

## Juvenile coral reef fish use sound to locate habitats

C. A. Radford · J. A. Stanley · S. D. Simpson ·  
A. G. Jeffs

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**Abstract** There is limited knowledge of the orientation cues used by reef fish in their movement among different habitats, especially those cues used during darkness. Although acoustic cues have been found to be important for settlement-stage fish as they seek settlement habitats, only a small number of studies support the possible role of acoustic cues in the orientation of post-settled and adult reef fish. Therefore, the aim of this study was to determine whether habitat-specific acoustic cues were involved in the nocturnal movements of juvenile reef fish to small experimental patch reefs that were broadcasting sound previously recorded from different habitats (Fringing Reef, Lagoon, Silent). Juvenile fish arriving at each patch reef were caught the next morning by divers and were identified. There were a greater number of occasions when juvenile fish (from all species together) moved onto the patch reefs broadcasting Fringing Reef and Lagoon sound (43 and 38%, respectively) compared to Silent reefs (19%) ( $\chi^2 = 33.5$ ;  $P < 0.05$ ). There were significantly more occasions when juvenile fish from the family Nemipteridae were attracted to the patch reefs broadcasting Lagoon sound (63%) versus those reefs broadcasting either Fringing Reef sound (31%) or Silent (6%). In contrast, there were more occasions when juveniles from the family Pomacentridae were attracted to the patch reefs broadcasting Fringing Reef sound (56%) than either Lagoon (24%) or

Silent patch reefs (20%) ( $\chi^2 = 19.5$ ;  $P < 0.05$ ). These results indicate that some juvenile fish use specific habitat sounds to guide their nocturnal movements. Therefore, the fish are able to not only use the directional information contained in acoustic cues, but can also interpret the content of the acoustic signals for relevant habitat information which is then used in their decision-making for orientation.

**Keywords** Habitat selection · Ambient underwater sound · Orientation cues · Coral reef fish · Post-settlement movement · Patch reefs

### Introduction

The guidance mechanisms for juvenile and adult reef fish moving successfully between locations and habitats are not well understood; however, these movements are critically important for effective foraging and breeding, as well as post-settlement dispersal and recruitment into adult habitats (Ogden and Quinn 1984; Cocheret de la Morinière et al. 2002; Odling-Smee et al. 2006). Diurnal reef fish are rarely observed transiting between habitats in open water during the day, although the diel migration between habitats by a wide variety of coral reef fish species is a well-described phenomenon that occurs during crepuscular and night periods (Ogden and Buckman 1973; Ogden and Quinn 1984; Mazeroll and Montgomery 1995, 1998; Kopp et al. 2007). This migration includes many nocturnal reef fish, such as cardinalfishes (Apogonidae) and squirrelfishes (Holocentridae), which forage in habitats away from the reef at night, but return to coral reefs to shelter during daylight hours (Hobson 1965, 1973; Marnane 2000; Kolm et al. 2005). For example, adults of the grey snapper, *Lutjanus griseus*, like many other members of the Lutjanidae, shelter in structurally complex

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C. A. Radford · J. A. Stanley · A. G. Jeffs (✉)  
Leigh Marine Laboratory, University of Auckland,  
PO Box 349, Warkworth 0941, New Zealand  
e-mail: a.jeffs@auckland.ac.nz

S. D. Simpson  
School of Biological Sciences, University of Bristol,  
Woodland Road, Bristol BS8 1UG, UK

habitats such as coral patch reefs, mangroves, boulders, channels and notches during the day, but move out to forage on seagrass beds during the night (Robblee and Zieman 1984; Rooker and Dennis 1991; Nagelkerken et al. 2000; Ouzts and Szedlmayer 2003). In addition to diel migrations, the grey snapper also undertakes seasonal migrations to more distant spawning grounds located at offshore reefs (Sheridan and Hays 2003; Luo et al. 2009). Furthermore, juveniles settle and reside in seagrass bed habitats for up to 10 months before migrating to shelter in more structurally complex habitats during the day (Faunce and Serafy 2007).

The diel migrations from sheltering to feeding habitats tend to occur under low light, or no light conditions, which is thought to reduce the predation risk from visual predators, which are abundant on reef margins (McFarland et al. 1979; Rickel and Genin 2005). In poor ambient light conditions, it is unlikely that visual or celestial cues guide the nocturnal movements of reef fish between habitats, although they may be of some use over relatively short distances (<100 m) when some daylight is present (Montgomery et al. 2006). Therefore, sensory cues that have the potential to operate over longer distances may become important for the orientation of reef fish at night and in poor light conditions. The most important long distance orientation cues are likely to be chemical and acoustic cues that may operate over distances of >100 m, and both types of cue also have the potential to carry information on both the direction and the type of habitat from which they emanate (Kingsford et al. 2002; Montgomery et al. 2006). The low attenuation of sound in water allows acoustic signals to propagate quickly over large distances independent of water movement (Urick 1983). Furthermore, recent research has shown that different habitats in shallow coastal environments can be characterised by the acoustic signals they produce, due to the differences in biological noises generated by the fauna residing in the habitats (Radford et al. 2010; Kennedy et al. 2010). The contribution of snapping shrimp, urchins, fish and other noise-producing organisms varies in different habitats, and these unique acoustic differences between habitats provide the potential for habitat-specific underwater sound to be an effective orientation cue for organisms moving among marine habitats.

