

Auditory sensitivity in settlement-stage larvae of coral reef fishes

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Abstract The larval phase of most species of coral reef fishes is spent away from the reef in the pelagic environment. At the time of settlement, these larvae need to locate a reef, and recent research indicates that sound emanating from reefs may act as a cue to guide them. Here, the auditory abilities of settlement-stage larvae of four species of coral reef fishes (families Pomacentridae, Lutjanidae and Serranidae) and similar-sized individuals of two pelagic species (Carangidae) were tested using an electrophysiological technique, auditory brainstem response (ABR). Five of the six species heard frequencies in the 100–2,000 Hz range, whilst one carangid species did not detect frequencies higher than 800 Hz. The audiograms of the six species were of similar shape, with best hearing at lower frequencies between 100 and 300 Hz. Strong within-species differences were found in hearing sensitivity both among the coral reef species and among the pelagic species. Larvae of the coral reef species had significantly more sensitive hearing than the larvae of the pelagic species. The

results suggest that settlement-stage larval reef fishes may be able to detect reef sounds at distances of a few 100 m. If true hearing thresholds are lower than ABR estimates, as indicated in some comparisons of ABR and behavioural methods, the detection distances would be much larger.

Keywords Auditory brainstem response · Coral reef fish · Larvae · Settlement-stage

Introduction

It is now clear that larvae of coral reef fish are able to orientate in the pelagic environment and control their dispersal through active swimming (Leis et al. 1996; Stobutzki and Bellwood 1997, 1998; Leis and Carson-Ewart 1999, 2003), and recent research indicates that settlement-stage larvae of coral reef fishes may use sound as a cue to locate settlement sites (Tolimieri et al. 2000, 2004; Leis et al. 2002, 2003; Simpson et al. 2004, 2005; Leis and Lockett 2005). Most coral reef fishes have a bipartite lifecycle, and the pelagic larval phase is spent in the open water environment away from the reef. At the end of this stage, the larvae must locate a coral reef upon which to settle. Dispersal of larvae during this phase was once thought to be passive, and settlement location determined entirely by currents (Roberts 1997). It is now clear, however, that larvae are able to return to natal reefs, and in some cases, locally spawned larvae can account for as much as 60% of all recruits (Jones et al. 1999, 2005; Swearer et al. 1999; Taylor and Hellberg 2003; Almany et al. 2007; Planes et al. 2009). Sensory cues almost certainly play a role in location of coral reef settlement habitats with chemical and sound cues being the most likely candidates. Sound propagation underwater is very

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effective, as sound travels 4.4 times faster in water than it does in air and travels long distances with little attenuation (Rogers and Cox 1988). So, the sound emanating from a coral reef could be used by a settlement-stage fish larva to find coral reefs (Kingsford et al. 2002; Leis and McCormick 2002). But, for reef sound to be a cue that larvae can utilize, the larva must be able to detect sound of the appropriate frequencies and intensities.

Little is known about the auditory capabilities of the larvae of coral reef fishes at settlement. Previously, they were believed to be quite limited (Myrberg and Fuiman 2002) and auditory assessment of juveniles of two pomacentrid damselfish species, *Stegastes partitus* and *S. variables* showed relatively poor auditory thresholds in comparison with conspecific adults (Kenyon 1996). However, several field studies show that settlement-stage larvae can detect and respond to reef sound. Studies using light traps show that traps with a speaker broadcasting reef sounds attracts more larvae than silent traps that do not broadcast sounds (Tolimieri et al. 2000; Leis et al. 2003; Simpson et al. 2004). Larvae are also capable of localizing a sound source—in binary choice chambers more larvae of damselfishes (Pomacentridae) moved towards nocturnal reef sound than away from it (Tolimieri et al. 2004; Leis and Lockett 2005). Further, larvae in situ are able to differentiate artificial sound (pure tones) from natural sound (coral reef sound) and alter their behaviour in the presence of broadcast nocturnal reef sound (Leis et al. 2002). Sound also can enhance settlement of larval coral reef fishes to artificial reefs (Simpson et al. 2005). However, none of these field studies attempted to measure the distance over which sound could be detected by the fish larvae. One physiological study on the auditory sensitivities of the sergeant major damselfish, *Abudefduf saxatilis*, suggested that, based on certain assumptions, sound could not aid *A. saxatilis* larvae in navigation, except over short (<1 km) distances (Egner and Mann 2005).

