frequencies >700 Hz (Ramcharitar et al. 2006).

The central question still remains: Can teleost larvae use their auditory abilities to detect and locate reefs prior to settlement? This question has broad implications for ecological modelling of reef interconnectivity and has been the focus of intense research interest in the last 5 yr. The data from the current study cannot definitively answer the question of acoustic attraction, but they do provide substantial new information upon which to base new estimates. Estimating the distance from which larvae can hear a reef is subject to a number of assumptions and to the local soundscape. First, factors related to the reef and its surroundings are vital: that is, the sound quality and quantity (i.e. frequency distribution and decibel level) at the reef itself and whether the sound propagates in a spherical or cylindrical manner (Urick 1983). Spherical sound spreading assumes a point sound source in an infinitely deep and non-stratified ocean and that the sound spreads equally in all directions. Although this does not exactly match any reef situation, it would most closely approximate a situation at an oceanic reef, where the bottom drops off very rapidly with distance and where the water column is unstratified and there is no reflection from the surface. Cylindrical spreading assumes that the sound reflects perfectly from both the bottom and the air–water interface and most closely approximates a situation of a reef on the continental shelf. In reality, any situation will be somewhere in between the extremes predicted by the spherical and cylindrical spreading models, but just how different it is from either will have overriding influence for the magnitude of the sound at any distance from the reef, ranging up to an order of magnitude difference in decibel values (which itself is a logarithmic measure). In addition, reefs are not point sources of sound, rather they produce sound along the reef continuum, which complicates any attempt to calculate sound levels at a distance from them. In short, the sound level at any distance from a reef will be strongly site dependent and time dependent, because reef sound levels vary temporally (Cato 1978).

A second set of influences comes from the assumptions that must be made to 'correct' electrophysiological measures of hearing sensitivity. Studies of adult fishes have shown that behavioural measures of hearing ability (usually derived from behavioural conditioning) are 10 to 30 dB more sensitive than are electrophysiological measures like AEP (Gorga et al. 1988, Kojima et al. 2005). Thus, the latter must be 'corrected' if they are to be useful to estimate detection distances in the field, but the increase in detection distance estimates provided by assuming spherical spreading and a 10 dB 'correction' are 3- to 4-fold, whereas, a 30 dB 'correction' provides an increase in detection distance of 30- to 50-fold (10- and 100- to 1000-fold, respectively, with cylindrical spreading). Unfortunately, appropriate 'corrections' for the species studied here are not available for any life-history stage, nor are any such corrections available for larvae of any fish species, primarily due to the near impossibility of obtaining behavioural estimates of hearing ability for larval stages. Finally, physiological thresholds have thus far been based on tone bursts, but the soundscape from a reef encompasses a wide range of frequencies and may well stimulate the fish ear or brain quite differently and, at different levels, than a tone burst (Kozloski & Crawford 2000, Wysocki & Ladich 2003, Maruska & Tricas 2009).

It is also unknown what frequencies of the reef sound spectra larvae may use to locate a reef. High-frequency segments of reef noise (570 to 2000 Hz) attracted greater numbers of settlement-stage larvae to artificial reefs and light-traps (Simpson et al. 2008a, b); however, our results show that hearing sensitivity of the larvae tested decreases at >800 Hz. Thus, it is likely to be the 500 to 1000 Hz segment of the reef noise that the larvae are responding to. Radford et al. (2010) show that, in many marine environments, the bulk of the sound energy is at frequencies >800 Hz, that is, at frequencies where fish larvae and many adults have low hearing sensitivity. While the Radford et al. (2010) study was conducted in a different environment than the current study (temperate versus tropical), it clearly demonstrates that reef sound signatures can have a substantial amount of energy outside the range of fish hearing. Therefore, it is important that studies of larval orientation take the hearing abilities of larvae into account and pay particular attention to lower frequency bands rather than simply assuming that the distribution of sound energy in the sea reflects that used by the animals living in it.