Despite the potential value of these habitat-specific orientation cues, there is little direct empirical evidence that reef fish use acoustic and chemical cues to locate or avoid specific habitats. For acoustic cues, the strongest evidence comes from a number of studies that have investigated the behaviour of settlement-stage reef fish and have shown some species orientate towards coral reef sound, presumably to locate suitable sites for settling (Tolimieri et al. 2000, 2002, 2004; Leis et al. 2002; Simpson et al. 2004, 2005, 2008a). Only one study has

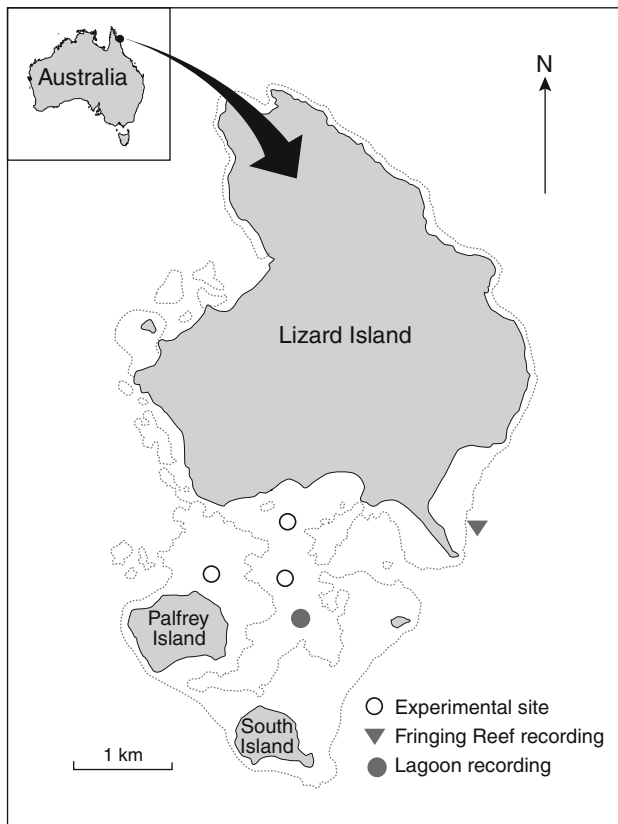
examined the possible role of sound cues for coral reef fish at later life stages moving among benthic habitats, which found that a greater number of juvenile fish species were attracted to small experimental patch reefs where coral reef sound was broadcast overnight, compared to patch reefs without broadcast sound (Simpson et al. 2008b). Also, juvenile apogonids, gobies and pinguipedids were found to be more abundant on the noisy experimental patch reefs. Marked differences were also found in the movement of adult and juvenile fish to patch reefs that were broadcasting coral reef sound that had been filtered into separate low- (<570 Hz) and high-frequency (>570 Hz) components (Simpson et al. 2008b). The authors concluded that these observed differences in fish movements in relation to the high- and low-frequency components of broadcast reef sound could be due to reef fish utilising different acoustic elements to discriminate between different habitat types; however, this possibility was not specifically tested. Therefore, the aim of this current study was to determine whether juvenile reef fish can use habitat-specific acoustic cues to discriminate between habitats whilst making nocturnal movements. For this, the study site on the Great Barrier Reef and methodology already developed by Simpson et al. (2008b) were utilised, but with natural ambient sound recorded from two distinct local habitats being broadcast at the experimental patch reefs.

## Materials and methods

The study was undertaken in the nearshore waters of the Lizard Island Group, which is a complex of small islands and reefs on the mid-shelf, situated 30 km from the Australian mainland and 19 km from the outer barrier reefs that follow the edge of the continental shelf (Fig. 1). The majority of the waters surrounding this island group, including the study site, are in a Marine National Park Zone that excludes fishing activities.