The current study aimed to directly determine the auditory capabilities of settlement-stage larvae of several species of coral reef fish and to compare these to the auditory thresholds of pelagic fishes of similar sizes. The audiograms of four species of reef fishes at settlement were compared with those of two species of non-reef fishes of similar size. The audiograms of the reef fishes *Lutjanus carponotatus*, *Pomacentrus amboinensis* and the non-reef fishes *Elagatis bipinnulata* and *Gnathanodon speciosus* are from the present study. The audiograms of the reef fishes *Pomacentrus nagasakiensis* and *Plectropomus leopardus* are from Wright et al. (2005) and Wright et al. (2008). Using these auditory capabilities, and published information on underwater ‘soundscapes’ in coral reef areas, an estimate of the spatial scales over which larval reef fishes might be able to hear coral reefs is calculated.

Materials and methods

Animals

Larvae were collected using light traps deployed overnight in open water, 100–200 m seaward of the reefs off Lizard Island on the Great Barrier Reef, Australia (14°40'S, 145°27'E). Testing of auditory capabilities took place on the day of capture, meaning all species examined were settlement or comparable stage (Choat et al. 1993). The size range of the larvae varied considerably among species, but much less so within species (Table 1).

Auditory brainstem response

Although some species can take a week to fully metamorphose, larvae of most fish species quickly and irreversibly metamorphose into juveniles after settlement. So, for a study on the hearing ability of settlement-stage larval fish, it was not possible to use conditioning behavioural assessments of hearing abilities because training of the subject is required. The electrophysiological method, auditory brainstem response (ABR) has been used extensively to measure mammalian auditory thresholds, and has more recently been adapted for work in fish (e.g. Corwin et al. 1982; Kenyon et al. 1998). The ABR measures the electrical potential generated in response to sound in the eighth cranial nerve and brainstem auditory nuclei. As the technique allows rapid measurements of auditory ability to be taken, it is ideal for the study of hearing capabilities of settlement-stage fish larvae (Higgs et al. 2002).

Auditory assessments were conducted on four species—two of the species, *P. amboinensis* (Pomacentridae) and *L. carponotatus* (Lutjanidae) settle on the reef at the end of their pelagic phase [as do *P. nagasakiensis* (Wright et al. 2005) and *P. leopardus* (Wright et al. 2008)], whereas the two carangid species, *E. bipinnulata* and *G. speciosus* remain in the pelagic environment as adults. Light trap catches of each species varied and were unpredictable, resulting in different numbers of each species being tested. Sample sizes and standard lengths (SL) for each species are given in Table 1. Most species of reef fishes settle within a relatively narrow, species-specific, size range (Leis and McCormick 2002), and this determined the sizes of the reef fish larvae used. Carangids of similar sizes were used for the comparison.

For ABR testing, fish were completely submerged underwater in a PVC (0.5 mm thick) tank 1.17 m long with a diameter of 0.25 m. Larvae were positioned laterally upon a piece of clay on a Perspex slide attached at a perpendicular angle to a plastic pipette (fish holder). Staples were positioned loosely around the fish's body as a restraint. No muscle relaxants or anaesthetics were needed

Table 1 Summary of all ABR data for all species of reef and pelagic individuals

Freq. (Hz)	SL dB re 1 μ Pa	<i>P. nagasakiensis</i> 12–15 mm		<i>P. amboinensis</i> 12–13 mm		<i>P. leopardus</i> 17–22 mm		<i>L. carponotatus</i> 23–27 mm		<i>E. bipinnulata</i> 14–28 mm		<i>G. speciosus</i> 20–31 mm	
		R	NR	R	NR	R	NR	R	NR	R	NR	R	NR
100	150	8	0	7	0	8	0	6	0	4	0	4	0
200	150	8	0	5	0	8	0	6	0	4	0	4	0
300	150	7	0	7	0	7	0	5	0	4	0	4	0
400	150	7	0	7	0	7	0	5	0	3	1	4	0
500	150	7	0	6	0	7	0	5	0	4	0	3	0
600	145	9	0	7	0	13	0	6	0	5	0	4	0
700	140	7	0	3	0	7	1	5	0	2	1	2	0
800	145	5	2	4	0	6	2	3	2	3	1	3	0
1,200	140	1	4	2	3	1	7	1	4	0	4	1	1
2,000	150	2	5	2	5	4	3	3	0	0	4	3	0

