Journal of Fish Biology (2008) **72,** 2543–2556
doi:10.1111/j.1095-8649.2008.01864.x, available online at http://www.blackwell-synergy.com

Auditory and olfactory abilities of larvae of the Indo-Pacific coral trout *Plectropomus leopardus* (Lacepède) at settlement

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(Received 5 February 2007, Accepted 18 February 2008)

Auditory and olfactory abilities of settlement-stage larvae of the coral trout *Plectropomus leopardus* (Pisces: Serranidae) were tested electrophysiologically to determine if these senses are sufficiently developed to aid larvae in detection of settlement habitats on coral reefs. *Plectropomus leopardus* larvae detected sounds from 100 to 2000 Hz with hearing most sensitive at the frequencies of 100, 200 and 600 Hz. The olfactory response of *P. leopardus* was similar for the two amino acids tested and for the water conditioned by conspecifics. Auditory and olfactory abilities of *P. leopardus* are well developed at settlement-stage, and apparently sufficient to detect auditory and olfactory cues from reefs.

Key words: auditory brainstem response; coral reef fish; electro-olfactogram; larvae; sensory abilities; settlement-stage.

INTRODUCTION

The coral trout *Plectropomus leopardus* (Lacepède), is an ecologically and commercially important fish in large parts of the tropical Indian and Pacific Oceans. This large epinepheline serranid is a top carnivore in many coral reef communities and plays a major role in the structure of these communities (Randall & Hoese, 1986). In Australia, *P. leopardus* is a major commercial finfish (Kailola *et al.*, 1993), targeted by the live fishing industry (Mapstone *et al.*, 2003) as well as recreational fishers (Williams, 2002).

Management of reef fishes is increasingly based on the use of marine protected areas (MPAs). MPAs are expected to serve the somewhat contradictory purposes of replenishing the populations of fishes within their borders through self-recruitment (*i.e.* lack of dispersal), and replenishing unprotected populations outside their borders through dispersal of eggs and larvae produced

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within their borders. To understand if these objectives can be met, and to determine the best spatial scaling and location of MPAs, it is important to understand dispersal during the pelagic larval stage. Previously, dispersal was assumed to be a primarily physical process (Roberts, 1997) but recent evidence indicates that behaviour of the larvae, particularly their swimming and sensory capabilities, may play an important role in dispersal (Leis & Carson-Ewart, 1997; Stobutzki & Bellwood, 1997; Tolimieri *et al.*, 2000, 2004; Bellwood & Fisher, 2001; Simpson *et al.*, 2004, 2005; Leis & Lockett, 2005). If behavioural control of dispersal is important, then the scale over which larval dispersal occurs will differ substantially from that predicted by physical processes alone.

Like the majority of coral reef fish larvae, *P. leopardus* has a bipartite life cycle (Leis, 1991). The larval stage of the life cycle of *P. leopardus* is presumably spent in the pelagic blue-water environment. As the demersal adults are relatively sedentary (Zeller *et al.*, 2003), it is during the larval phase that dispersal occurs and the larvae were thought to drift passively with the currents. Recent research, however, has shown that *P. leopardus* larvae are far from passive, being able to swim at speeds greater than the local ambient currents (Leis & Carson-Ewart, 1999; Leis & Fisher, 2006). The larvae of *P. leopardus* undergo settlement and metamorphosis onto coral reefs after 19–31 days, settling at an average size of 16·8 mm standard length (L_S) (Doherty *et al.*, 1994) and where they begin the demersal phase of the life cycle. For *P. leopardus*, and for other coral reef fishes, knowledge of how they locate a coral reef upon which to settle at the end of the pelagic larval phase remains scant, although settlement behaviour of *P. leopardus* has received some attention (Leis & Carson-Ewart, 1999). Given the well-developed swimming and orientation abilities of settlement-stage reef-fish larvae (Stobutzki & Bellwood, 1994, 1997, 1998; Leis *et al.*, 1996; Leis & Carson-Ewart, 1997, 1999, 2003; Leis & Fisher, 2006), and their ability to return to a natal reef (Jones *et al.*, 1999; Swearer *et al.*, 1999; Taylor & Hellberg, 2003), sensory abilities may be important in the location of a settlement habitat. Several behavioural studies have demonstrated that the auditory and olfactory senses of larvae of coral reef fishes are involved in directional movement (Elliott *et al.*, 1995; Arvedlund *et al.*, 1999; Tolimieri *et al.*, 2000, 2004; Atema *et al.*, 2002; Leis *et al.*, 2002, 2003; Leis & Lockett, 2005).