### Habitat sound recordings

During calm conditions over the new moon period of December 2008, underwater recordings were taken from two locations with distinct habitats at Lizard Island; (1) Fringing Reef—a frontal fringing reef offshore from Coconut Beach on the eastern side of Lizard Island and composed of a diverse range of coral species—14°41′ 01.31″S 145°28′ 20.85″E; 2) Lagoon—a lagoon in the centre of the Lizard Island Group with an extensive sandy seafloor well inside of the fringing reefs with the nearest reef >250 m away—14°41′ 29.58″S 145°27′ 27.84″E (Fig. 1). Recordings were taken using remote hydrophone units consisting of a HTI-96-MIN hydrophone connected



**Fig. 1** Location of the study site at Lizard Island, Great Barrier Reef, Australia, showing the location of the Fringing Reef and Lagoon recordings, and the location of the three experimental sites where sets of patch reefs were established

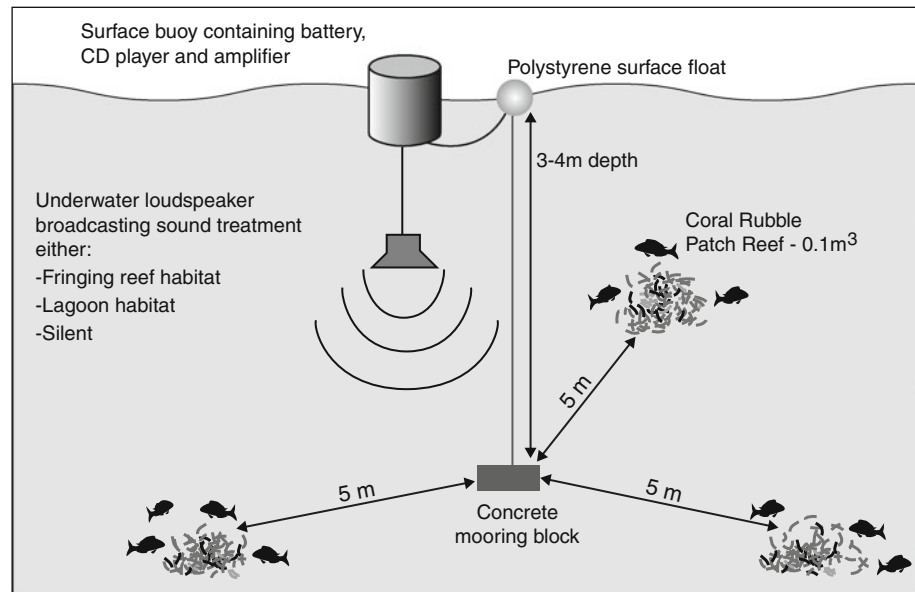
to a digital recorder in an underwater housing (details in Radford et al. 2008a, b) that was programmed to record for 10 min every hour during dusk. A remote hydrophone was installed in 7-m water depth at the Fringing Reef habitat and 12 m in the Lagoon habitat on 1 December 2008 and ran for 3 days. A selection of 4-min segments of the ambient underwater sound that were recorded during dusk for each habitat were transferred to CD and used for subsequent broadcast experiments to prevent pseudoreplication (Slabbekoorn and Bouton 2008). Only recordings that were taken during these periods of calm weather were used to eliminate abiotic underwater sound sources, such as waves crashing onto reefs. One of the 4-min segments was randomly selected for each habitat and transferred to a PC and analysed using Matlab software with spectral analyses codes specifically written for these recordings. Five randomly selected 10-s samples from the 4-min recording were used to produce acoustic power spectra for each habitat using a fast fourier transformation analysis, which was smoothed with an 11-point triangular window. Data were also high pass filtered to 51 Hz to remove any 50-Hz interference and hydrostatic effect caused by surface waves. For each of the five randomly selected subsamples,

the total sound intensity (rms expressed as dB re 1  $\mu$ Pa) was calculated and then used to generate a mean sound intensity.