The data for *P. nagasakiensis* and *P. leopardus* are from Wright et al. (2005) and Wright et al. (2008), respectively. The maximum SPL is given for each frequency (see Sect. “Methods” for further details). The reef species are on the left of the table, and the pelagic species on the right. The “R” column indicates the number of individual fish that responded at each frequency, whilst “NR” indicates the number of fish that showed no response at each frequency

for these experiments. A micromanipulator positioned the fish holder in the tank, at a depth of approximately 12 cm. An underwater speaker (University Sound UW-30) was placed near the opposite end of the tank, approximately 0.75 m from the fish.

Auditory stimuli were produced by a sound module (Tucker-Davis technologies, TDT, Gainesville, Florida) operated by a computer running SigGen (Version 4.4) and BioSig (Version 4.4) software. The TDT apparatus linked to the underwater speaker delivered tone bursts (10 ms duration with a 2 ms rise fall time gated through a Hanning Window) with frequencies of 100–2,000 Hz, the expected range of fish hearing (Fay and Megala-Simmons 1999). The presentation order of the frequencies was conducted randomly. Sound levels were increased in 5 dB increments for each frequency until a stereotypical ABR was seen, and then continued for at least another 10 dB to examine suprathreshold responses. Speaker limitations meant that not all frequencies tested could be played to the same sound pressure level (SPL; see Table 1 for maximum SPLs). An average of 200 responses (100 from stimuli presented at 90° and 100 from stimuli presented at 270° to cancel stimulus artefacts) was taken for each SPL at each frequency. Acoustic calibration was carried out daily using a High Tec Inc. HTI-96 Min Series hydrophone (sensitivity –163.7 dB V/1 μ Pa) placed in the fish holder. An oscilloscope was then used to measure SPL at each frequency, which was then attenuated through BioSig to output the desired decibel levels.

Stainless steel subdermal electrodes (Rochester Electro-medical Inc., Tampa, Florida) were used to collect ABRs.

Two electrodes were used—the recording electrode was positioned dorsally, just posterior to the operculum whilst the reference electrode was placed dorsally in the nasal region. Each electrode was insulated with fingernail varnish, except the tip, and was positioned by a micromanipulator. Auditory threshold was defined as the lowest level at which a clear response could be detected with ABR and was done visually. Visual detection has been shown to produce comparable results to the use of statistical approaches (Mann et al. 2001).

Data analysis

The number of test subjects available was dependent upon light trap catches, so the numbers of individuals tested for each species was unbalanced. Therefore, generalized linear modelling was used to compare the auditory sensitivities of the different species. Where significant differences were found, Bonferroni post hoc tests were conducted. To assess whether size and pelagic larval duration (PLD) were correlated with hearing sensitivity, Kendall’s test for correlation was carried out. For all tests, the significance level was $\alpha = 0.05$.

Results

The shape of the ABR waveform differed depending on the frequency or sound type being played. Low frequency tone bursts (100 and 200 Hz) produced a response waveform with two or more waves after the stimulus ended.

In contrast, all other frequency tone bursts produced the typical ABR response waveform, dropping away from the horizontal in response to the stimulus before rising sharply back above the horizontal (Fig. 1).

The hearing sensitivities of the coral reef species were significantly different (GLM, $F = 10.1$, $df = 3$, $P < 0.001$). Of the four species of reef fish tested, *L. carponotatus* had significantly lower hearing thresholds than the other three species ($P < 0.001$, *P. amboinensis* and *P. leopardus*; $P < 0.05$, *P. nagasakiensis*; Fig. 2). The auditory abilities of the other three species were similar in some cases, for example, *P. nagasakiensis* and *P. leopardus*, and *P. amboinensis* and *P. leopardus*. Unexpectedly, the hearing sensitivities of the two damselfish species from the same genus, *P. nagasakiensis* and *P. amboinensis*, were significantly different ($P < 0.05$). Hearing sensitivity was found to be independent of both size at settlement and PLD for the four coral reef species [Kendall's correlation, $P > 0.05$, $n = 6$ (size), $n = 4$ (PLD)].