To investigate the sensory abilities of *P. leopardus*, the current study used the electrophysiological techniques of auditory brainstem response (ABR) and electro-olfactogram (EOG) to measure the auditory and olfactory abilities of larval *P. leopardus* at the stage that they would normally search for a settlement site and be making the pelagic–demersal transition, and determine whether these senses are developed sufficiently to potentially assist *P. leopardus* in the detection of a coral reef habitat.

MATERIALS AND METHODS

Larvae were collected using light traps deployed overnight, 100–200 m seaward of the reefs off Lizard Island on the Great Barrier Reef, Australia (14°40′ S; 145°27′ E) during the months of December 2005 and January 2006. The light traps were set in water 10–15 m deep and were emptied at dawn. Testing of sensory abilities took place on the day of capture. The larvae tested ranged from 17 to 22 mm L_S, with an average of

19·1 mm L_S. All physiological testing was carried out under the University of New South Wales, Animal Care and Ethics permit 03/54.

AUDITORY PHYSIOLOGY

Auditory abilities of settlement-stage *P. leopardus* were measured using ABR. Originally used in mammalian audition studies, the technique has been adapted for audition studies on fishes (Corwin *et al.*, 1982; Kenyon *et al.*, 1998). Auditory brainstem response requires no behavioural conditioning or training of an animal and provides an instantaneous measurement of audition.

The ABR methodology used was adapted from Higgs *et al.* (2003). Sample sizes for ABR are listed in Table I. An attempt was made to measure the full range of frequencies on each fish, however, this was not always successful. In total, 15 fish were tested. All evaluations of hearing ability were carried out in a tank constructed from 5 mm thick PVC pipe, 0·25 m in diameter and 1·17 m long, lying horizontally. The tank had an aperture of 1 m by 0·15 m allowing a free water surface area of *c.* 0·15 m^2. The larvae were placed at one end of the tank, 0·76 m away from an underwater speaker (University Sound UW-30; San Diego, CA, U.S.A.) positioned vertically at the opposite end of the tank. Larvae were restrained using a 'fish holder', constructed from a perspex slide attached (at a perpendicular angle) to a plastic pipette. The larvae were positioned on their side on clay resting on the fish holder, and staples loosely placed around their bodies. The fish holder was positioned in the tank using a micromanipulator at approximately half the tank's depth (0·12 m), and was completely submerged for testing leaving the fish's head *c.* 100 mm below the surface. No anaesthetics or muscle relaxants were used in these experiments. As a control, dead fish were also tested in the apparatus, and at no time did a dead fish produce a response similar to the responses of the experimental animals (Fig. 1).

Physiological equipment by Tucker-Davis Technologies (TDT; Gainesville, FL, U.S.A.) controlled by a computer running TDT SigGen (Version 4.4) and BioSig (Version 4.4) software was used to present auditory stimuli. Tone bursts of 10 ms duration with a 2 ms rise–fall time gated through a Hanning window were played, at frequencies of 100, 200, 300, 400, 500, 600, 700, 800, 1200 and 2000 Hz, covering the expected range of fish hearing (Fay & Megala-Simmons, 1999). Sound intensity was increased in 5 dB increments until a stereotypical ABR was observed at each frequency. Measurements were continued to at least 10 dB above threshold to ensure that the size of the response grew in magnitude with an increase in decibel level. The maximum sound pressure level (SPL) played was 140–150 dB. Calibration of acoustic intensities was

TABLE I. Summary of auditory brainstem response data for *Plectropomus leopardus*. A total of 15 fish was tested

Frequency (Hz)	Number of larvae tested	Response	No response
100	8	8	0
200	8	8	0
300	7	7	0
400	7	7	0
500	7	7	0
600	13	13	0
700	8	7	1
800	8	6	2
1200	8	1	7
2000	7	4	3