#### Sound playback experiment

A similar experimental method to that previously deployed by Simpson et al. (2008b) was used that combines artificial patch reefs with broadcast underwater sound to create pseudonatural acoustic and habitat conditions that are suitable for testing the in situ behaviour of nocturnally active fish. During the new moon period of December 2008–January 2009, three sites of a similar depth (3–4 m) on a bare sandy seafloor and each separated by at least 300 m were selected at Lizard Island using information from aerial photographs and scuba surveys to ensure they were located at least 250 m from the nearest established reef habitat (Fig. 1). At each of the three sites, a mooring was deployed consisting of a concrete block with a mooring rope running to a polystyrene surface float (Fig. 2). In an equidistant triangle around the mooring (each 5-m distant from the concrete block), three patch reefs (0.1 m<sup>3</sup> each) were built out of dead coral rubble collected from the edge of a living reef in the same vicinity. The three small patch reefs were used to increase sampling effort whilst avoiding the use of larger patch reefs which can be difficult for divers to clear effectively. The three spatially separated patch reefs also allowed the divers to service all three reefs on a single dive and remain within the multiple dive safety requirements for this research station. For nine consecutive nights commencing on 28 December 2008, an underwater sound system was deployed at each of the three sites by attaching it to the mooring float at dusk, which was at 1650 h (Geoscience Australia—<http://www.ga.gov.au>). Diver observations during the civil twilight period indicated that juvenile fish were arriving at the reefs after nightfall and not during the dusk period. Each identical sound system consisted of a battery, CD player and amplifier housed inside a floating buoy to which an underwater speaker (Lubell Labs Inc., Columbus, OH; LL964, frequency response 0.2–20 kHz) was suspended 2 m underneath. The broadcast sound was of similar composition to the high-quality digital recording used as the input for the sound system (Simpson et al. 2004; Lubell Laboratories 2010; Stanley et al. 2010). Each night one of three different treatments was randomly allocated to each of the three sites so that each site had three nights of each treatment, in order to randomise for any possible effects related to the site itself. The three treatments consisted of a 4-min underwater sound recording played throughout the night of either Fringing Reef habitat or Lagoon habitat, or a Silent system with a blank CD. The Silent treatment was used to control the behaviour of reef

**Fig. 2** Experimental apparatus showing the configuration of the reefs and the underwater sound broadcast equipment that was used at each of the three experimental sites



fish in relation to the experimental apparatus independently of the presence of the broadcast habitat sound. For each night, a different recording taken from each habitat was broadcast to prevent pseudoreplication due to repeatedly using the identical sound sample from a source habitat (Slabbekoorn and Bouton 2008). The broadcast sound levels for Fringing Reef and Lagoon habitat were set to the same level for all habitat recordings (156 dB re 1  $\mu$ Pa at 1 m) by recording the broadcast sound level with a calibrated hydrophone (HTI-96-MIN, flat frequency response 20 Hz–30 kHz) and adjusting the power output on the amplifier of the sound system. Immediately prior to the experiment commencing, the background levels of ambient underwater sound were measured in an area near to the study sites and were found to be peak at 132.4 dB re 1  $\mu$ Pa during dusk and fall off to 126.7 dB re 1  $\mu$ Pa during the night. Therefore, given the broadcast sound levels in this study (156 dB re 1  $\mu$ Pa at 1 m), we would expect this broadcast sound to be audible above ambient background sound levels to juvenile fish in the immediate vicinity of the sound source and the patch reefs, i.e. within 50 m (Simpson et al. 2004). Beyond this, the exact distance that the broadcast sound source would be detectable by juvenile fish depends on their individual hearing abilities, which are poorly described in juvenile reef fish, but are known to vary substantially among species (Kenyon 1996; Wright et al. 2005). Early the following morning, the juvenile fish that had arrived on each patch reef overnight were collected by scuba divers using clove oil anaesthetic and hand nets. The captured fish were photographed with a digital camera against a scale bar for later identification and then released to a location well away from the study site. The size of the captured fish was assessed in relation to existing size

records to ensure that they were established juveniles and not immediate post-larval settlers or adults. A number of settling fish were captured, but were excluded from the analyses.

#### Statistical analyses

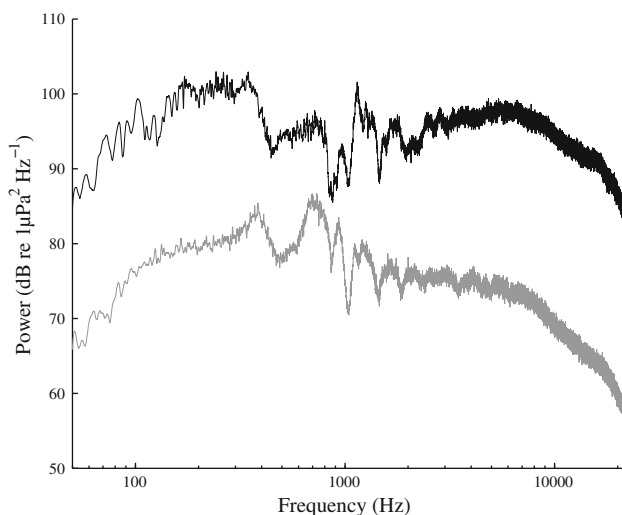
The frequency of different numbers of fish for each species arriving at each patch reef for each night regardless of treatment was calculated and tested against a modelled Poisson distribution to determine the independence of the data, i.e. each individual fish arrived at patch reefs independently of others arriving at the same reef (Zar 1999). These arrival data were not independent ( $\chi^2 = 9.48$ ;  $P < 0.01$ ), as fish were present on patch reefs in groups more often than would be expected by chance, possibly due in part to the innate schooling behaviour of many fish species. Consequently, statistical comparisons between treatments that relied on independence of data could only be made for events, i.e. occasions when one or more individuals of the same species arrived at a patch reef. Chi-square tests were used to determine whether the proportions of fish arrival events were unequal among the three sound treatments (Zar 1999). The frequency of arrival events for each species at every patch reef for every night of each of the three sound treatments was pooled. The data were then pooled again for all species and separately for each family of fish which was represented in the samples. Pooling was necessary to sufficiently increase the size of samples because of the generally small numbers of arrival events on each patch reef each night for an individual species. Chi-square tests were used to compare the distribution of observed and expected frequency of arrival