The two pelagic species had significantly different hearing sensitivities—*G. speciosus* had more sensitive

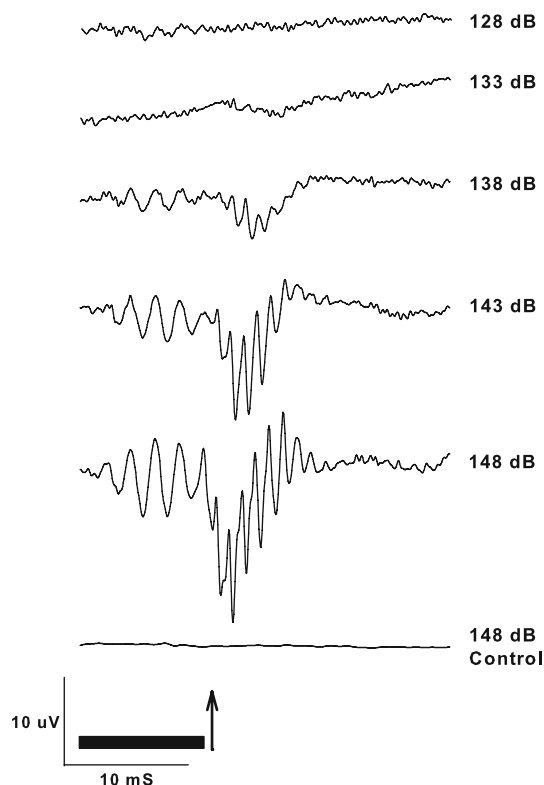


Fig. 1 Auditory brainstem response to a 600 Hz tone burst for *Pomacentrus nagasakiensis*. All intensities are expressed as dB re $1 \mu\text{Pa}$. The bar represents stimulus duration and the arrow indicates the start of the response. Auditory threshold or the lowest SPL to show a definitive response occurred at 133 dB for 600 Hz in this example. No response occurred for any dead controls

hearing than *E. bipinnulata* (GLM, $F = 8.8$, $df = 1$, $P < 0.01$; Fig. 3). The audiogram of *E. bipinnulata* was flatter than the audiogram of *G. speciosus* which had a wider range of auditory thresholds.

Comparison of the two ecological groups showed that the coral reef species had significantly more sensitive hearing than their pelagic counterparts (GLM, $F = 13.5$, $df = 1$, $P < 0.001$; Fig. 4). The two audiograms were similar in shape; however, the coral reef species had more sensitive hearing for all frequencies except 1,200 Hz.

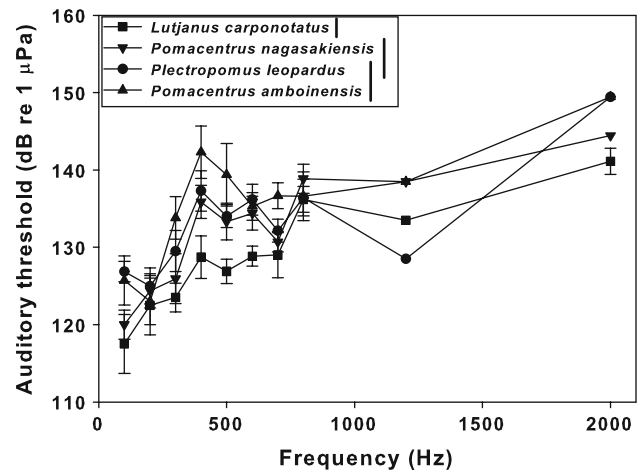


Fig. 2 Auditory thresholds for settlement-stage larvae of four species of coral reef fishes: *Pomacentrus nagasakiensis* (inverted filled triangle), *Pomacentrus amboinensis* (filled triangle), *Plectropomus leopardus* (filled circle) and *Lutjanus carponotatus* (filled square). All values are means \pm standard errors. On the legend, species linked by a vertical line do not differ in their hearing sensitivities, whilst those not linked by a line have significantly different hearing sensitivities