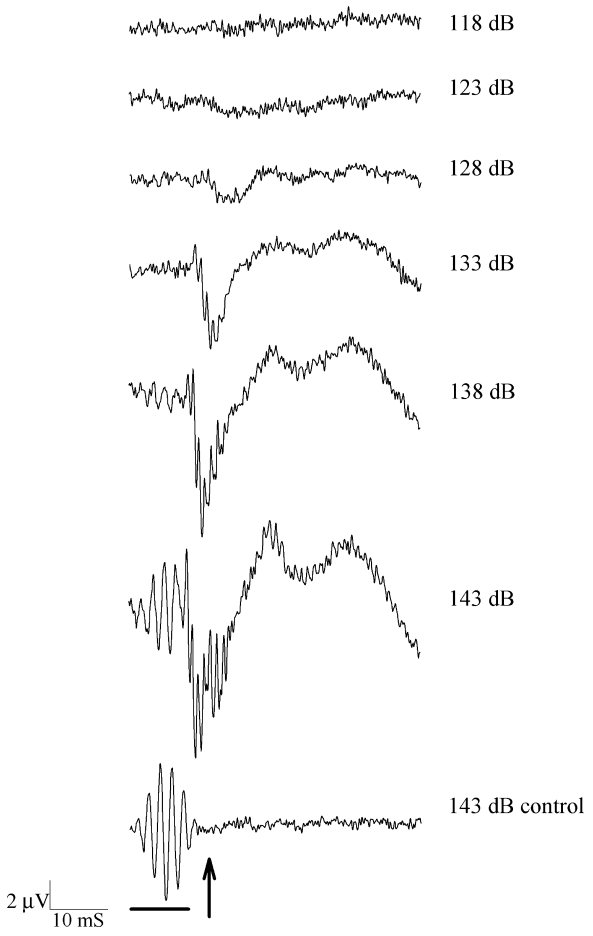

FIG. 1. Example response waveform for *Plectropomus leopardus* to a 600 Hz tone burst. The bars under the trace indicate the time of the stimulus presentation and the ↑, indicates the position of the response. Auditory threshold, or the lowest sound pressure level (SPL) to show a response in the example waveforms occurred at 123 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.

done using a HighTech Inc. (Gulf Port, MS, U.S.A.) HTI-96 Min Series hydrophone (sensitivity −163·7 dB V/1 μPa) which was placed in the position of the fish holder before experiments began. A digital oscilloscope (Tektronix TDS 1002; Beaverton, OR, U.S.A.) was used to measure RMS output at each frequency. The speaker output was then adjusted so that BioSig would output the desired decibel levels. To test for possible distortion of the waveform at the position of the fish, stimuli were presented with the hydrophone placed in the position of the fish and captured on computer for analysis. Although the 100 Hz signal did show some tank effects (Fig. 2), all other frequencies were transmitted with limited distortion (Fig. 2). Due to equipment limitations it was not possible to measure particle motion in the experimental set-up so all hearing estimates are expressed in units of sound pressure (dB re 1 μPa). While fishes are able to detect both pressure and displacement, expressing hearing in units of sound pressure makes the current study more directly comparable to other studies of fish hearing and to studies of reef noise, all of which measure sound in pressure units.