events. Significant test results were ranked and sequentially tested against serially adjusted significance level, but retaining an overall  $\alpha = 0.05$  until the significance test produced a non-significant result establishing the limit of the significance testing (Holm 1979). This method of Holm-Bonferroni correction of significance protects against cumulative type I error as a result of multiple testing of the same data set.

## Results

### Habitat sound recordings

The mean ambient sound level at the Fringing Reef habitat (144.5 dB re 1  $\mu\text{Pa}$ ) at dusk was significantly higher than the Lagoon habitat (122.4 dB re 1  $\mu\text{Pa}$ ) ( $t = 2.89$ ,  $P < 0.05$ , Fig. 3). The spectral composition of the two habitats was also different, with the greatest difference observed above 500 Hz (Fig. 3). Between 500 and 1,000 Hz, the Fringing Reef habitat had a broader band of sound intensity over 500–800 Hz and a narrow peak at 1,000 Hz, whereas the Lagoon habitat had a sharp rise in sound intensity at 700 Hz and a marked fall in intensity at 1,000 Hz. From 2 to 22 kHz, the Lagoon habitat had a gradual decrease in intensity with increasing frequency, while the Fringing Reef habitat had an increase in intensity from 2 kHz, which peaked at 6 kHz followed by a slow decrease in intensity to 22 kHz. It is in the 2- to 22-kHz bandwidth that there is the greatest difference between the two habitats in the overall sound intensity, i.e. around 30 dB re 1  $\mu\text{Pa}^2\text{Hz}^{-1}$ . Both habitats have a similar spectral composition below 500 Hz, with a peak at 400 Hz then a pronounced drop in intensity at 500 Hz.