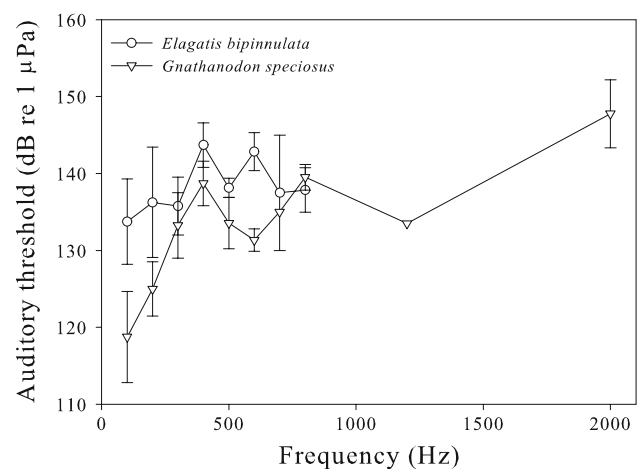


Fig. 3 Audiogram for the two species of pelagic larvae tested: *Gnathanodon speciosus* (open triangle) and *Elagatis bipinnulata* (open circle). Values are means \pm standard errors. The hearing sensitivities of the two species were significantly different

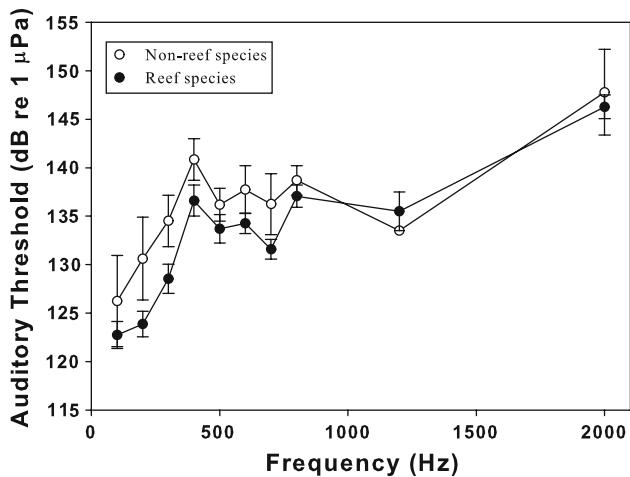


Fig. 4 Auditory thresholds for reef species (filled circle) and pelagic species (open circle). All values are means \pm standard errors. The hearing sensitivities of the two groups were significantly different

Discussion

Studies of auditory capabilities of fishes have previously been focused on adults, with only a few investigations of the hearing abilities of larvae or juveniles. These include the freshwater zebrafish *Danio rerio* (Higgs et al. 2002, 2003), post-settlement juveniles of the damselfish species *S. partitus* and *S. variabilis* (Kenyon 1996), *A. saxatilis* (Egner and Mann 2005) and *P. nagasakiensis* (Wright et al. 2005, 2007), and settlement-stage larvae of a serranid, *P. leopardus* (Wright et al. 2008), and a pomacentrid, *P. nagasakiensis* (Wright et al. 2005, 2007). The current study is the first to investigate and compare the hearing abilities of settlement-stage larvae of several different coral reef fish species and of similar size juveniles of pelagic species, providing valuable information on hearing sensitivities of larval fish at this stage.

The relative auditory capabilities of larvae of the tested species would not have been predicted by available information on adult hearing capabilities. Among the larvae, the lutjanid *L. carponotatus* had more sensitive hearing than the two pomacentrids (Fig. 2) which contrasts with the situation in adults (Myrberg and Fuiman 2002), where a species of *Lutjanus* (*apodus*; Tavalga and Wodinsky 1963) had less sensitive hearing at frequencies > 300 Hz than did six pomacentrid species (Myrberg and Spires 1980). A comparison between the hearing sensitivities of the settlement-stage larvae of two pomacentrid species (this study) and post-settlement juveniles of two other pomacentrid species showed both similarities and differences (Fig. 5). Hearing of post-settlement *A. saxatilis* (Egner and Mann 2005) was more sensitive than the other species at lower frequencies (100–300 Hz), similar at 800 Hz and less sensitive at the frequencies higher than 800 Hz. *Stegastes*