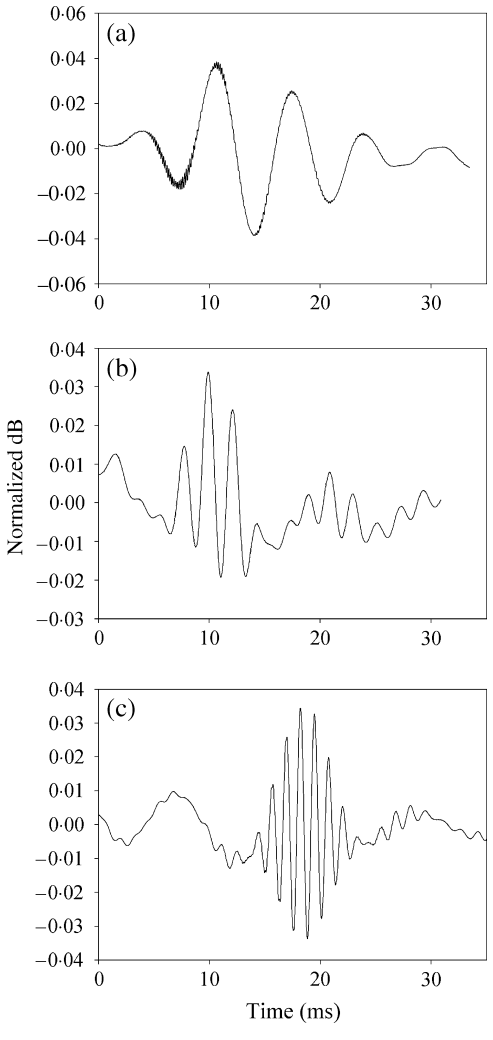

FIG. 2. Time waveforms of auditory stimuli for (a) 100, (b) 400 and (c) 800 Hz presentations as detected by a hydrophone at the position of the fish holder. The 100 Hz signal was slightly distorted (approximate frequency at hydrophone = 140 Hz) but the rest of the frequencies were transmitted with high fidelity.

Two stainless steel sub-dermal electrodes (Rochester Electromedical Inc., Tampa, FL, U.S.A.) coated in nail varnish for insulation (except the tip), were used to collect responses. The tip of each electrode was placed subcutaneously: the recording electrode was placed dorsally, posterior to the operculum whilst the reference electrode was placed dorsally in the nasal region. Micromanipulators were used to position each electrode. Responses were obtained from 200 stimulus presentations at each intensity and frequency (100 from stimuli presented at 90° phase and 100 from stimuli presented at 270° phase with different phase responses averaged to cancel stimulus artefacts).

The auditory threshold was the lowest level at which a clear response could be determined. Visual determination was used to detect auditory thresholds. Examples of ABR responses can be seen in Fig. 1.

OLFACTORY PHYSIOLOGY

Olfactory ability of settlement-stage *P. leopardus* individuals was determined using EOG. The EOG technique measures olfactory transduction by recording the change in the negative electrical potential at the surface of the nasal epithelium. The EOG methodology used was similar to other studies (Caprio, 1978; Wright *et al.*, 2005). Six *P. leopardus* larvae were tested by restraining them on their side, wrapped in a wet piece of tissue on a perspex stand. Oxygenated water was delivered in a constant flow-through the mouth and over the gills *via* a mouth tube (the water did not flow over the nose). Each individual was only tested once with different odours presented in random order, and no muscle relaxants or anaesthetics were needed. All EOG work was carried out in a grounded steel mesh Faraday cage, to minimize background electrical noise.

Responses were obtained using two stainless steel electrodes (Rochester Electromedical Inc.), which were coated in nail varnish (except the tips) for insulation. Micromanipulators positioned the electrodes, with the recording electrode placed into the excurrent nostril hole, and the reference electrode *c.* 10 mm away from the nostril on the ipsilateral side of the skin. The nasal cavity was constantly perfused with 24° C sea water from the Lizard Island Research Station (LIRS) seawater system (background flow) *via* an odour delivery tube placed over the posterior nostril. The background flow was manually switched to the test solution for a period of 5 s for each test, eliminating the possibility of a mechanical response as no change in flow rate occurred between this switch. Care was also taken to ensure no air bubbles were introduced to the flow during the change in water delivery. The amplified response (Grass-Telefactor CP122 Amplifier; West Warwick, RI, U.S.A.) was observed and recorded using an oscilloscope (Tektronix TDS1002; Tektronix, Richardson, TX, U.S.A.) and computer running Wavestar software (Version 2.6). The EOG response magnitude was measured from baseline to peak of the response and converted to mV using the amplifiers calibration scale.

The test stimulants used in this study were solutions of the amino acids L-alanine and L-proline (approximate concentrations 10^{-5} M) and conspecific conditioned sea water (CW). To make CW, 15 randomly selected *P. leopardus* larvae were placed in 300 ml of sea water with an airstone for a period of 1 h (these larvae were not the test subjects). The CW was used undiluted within 3 h. The preparation of all test waters was done using the background water and kept at the same temperature as the background water to ensure that any response seen was not due to those differences. Olfactory acclimation was minimized by allowing at least 2 min between exposures to test solutions. Dead fish controls, background water controls (*i.e.* water from the LIRS flow-through seawater system that has not been conditioned) and live controls where the electrode was placed on a different body part were run to ensure that all responses seen were genuine evoked potentials; at no time did control traces look similar to positive responses (Fig. 3).