**Fig. 3** Spectral composition of the two sound treatments, *Black Line* Fringing Reef; *Grey Line* Lagoon

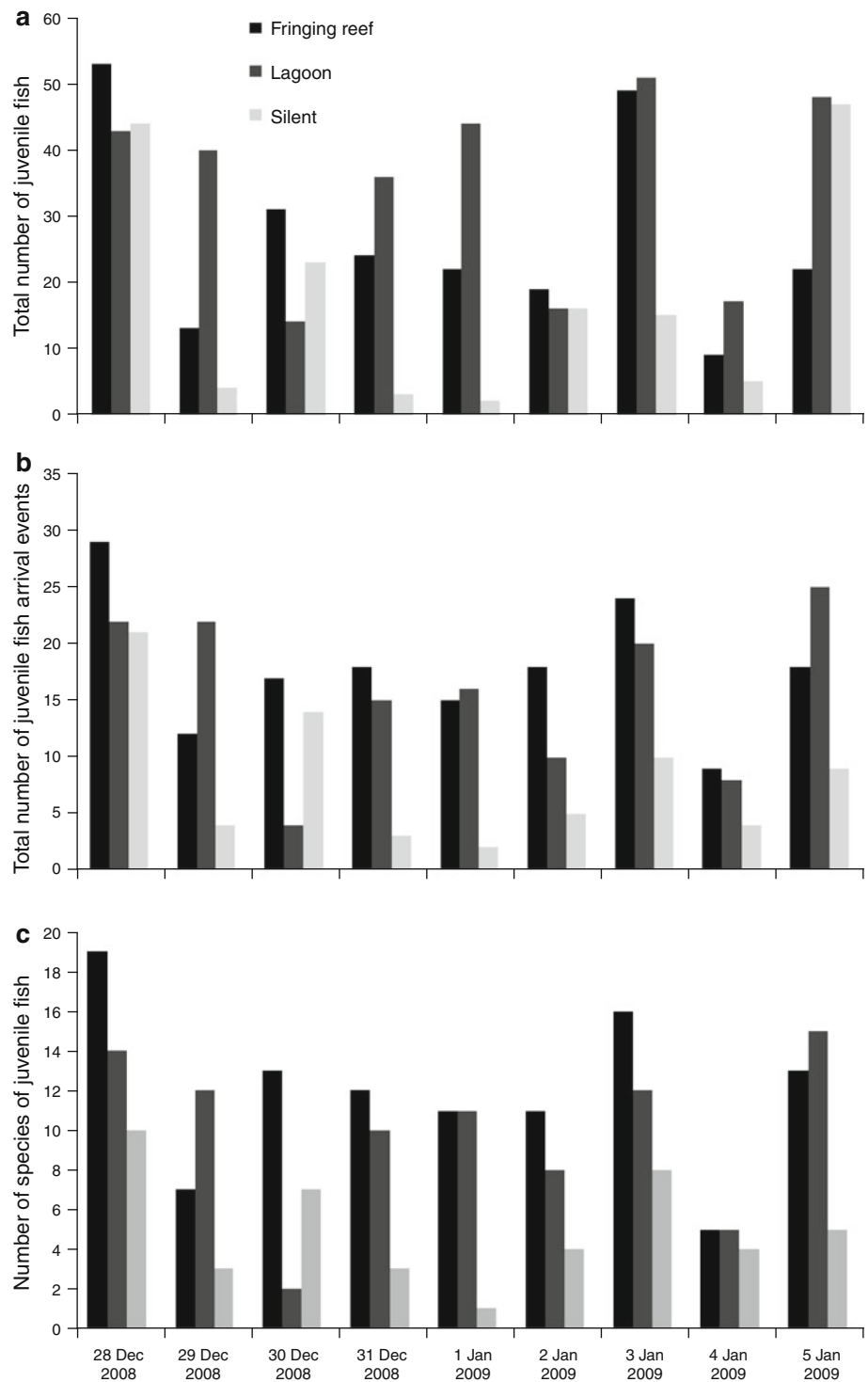
### Sound playback experiment

In total, 714 juvenile fish from 32 different species and 19 families were collected during nine nights of sampling from the patch reefs (Table 1). The overall numbers of juvenile fish that were caught each night across all sites and treatments varied, with total nightly catches ranging from 31 to 140 (Fig. 4a). Sites broadcasting Lagoon sound had the highest catches of the three treatments for 6 out of 9 nights, and sites broadcasting Fringing Reef sound on 3 out of 9 nights. The number of occasions when one or more juveniles of any species arrived at patch reefs was also variable among nights (Fig. 4b). Sites broadcasting Fringing Reef sound had the highest number of occasions when one or more juveniles of any species arrived at patch reefs for 6 out of 9 nights, and sites broadcasting Lagoon sound on 3 out of 9 nights. The number of different species arriving at each site each night varied in general concordance with overall total catches (Fig. 4c). Sites broadcasting Fringing Reef sound attracted the highest variety of species for the night on 5 out of 9 nights, and sites broadcasting Lagoon sound on 2 out of 9 nights, and for the

**Table 1** Summary of numbers of juvenile fish attracted to experimental patch reefs near Lizard Island that were broadcasting either sound from a Fringing Reef habitat or Lagoon habitat, or were silent

Grouping	Fringing reef	Lagoon	Silent	Total
Total number of fish	242	309	163	714
Percentage of total fish	33.9	43.3	22.8	100
Total number of families	18	16	13	19
Total number of species	32	27	15	32
Nemipteridae	32	70	13	115
Pomacentridae	58	29	21	108
Lutjanidae	23	21	30	74
Lethrinidae	14	59	0	73
Apogonidae	9	25	39	73
Acanthuridae	25	15	14	54
Gobiidae	14	28	12	54
Pinguipedidae	10	22	7	39
Scaridae	15	8	5	28
Blenniidae	6	10	10	26
Tetraodontidae	10	5	7	22
Balistidae	5	10	1	16
Serranidae	8	3	2	13
Chaetodontidae	6	1	0	7
Pseudochromidae	1	2	2	5
Siganidae	4	0	0	4
Syngnathidae	0	1	0	1
Labridae	1	0	0	1
Holocentridae	1	0	0	1

**Fig. 4** Catch of juvenile fish at patch reefs with different sound treatments (Fringing Reef, Lagoon, Silent) for individual nights of 28 December 2008–5 January 2009; **a** Total number of juvenile fish caught for each treatment for all three patch reefs within the treatment, **b** Total number of arrival events for juvenile fish at the three individual patch reefs within the treatment, **c** Total number of species for all three patch reefs within the treatment combined



remaining 2 nights, these two sites caught the same number of species.