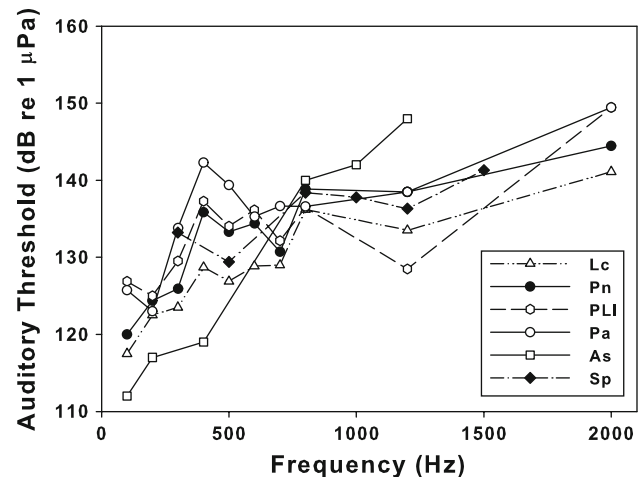


Fig. 5 Audiogram of six species of coral reef fishes. Settlement-stage larvae of *Pomacentrus nagasakiensis* (Pn, 12–15 mm, Wright et al. 2005), *Pomacentrus amboinensis* (Pa, 12–13 mm, this study), *Plectropomus leopardus* (PLI, 17–22 mm, Wright et al. 2008), *Lutjanus carponotatus* (Lc, 23–27 mm, this study), post-settlement *Abudefduf saxatilis* (As, <30 mm, Egner and Mann 2005) and post-settlement *Stegastes partitus* (Sp, 12–14 mm, Kenyon 1996)

partitus (Kenyon 1996) and the two pomacentrid species (*P. amboinensis* tested in this study, and *P. nagasakiensis* from Wright et al. 2005) had roughly similar hearing sensitivity. This is surprising considering hearing sensitivities determined with behavioural conditioning (*S. partitus*) are usually better than those measured by electrophysiological methods like ABR (the other 3 pomacentrid species). All species had convergent hearing sensitivities around the frequency of 800 Hz.

Such comparisons must be done with caution, however, as methods differed amongst studies—electrophysiological tests in this study and Egner and Mann (2005) versus behavioural tests in Tavalga and Wodinsky (1963), Myrberg and Spires (1980) and Kenyon (1996). Audiograms from the same species can differ between methods (Kenyon et al. 1998). Both behavioural and electrophysiological approaches have their merits. Behavioural tests seem to be more sensitive than electrophysiological methods by 10–30 dB (Gorga et al. 1988; Kenyon et al. 1998; Kojima et al. 2005). Electrophysiological tests have the advantage of not requiring behavioural training, which in the case of transient larval stages is not possible. Methodologies of electrophysiological testing can also vary. Responses were obtained in this study from an average of 200 stimulus presentations, whereas Egner and Mann used an average of 2000 stimulus presentations. The higher number of averages used in the Egner and Mann study would decrease background electrical noise, possibly resulting in thresholds as much as 10 dB lower (Mann, personal communication).

The auditory sensitivities of the larvae are reported in the current study in relation to the pressure component of the sound stimulus. In reality, the larvae likely respond to both the pressure and particle components of the sound wave and thus true auditory sensitivities may differ from those reported here, although auditory bandwidth would not be expected to change. Measurements of particle motion were not possible for the current study; however, the auditory sensitivities reported here in relation to sound pressure are still of value. All previous studies cited here reporting auditory thresholds of fishes are measured in sound pressure; therefore, auditory thresholds determined in this study can be directly compared to previous research. Sound pressure is also used in the measurement of coral reef noise in the ocean—particle motion measures of coral reef noise remain undetermined in the ocean and there is no quantification of how the particle motion component of the sound wave changes with distance. With these limitations in mind, analysis of sensitivities in terms of pressure allow for comparisons to previous work and also allow direct estimations of sensitivities in regards to published noise levels from coral reefs. Information on sensitivity to particle motion would be of value for future work, but until the acoustic signatures of coral reefs are better modelled in terms of particle motion (Mann et al. 2007), any estimation of detection distance for this metric remains problematic.

Contrary to this study, the few comparisons of auditory ability of adult fishes within a genus, suggest that similar species have similar auditory thresholds, and thus similar mechanisms of sound detection (Myrberg and Spirens 1980). Such comparisons are complicated, however, because previous studies were not based on statistical testing. The similarity in hearing ability of similar species reported in Myrberg and Spirens (1980) and Kenyon (1996) may be correct, but without statistical testing this remains unclear.

The difference found here in hearing abilities in larval stages of two congener species has potentially far reaching implications. Generalisations of hearing abilities from one or two measured species to congeners or confamilials may be incorrect. Management strategies and models of dispersal may need to account for differences in hearing abilities amongst species, as one model cannot necessarily be generalized for even closely related species, not to mention to species in other families. In addition, the question of the impact of anthropogenic noise (McCauley et al. 2003) in the ocean may need to be addressed on a species-by-species basis—some species could be more adversely affected by increased levels of anthropogenic noise than others. For example, anthropogenic noise could mask sounds that are important for orientation. More work needs to be done in this area, however, as a statistical difference in hearing ability may not be biologically

significant and may not be apparent in the coral reef environment.