STATISTICAL ANALYSES

To test the hypothesis that hearing sensitivities differed across the frequency range, generalized linear modelling (GLM) was used due to the unbalanced nature of the datasets. Where significant differences were found, Bonferroni *post hoc* tests were conducted. Significant differences in EOG responses to different odour types were also assessed using GLM, and Dunnett's test was used *post hoc* to compare each odour type to the control and background level. For all tests, the significance level was $\alpha = 0{\cdot}05$.

RESULTS

AUDITORY PHYSIOLOGY

The ABR waveforms produced for settlement-stage *P. leopardus* were typical of the ABR shape: a sharp drop away from the horizontal followed by a rise

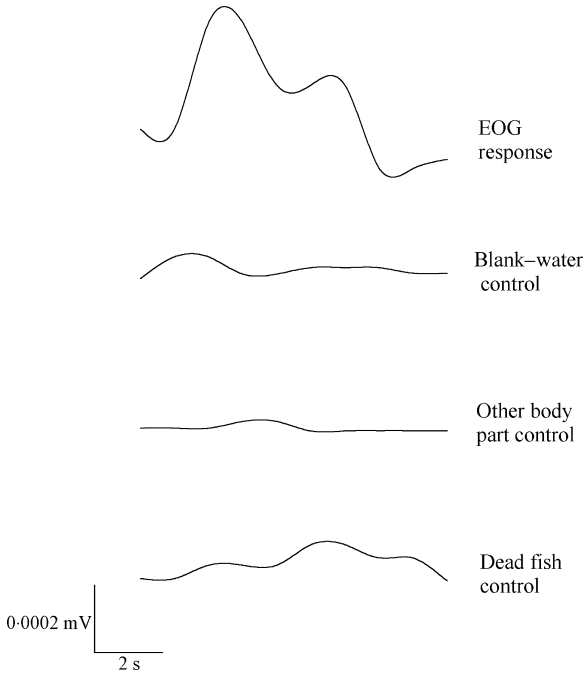

FIG. 3. Example of electro-olfactogram (EOG) waveforms (mV) for *Plectropomus leopardus* produced in response to the amino acid L-alanine. Responses to L-proline and conspecific conditioned sea water were similar.

(Fig. 1). Amplitude of the responses increased as the magnitude of the SPL increased. Waveforms in response to tone bursts at all frequencies were similar in appearance, except for 100 and 200 Hz, where more peaks occurred in the waveform. A response was obtained in all individuals at all frequencies up to and including 600 Hz (Table I). At higher frequencies, a response could not always be elicited, and at some frequencies, a majority of individuals had no detectable ABR to the highest sound intensity the system could generate. Thus, the mean sensitivity values for frequencies >700 Hz plotted in Fig. 4 are minimal threshold estimates.

Hearing sensitivity of settlement-stage *P. leopardus* varied among frequencies (GLM, $F_{8,59}$, $P < 0{\cdot}001$). The hearing of *P. leopardus* was most sensitive (threshold lowest) at a range of frequencies including 100–300 Hz and 500 and 700 Hz (Fig. 4). No significant differences in sensitivity were found at frequencies between 100 and 800 Hz except that hearing at 100 and 200 Hz was significantly more sensitive than at 400, 600, 800 and 2000 Hz (Fig. 4). The plotted value for hearing ability at 1200 Hz probably overestimates actual mean sensitivity, as only one response was obtained out of eight trials (Table I).

OLFACTORY PHYSIOLOGY

Response waveforms for EOG responses were typical, rising sharply and then falling gradually as the test odour washed away (Fig. 3). Responses to