The greatest total numbers of individuals sampled from all patch reefs for all nights were from the Nemipteridae (115 juvenile fish), followed by the Pomacentridae (108), Lutjanidae (74), Lethrinidae (73) and Apogonidae (73) (Table 1). There was a trend for a greater variety of fish

species to be attracted to the Fringing Reef sound treatment (32), followed by the Lagoon sound treatment (27), with the lowest number of different species arriving at the Silent treatment (15). Likewise, there was a significant difference in the distribution of the unique species among the sound treatments ( $\chi^2 = 15.9$ ;  $P < 0.05$ , Table 2). A unique species was an individual species of fish that was only sampled



**Table 2** Summary of total number of different species, numbers of unique species, and the numbers of events of when juvenile fish from individual species were attracted to an experimental patch reef near Lizard Island that were broadcasting sound either from a Fringing Reef habitat or Lagoon habitat, or were Silent

Grouping	Fringing reef	Lagoon	Silent	Total	$\chi^2$	<i>P</i>	<i>P</i> corrected
Total number of species	32	27	15	32	7.1	0.05	N.S.
Number of unique species	11	2	0	13	15.9	0.001	0.05
All fish species	160	142	72	374	33.5	0.001	0.05
Percentage of all fish species	42.8	38.0	19.3	100			
Pomacentridae	47	20	17	84	19.5	0.001	0.05
Nemipteridae	11	22	2	35	17.2	0.001	0.05
Gobiidae	9	16	9	34			
Acanthuridae	14	8	10	32			
Lutjanidae	11	10	5	26			
Pinguipedidae	9	12	5	26			
Apogonidae	6	12	6	24			
Scaridae	12	7	2	21	7.1	0.05	N.S.
Blenniidae	4	7	6	17			
Lethrinidae	7	9	0	16	8.4	0.05	N.S.
Balistidae	4	9	1	14	7.0	0.05	N.S.
Tetraodontidae	6	3	5	14			
Serranidae	7	3	2	12			
Chaetodontidae	6	1	0	7			
Pseudochromidae	1	2	2	5			
Siganidae	4	0	0	4			
Syngnathidae	0	1	0	1			
Labridae	1	0	0	1			
Holocentridae	1	0	0	1			

*P* corrected values were corrected with the Holm–Bonferroni method to control inflated type I errors resulting from multiple significance testing on the same data set

from one sound treatment over the entire study. Juvenile fish from eleven species were unique to the Fringing Reef sound treatment. This included five species from the Pomacentridae, one species from each of the Chaetodontidae, Labridae, Serranidae, Nemipteridae, Holocentridae and Siganidae. Only two unique species were sampled on reefs with Lagoon sound treatment (Chaetodontidae and Syngnathidae), and no unique species were sampled on the Silent treatment.

Overall, there was a tendency for higher total numbers of juvenile fish to be attracted to patch reefs broadcasting either Lagoon sound (309 fish, 43%) or Fringing Reef sound (242 fish, 34%) compared to Silent reefs (163 fish, 23%) (Table 1). Individual fish did not arrive at the patch reefs independently of conspecifics ( $\chi^2 = 9.48$ ;  $P < 0.01$ ). On 241 occasions, a lone individual of a species was found on a patch reef, regardless of the habitat sound treatment. In contrast, on 71 occasions, a pair of juveniles of the same species was sampled from a patch reef, on 23 occasions three individuals were sampled, and on 39 occasions four or more individuals were sampled from a patch reef. The

largest group of the same species sampled from one patch reef was 34 juvenile apogonids. There was insufficient  $\alpha$  to control for the familywise error rate for statistically examining the independence of arrival for juveniles of all 32 fish species; however, a visual examination of the arrival data suggested that for most species the arrival of individuals was not independent. As a result, statistical comparisons between the sound treatments could only be made for events, i.e. occasions when one or more individuals of the same species arrived at a patch reef. Overall, for all species, there were a greater number of occasions when juvenile fish were attracted onto the patch reefs broadcasting sound; Fringing Reef sound (43%), Lagoon sound (38%) versus Silent reefs (19%) ( $\chi^2 = 33.5$ ;  $P < 0.05$ , Table 2). Also, for the family Nemipteridae, there were significantly more occasions when juvenile fish were attracted to the patch reefs broadcasting Lagoon sound (63%) versus those reefs broadcasting either Fringing Reef sounds (31%) or Silent (6%) ( $\chi^2 = 17.2$ ;  $P < 0.05$ , Table 2). There was a trend for members of the Balistidae to be attracted to the patch reefs broadcasting

Lagoon habitat sound; however, this was not within the level of significance calculated for familywise error (Table 2). In contrast, there were more occasions when juveniles from the family Pomacentridae were attracted to the patch reefs broadcasting Fringing Reef sound (56%) than either Lagoon (24%) or Silent patch reefs (20%) ( $\chi^2 = 19.5$ ;  $P < 0.05$ , Table 2). There was also a trend for members of the Scaridae to be attracted to the patch reefs broadcasting Fringing Reef habitat sound; however, this was not within the level of significance calculated for familywise error (Table 2). Members of the Lethrinidae tended to be attracted to both Fringing Reef and Lagoon habitats, as opposed to Silent habitat but again this trend was not significant (Table 2).