Increased hearing sensitivity was not related to a longer PLD. Whilst *L. carponotatus* had the most sensitive hearing and the longest PLD (33–38 days) (Jones and Williamson, personal communication), the long PLD of *P. leopardus* (25.2 days; Doherty et al. 1994) did not correlate with an increased hearing sensitivity. Also, both pomacentrid species have similar PLDs (*P. nagasakiensis* average PLD 19 days versus *P. amboinensis* average PLD 19.8 days; Kerrigan 1996); however, the hearing of *P. nagasakiensis* is more sensitive than that of *P. amboinensis*. Increased hearing sensitivity was also found to be independent of size at settlement. For example, the hearing sensitivities of *P. leopardus* and *P. amboinensis* were not significantly different even though *P. leopardus* has a larger size at settlement than *P. amboinensis* (19.6 and 12.5 mm SL, respectively). It should be noted, however, that the power of these tests was low due to small sample sizes.

The two ecologically distinct groups of fish tested, reef versus pelagic, had significantly different hearing sensitivities. The larvae of coral reef fishes had more sensitive hearing at all frequencies tested compared to the pelagic species (with the exception of 1,200 Hz, where hearing sensitivity was poor in all species and did not differ between the two groups). This disparity in hearing ability between the two groups might be attributed to the requirement that coral reef fish larvae must locate a reef for settlement, something not needed by pelagic species. It would be expected that a larva that used sound in settlement site location would have more sensitive hearing than a similar size individual that does not settle. However, given that the pelagic species were of a different family than the coral reef species, the differences in hearing documented here may have a phylogenetic rather than an adaptational basis.

Several pieces of information are required to predict the spatial scale over which a larva might be able to detect sound coming from a reef: (1) the hearing sensitivity of the fish; (2) the masking by background noise; (3) the level of sound radiated by the reef and (4) the reduction in level as the sound radiates away from the reef (i.e. propagation loss). The information on hearing thresholds of larvae presented here suggests that these thresholds are too high for the larvae to be able to detect background noise (see Cato 1978, 1980 for typical background noise in comparable environments), meaning masking by background noise can be ignored. Propagation loss for sound underwater is complex and varies widely depending on environmental conditions such as sound speed profile, water depth and bottom acoustic properties (Urick 1983). A rather simplistic approach was adopted to estimate the distance over which larvae of coral reef fish species might

detect and use sound cues. The audiogram of one of the species, *L. carponotatus*, was compared to published levels of reef sound at two differing distances from Feather Reef (Great Barrier Reef), the first measured at 4.3 km from a reef (McCauley 1997) and the second estimated at a distance of 0.27 km from the same reef after assuming that propagation loss over this distance would be according to spherical spreading (Egner and Mann 2005). Given that reef sound is a broadband sound, an adjustment needed to be made to the audiogram of *L. carponotatus*, as this was in response to tones at set frequencies rather than broadband sound. The same adjustment of tonal thresholds was used by Egner and Mann (2005) which they applied to