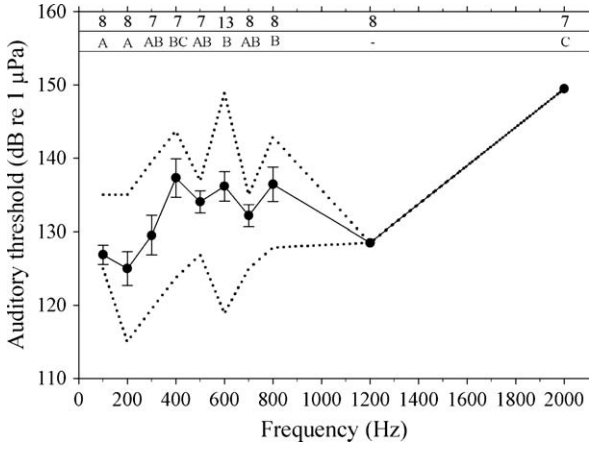

FIG. 4. Mean ± S.E. auditory thresholds for settlement-stage *Plectropomus leopardus* in response to tone bursts for a frequency range of 100–2000 Hz. · · · , the range of responses: the upper, the response by the least sensitive individual at each frequency and the lower, the response by the most sensitive individual at each frequency. The first row of the table at the top of the graph gives the total number of fish tested for each frequency, and the second row indicates significant differences between frequencies: those frequencies with a different uppercase letter are significantly different ($P < 0{\cdot}05$) (only one response was obtained for 1200 Hz, so this frequency was not included in the statistical testing).

the three odorants were significantly greater than both the background water control and the background level running throughout the experiment (GLM, $F_{4,31}$, $P < 0{\cdot}001$). No significant difference was found in the olfactory responses of *P. leopardus* to the three odours tested, alanine, proline and CW (Fig. 5).

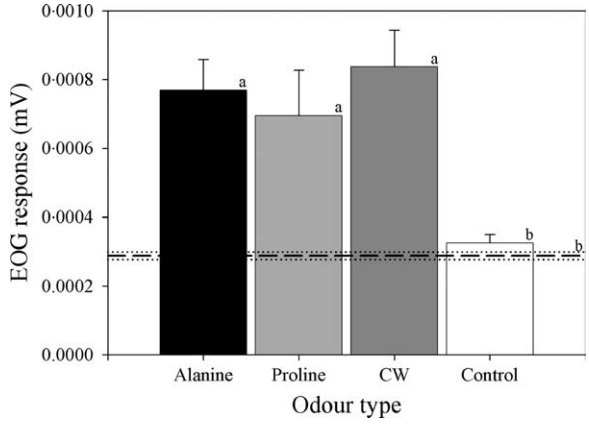

FIG. 5. Mean ± S.E. electro-olfactogram (EOG) responses to odour stimulants [alanine, proline and conspecific conditioned sea water (CW)] for settlement-stage *Plectropomus leopardus* ($n = 6$), including responses to the background water control (water that was not conditioned). – –, the average background level (mV); · · · , S.E. Significant differences between odorants, the control and the background level are indicated by different lowercase letters.

DISCUSSION

AUDITORY PHYSIOLOGY

The audiogram for settlement-stage *P. leopardus* showed a range of hearing sensitivities existed across the frequencies tested, with hearing ability differing significantly among frequencies (Fig. 4). Hearing ability tended to be most sensitive at lower frequencies. The audiogram of settlement-stage *Pomacentrus nagasakiensis* Tanaka the only other species for which an audiogram is available for settlement-stage larvae, had a similar shape to that of *P. leopardus* (Wright *et al.*, 2005). At most frequencies, the hearing ability at settlement stage of the two species was similar. At 100 and 2000 Hz, hearing of *P. nagasakiensis* was more sensitive than that of *P. leopardus*. Although it appeared that *P. leopardus* had more sensitive hearing at 1200 Hz, this apparent difference is suspect because the value for *P. leopardus* probably overestimated auditory ability. Juveniles of another species of coral reef fish, the pomacentrid *Abudefduf saxatilis* (L.), also tested using ABR (Egner & Mann, 2005), had more sensitive hearing than *P. leopardus* at the lower frequencies of 100, 200 and 400 Hz. At 800 Hz, the auditory thresholds of the two species were similar, and whilst *A. saxatilis* apparently could not detect 1400 and 1600 Hz, *P. leopardus* was able to detect the frequency of 2000 Hz, albeit at a relatively high SPL.

Although the hearing ability of adult *P. leopardus* has not been measured, the hearing ability of an adult of another serranid species has been measured behaviourally. Like settlement-stage *P. leopardus*, the hearing of the adult serranid *Epinephelus guttatus* (L.) was most sensitive at a frequency of 200 Hz (Tavolga & Wodinsky, 1963). Comparisons of hearing ability using different techniques must be done cautiously, and even results using the same technique in different studies on the same species can differ (Kenyon *et al.*, 1998). Further, behavioural testing of hearing ability has been found to be more sensitive than ABR estimates by *c.* 10–30 dB (Gorga *et al.*, 1988; Kenyon *et al.*, 1998), most probably because of the difficulty in detecting a response above the background noise of both the brain and the ABR set-up. The reported values of hearing sensitivity for adult *E. guttatus* were lower than those of settlement-stage larvae of *P. leopardus* but the hearing ability of the two species would be in a similar decibel range if the adjustment from behavioural to electrophysiological techniques (a 10–30 dB improvement of the latter) was made.