Therefore, calculating general detection distances is unlikely to provide useful estimates, but it is possible to calculate relative ontogenetic increases in detection range based on the AEP values provided here, because such relative measures cancel out many of the assumptions mentioned above. To do this, we followed

the methodology of Egner & Mann (2005) to calculate detection distances at Feather Reef, Great Barrier Reef, based on AEP measures, but, in addition to their assumption of spherical spreading of sound, we also calculated detection distances assuming cylindrical spreading. For each species, we compared the calculated detection distances for 100 and 500 Hz, for uncorrected AEP values and for corrections of 10 and 30 dB. Even the smallest larvae tested were able to hear, but their estimated 'uncorrected' detection distances were small. The actual estimates for 'uncorrected' detection distance in the Egner and Mann scenario ranged from about 15 to 400 m for the smallest larvae to about 40 to 1000 m for the largest larvae, assuming spherical spreading. For cylindrical spreading, the estimates were from 5 to 600 m and from 7 to 5000 m, respectively. In Table 1, we report, for each species, the range in values of the ratio of these estimates between the smallest and largest size class studied here as a measure of ontogenetic increase in detection distance.

Ontogenetic increases in detection distance were substantial for tropical species (1.5-to 10-fold for spherical spreading, 2- to 100-fold for cylindrical spreading), but increased by only 10 to 50% in the single temperate species (Table 1).

Our physiological experiments provide an estimate of the range of sounds that are detectable by fish and how hearing ability differs among species and among life-history stages. What is clear from the current data is that thresholds and bandwidths change ontogenetically, but pelagic larvae do have the ability to detect sounds relatively early in life (by 8 mm, the smallest larvae we could measure using the AEP methodology).

With the acceptance that larvae are capable of controlling their dispersal (Leis 2006), models of larval dispersal need to incorporate abilities such as swimming or hearing, where applicable (Leis 2007), to more accurately manage fish populations. The finding that auditory abilities are species specific means that models of dispersal incorporating sensory abilities may need to be tailored to individual species. Therefore, assessments of auditory ability of a species need to be conducted before a dispersal model can include the range over which sound may affect the trajectory of the larvae of that species. Audition, however, is not the only sensory ability that may be employed in habitat localisation — other possibilities include vision (Kingsford et al. 2002, Myrberg & Fuiman 2002), a magnetic sense (Wiltschko & Wiltschko 1995, Kingsford et al. 2002, Myrberg & Fuiman 2002), solar or lunar compass (Kings-

Table 1. Ontogenetic increase in the range of reef detection assuming a spherical or cylindrical model at 100 and 500 Hz. This range includes the measurements of tonal thresholds converted to spectral thresholds using an estimated critical bandwidth of 10% of the centre frequency (after Egner & Mann 2005), as well as a behavioural adjustment of from 10 to 30 dB, as behavioural methods of auditory determination are more sensitive than auditory-evoked potential (see Gorga et al. 1988, Kojima et al. 2005). SL: standard length

Species	Size class (SL, mm)		Ontogenetic increase in range	
	Smallest	Largest	Spherical model	Cylindrical model
Caranx ignobilis	9–13	19–23	1.5–4.0×	2.4–100×
Epinephelus coioides	9–13	24–28	6.6–10.0×	17.5–52.6×
Epinephelus fuscoguttatus	14–18	24–28	1.8–2.3×	2–5×
Eleutheronema tetradactylum	14–18	19–23	2.2–7.8×	8.3–66.7×
Macquaria novemaculeata	9–13	14–18	1–1.5×	1.2–1.4×

ford et al. 2002, Leis & Carson-Ewart 2003) and chemical cues (Sweatman 1988, Elliott et al. 1995, Ohman et al. 1998, Arvedlund et al. 1999, Atema et al. 2002, Lecchini et al. 2005a,b, Wright et al. 2005, 2008). One or a few of these sensory abilities are likely to play a role in navigation to a settlement habitat, and the hierarchy of these sensory modalities should be determined before sensory abilities can be incorporated into a dispersal model.

The present study provides the first data on the ontogenetic development of hearing of fish larvae prior to settlement. It shows that the smallest larvae tested can hear and that hearing ability generally increases with growth to settlement and beyond; this means that the range over which they can hear biologically significant sound also increases greatly. The examination of auditory ability within families shows intraspecific variations, which needs to be considered in the application of sensory abilities in dispersive modelling of fish larvae. No one model of hearing ontogeny should be applied to all fish larvae.

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