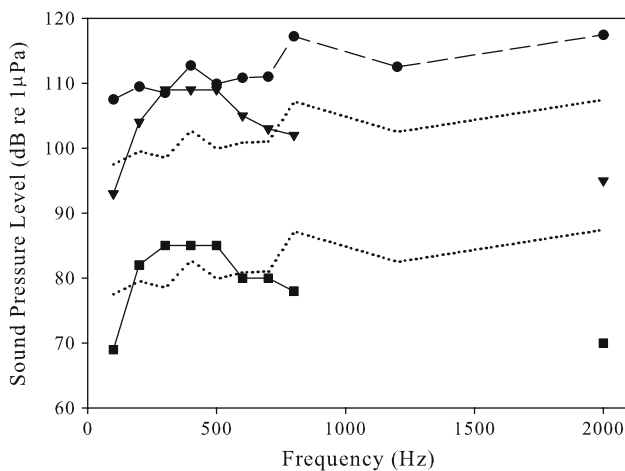


Fig. 6 Audiogram of *Lutjanus carponotatus* adjusted to take into account critical bandwidth of 10% of test frequency (Egner and Mann 2005; circles). The two dotted lines indicate the adjustment to account for the difference in ABR thresholds and behavioural thresholds—behavioural thresholds have been found to be 10–30 dB lower than ABR thresholds (Gorga et al. 1988). Reef sound recorded 4.3 km from Feather Reef (McCauley 1997) is indicated by the squares, whilst an estimate of the same reef sound 0.27 km away (Egner and Mann 2005) is indicated by the triangles. For frequencies where the solid lines are above the dotted lines, the larva can hear the reef sound of those frequencies

A. saxatilis but which was derived from studies of human hearing (Yost 1994): a critical bandwidth of 10% of the centre frequency. On this basis, sound emanating from a reef could be heard by larvae of *L. carponotatus* at least 0.27 km away from the reef (Fig. 6; Table 2 provides similar estimates for other reef species, which have less sensitive hearing). As mentioned previously, however, behavioural methods of auditory determination are more sensitive than ABR by about 10–30 dB (Gorga et al. 1988; Kojima et al. 2005). If it is assumed that a 30 dB behavioural adjustment applies, *L. carponotatus* could hear the same reef sound 4.3 km from the reef (Fig. 6).

The distance of detection of reef sound from Feather Reef for *L. carponotatus* cannot, however, be directly applied to all reefs. Underwater soundscapes are dependent on location and this will influence the distance of detection. For example, the depth of the water column, the type of substrate, size of reef and many other factors can affect the propagation of sound from a coral reef. If the auditory thresholds of *L. carponotatus* are compared with coral reef choruses recorded at another location, a different auditory detection range is likely to result. A chorus recorded 6 km from a Timor Sea reef by Cato (1978) reached 80 dB re 1 μPa between 500 and 700 Hz. Taking into account the widest behavioural adjustment of –30 dB, *L. carponotatus* can detect sounds of about 80 dB (for frequencies up to 700 Hz), meaning this species should be able to detect the 500–700 Hz portion of this reef chorus 6 km from the reef.

There are substantial uncertainties in these estimates of distances at which larvae might be able to detect reef sound, due to the uncertainties in the data and assumptions used. Shallow water propagation loss may approach cylindrical spreading at longer ranges if the bottom is highly reflective, whereas spherical spreading assumes no reflection from surface or bottom, and is more appropriate for deep water. The true situation for any location will lie somewhere between these extremes. Determining the difference between the ABR estimates of hearing threshold

Table 2 Ability of the larvae of the four coral reef species tested to detect reef sound either 0.27 km (Egner and Mann 2005) or 4.3 km (McCauley 1997) from a reef

Species	Adjusted (10% of frequency bandwidth)		Adjusted (10% of frequency bandwidth and –10 dB)		Adjusted (10% of frequency bandwidth and –30 dB)	
	0.27 km	4.3 km	0.27 km	4.3 km	0.27 km	4.3 km
<i>L. carponotatus</i>	✓	X	✓	X	✓	✓
<i>P. nagasakiensis</i>	X	X	✓	X	✓	✓
<i>P. amboinensis</i>	X	X	✓	X	✓	✓
<i>P. leopardus</i>	X	X	✓	X	✓	✓

A ✓ indicates that the species can hear reef sound over this range, whilst a X means that the species cannot detect reef sounds at this distance. The audiograms were adjusted to take into account frequency bandwidth of 10% of the test frequency in all columns, and a further adjustment of –10 and –30 dB, respectively, in columns 2 and 3 to account for the difference in ABR thresholds and behavioural thresholds (Gorga et al. 1988)

and the true threshold is crucial to making reliable estimates. For example, if the true threshold is 10 dB below the ABR threshold, the difference in distance would be a factor of 3 for spherical spreading or 10 for cylindrical spreading. If the true threshold is 30 dB below the ABR threshold, the difference in distance would be at least a factor of 30. There are also uncertainties in the value of the critical band and very limited information on how reef sound varies with distance. Such large uncertainties limit the extent that any conclusions can be drawn on the distances at which larvae can detect reef sounds. In all, this emphasizes the importance of empirical measures of sound propagation in an area of interest, and the need for research on the relationships between behavioural and electrophysiological measures of hearing ability in the species and life history stages of interest.

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