This study is the first measurement of hearing ability of the commercially and ecologically important epinepheline serranid, *P. leopardus*. The hearing ability of larval *P. leopardus* at the critical settlement-stage is comparable to that of other species. Field studies have provided conclusive evidence that settlement-stage larval fishes, including serranids, can detect and locate sources of reef noise (Leis *et al.*, 2003; Simpson *et al.*, 2004, 2005; Tolimieri *et al.*, 2004; Leis & Lockett, 2005), and the present study quantifies the hearing ability of settlement-stage larvae of one reef fish species (Fig. 4). Combined with data on the soundscapes near coral reefs, audiograms can help predict the spatial scales over which reef fish larvae detect sound sources such as reefs for use as settlement habitats. Using soundscape data taken 4·3 km from a reef (McCauley, 1997), Egner & Mann (2005) applied a spherical spreading model

to calculate sound levels in closer proximity to the reef. Using audiograms of post-settlement juveniles of the pomacentrid *A. saxatilis*, Egner & Mann (2005) estimated that the greatest distance that *A. saxatilis* could detect the reef was 0·54 km. While the reef system used in this study was not able to collect sounds, using the same data (McCauley, 1997) and the methods and assumptions of Egner & Mann (2005), it was estimated that settlement-stage larvae of *P. leopardus* would be able to detect a reef from at least as far as 0·135 km away at 300 Hz (Fig. 6). As mentioned above, ABR-derived hearing thresholds for *P. leopardus* are likely to be 10–30 dB less sensitive than behavioural thresholds (Gorga *et al.*, 1988; Kenyon *et al.*, 1998). Thus, taking this difference into account, *P.leopardus* would be able to hear reef sounds at 200–300 Hz when 4·3 km from the reef and at a broad range of frequencies at 0·27 km (Fig. 6). Estimating sound propagation underwater is complex, and it is not clear that the assumptions made by Egner & Mann (2005) are entirely appropriate for reefs located in relatively shallow water. A cylindrical rather than a spherical spreading model may be more appropriate in relatively shallow water (Urick, 1975). Reefs are also not point sources of sound, as assumed by Egner & Mann's (2005) model, rather they function as a line source (D. H. Cato, pers. comm.). Such assumptions can greatly influence the calculated soundscape. For example, if a model of cylindrical sound spreading (usually applicable in shallow water environments with reflective substrata) was assumed, the transmission loss over the same distance would only be half of that for a spherical spreading model.

OLFACTORY PHYSIOLOGY

This first determination of the olfactory ability of *P. leopardus* revealed that at settlement-stage, *P. leopardus* have the ability to detect amino acids as well as

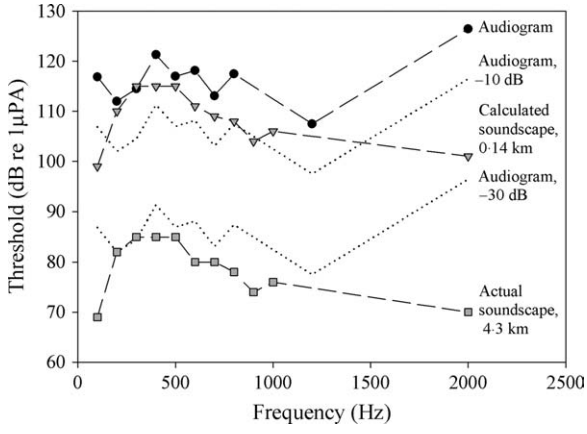

FIG. 6. Audiogram of *Plectropomus leopardus* adjusted to take into account frequency bandwidth of 10% of test frequency (Egner & Mann, 2005) (●). · · · ·, the adjustment to account for the difference in ABR thresholds and behavioural thresholds: behavioural thresholds have been found to be 10–30 dB lower than ABR thresholds (Gorga *et al.*, 1988). Reef noise recorded at a distance of 4·3 km from the reef (McCauley, 1997) is indicated (□), whilst an estimate of the same reef noise 0·27 km away (Egner & Mann, 2005) is also indicated (▽).

conspecifics (Fig. 5). Olfactory detection of both amino acids and conspecifics would be of value in the location of a coral reef at the time of settlement. As amino acids are present in all living organisms (Decho *et al.*, 1998), the density of living organisms in and around a reef would make it a concentrated source of chemical cues. Amino acid concentrations in sea water have been reported at levels (10^{-6}–10^{-5} M) (Kasumyan & Taufik, 1994) similar to those detected by settlement-stage larvae of *P. leopardus* in this study. The detection of conspecifics in an area would also indicate to settling larvae that a site was suitable for settlement. The presence or absence of conspecifics has also been shown to influence settlement in a number of coral reef fishes (Sweatman, 1988; Ohman *et al.*, 1998; Leis & Carson-Ewart, 2002). In addition to the utility of olfaction as a potential orientation and settlement cue, it may be important for other interactions such as predator avoidance and food location. The response to all odours tested was of similar magnitude, and also similar to the responses of pre-settlement *P. nagasakiensis* (Wright *et al.*, 2005), which are the only comparative data on physiological measurements of olfactory abilities in larvae of any marine fish.

Behavioural studies have shown that larval anemonefishes (Pomacentridae) use chemical cues from anemones to recognize and locate a host anemone (Elliott *et al.*, 1995; Arvedlund *et al.*, 1999). Further, settlement-stage larvae of several species of reef fishes (mostly apogonids) are capable of using chemical cues to distinguish and preferentially choose between coral reef lagoon water and oceanic water (Atema *et al.*, 2002). It has also been shown that the morphological mechanisms to detect chemical cues are present at the time of settlement in coral reef fishes; settlement-stage larvae of the families Apogonidae, Pomacentridae, Gobidae and Blennidae have well-developed noses with fully developed nares, accessory sacs and innervations to the olfactory bulb (Atema *et al.*, 2002). Atema *et al.* (2002) also demonstrated that apogonids at this stage sniff continuously, pumping water through their nares. The larvae of *P. leopardus* have two fully formed nares early during the pelagic stage, when they are between 8·1 and 8·7 mm L_S (Leis, 1986). So, given that the olfactory morphological structures are in place before and at settlement-stage, that larvae respond behaviourally to chemical cues and this study's physiological demonstration that settlement-stage larvae of coral reef fishes can indeed detect odours, it is plausible, if not likely, that olfaction plays a part in navigation by settlement-stage larvae at spatial scales relevant to the location of reefs.

Until recently, sensory abilities like hearing and olfaction of larval fishes were considered to be irrelevant to dispersal and settlement, either because the larvae lacked the swimming ability to use the sensory information for orientation and to locate a settlement habitat, or because the sensory abilities were not sensitive enough to be helpful (Myrberg & Fuiman, 2002). This study and other recent work on both senses (Arvedlund *et al.*, 1999; Tolimieri *et al.*, 2000, 2004; Atema *et al.*, 2002; Leis *et al.*, 2003; Simpson *et al.*, 2004, 2005; Leis & Lockett, 2005; Wright *et al.*, 2005; Arvedlund & Takemura, 2006; Leis, 2006) and swimming ability (Leis & Carson-Ewart, 1997, 1999; Stobutzki & Bellwood, 1997; Bellwood & Fisher, 2001; Leis & Fisher, 2006) have shown that both of these are misconceptions. It is now clear that larvae of many coral reef fishes at settlement-stage have excellent swimming abilities and sufficient sensory abilities that give the larvae the potential to control their dispersal

trajectories and actively find a settlement habitat. The challenging questions that remain are: When during ontogeny do these abilities develop? Do the larvae use these abilities to achieve results that differ substantially from passive drift, and if so, over what spatial and temporal scales? Answers to these questions are vital for effective management and protection of coral reef fish species.

This research was supported by ARC Discovery Grant DP0345876, DST International Sciences Linkages Grant IAP-IST-CG03-00442 and I. Suthers. The authors thank K. Poling for EOG apparatus design, technical advice and draft critiquing, R. Piola for laboratory assistance, D. Cato for technical advice on acoustics and tank design, and the staff at Lizard Island Research Station.

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