## Discussion

To the authors' knowledge, this study provides the first evidence that fish can discriminate sounds originating from different habitats. For all species combined, there were a greater number of occasions when juvenile fish were attracted onto the experimental patch reefs broadcasting Fringing Reef or Lagoon sound versus the Silent patch reefs. However, there were differences in the composition of juvenile fish attracted to patch reefs broadcasting Fringing Reef versus Lagoon sound. The juveniles of the second most sampled family Pomacentridae showed a marked nocturnal preference for Fringing Reef sound. The juveniles of species from this family are known to be strongly associated with coral reef and hard-bottom habitats (<http://www.fishbase.org>; Mellin et al. 2007). In addition, the Fringing Reef sound treatment tended to attract a greater variety of species and significantly more unique species than the Lagoon or Silent sound treatments. This included members of the Pomacentridae, Chaetodontidae, Holocentridae, Serranidae, Nemipteridae, Labridae and Siganidae. The juveniles of the species from these families mostly tend to be associated with coral reef habitats (<http://www.fishbase.org>; Choat and Bellwood 1991; Williams 1991; Mellin et al. 2007). For example, juvenile yellow-tail demoiselle, *Neopomacentrus azysron*, was unique to patch reefs broadcasting Fringing Reef sound, and this species usually dwells on outer reef slopes and frequently in the deeper surge channels or adjacent ledges (<http://www.fishbase.org>). Experimental patch reefs broadcasting Lagoon habitat sound tended to attract more juvenile fish than Fringing Reef or Silent sound treatments; however, this trend could not be statistically examined because fish were arriving at patch reefs in groups and were therefore not independent. However, for the family Nemipteridae, there were significantly more occasions when juvenile fish were attracted to the patch reefs

broadcasting Lagoon sound versus those reefs broadcasting either Fringing Reef sounds or Silent. Juveniles and adults of species in the Nemipteridae are strongly associated with Lagoon habitats as juveniles (<http://www.fishbase.org>; Choat and Bellwood 1991; Williams 1991). For example, juveniles of the bridled monocle bream, *Scolopsis affinis*, are solitary and tend to inhabit sheltered lagoons on sandy or muddy bottoms close to reefs (<http://www.fishbase.org>). Overall, these results are congruent with what might be expected, given the differences in the numbers of fish species found in these two natural habitats associated with coral reef environments (Roberts and Ormond 1987; Williams 1991; Brokovich et al. 2006; Knudby et al. 2010). Silent experimental patch reefs consistently had lower catches of juvenile fish than either the Fringing Reef or Lagoon sound treatments, despite having ambient background noise that was consistent with a natural Lagoon habitat. The reasons for this are not clear, but it must be related to the existence of the broadcast sound because the presence of the experimental equipment has been controlled for. It could be that the sound level used in this study, which was intended to be higher than ambient natural noise, had a wider influence in attracting juvenile fish.

The vast majority of the fish that were caught on the experimental patch reefs broadcasting sound were hearing generalists, including members of the two families, Nemipteridae and Pomacentridae, which showed significant responses to broadcast habitat sound in this current study. For some of these species such as members of the Pomacentridae, there is evidence from measurements of hearing thresholds that their hearing sensitivity is relatively low (Egner and Mann 2005; Wright et al. 2005). Regardless, juveniles of these species appear to have the capability to receive and interpret the composition of the sound that provides information on habitat.

Previous research has shown that some juvenile and adult coral reef fish will preferentially relocate to experimental patch reefs broadcasting sound from coral reef habitat versus patch reefs without broadcast sound (Simpson et al. 2008b). Furthermore, this previous study also found that broadcasting the high- (>570 Hz) and low- (<570 Hz) frequency components of coral reef habitat sound attracted different groups of fish species to the experimental patch reefs. Broadcasting the low-frequency component of coral reef sound tended to attract more adult fish from the Gobiidae and Blenniidae, as well as juveniles from the Apogonidae, whilst the high-frequency component attracted more juveniles from both the Gobiidae and Acanthuridae (Simpson et al. 2008b). The differences in these results may help to provide some initial insight into the component of habitat-specific sounds that fish are using to discriminate between different habitats. Different temperate reef habitat types have been shown to have distinctive



underwater sound signatures that vary not only in their overall spectral composition, but also in their overall sound intensity, as well as temporal differences in sound composition at a wide range of time scales (from milliseconds to months), that often reflect the patterns of acoustic activity of species resident in the habitats (Radford et al. 2008a, b, 2010). For example, one type of rocky reef habitat in New Zealand was characterised by greater sound intensity in the 800- to 2,500-Hz frequency band during dusk and the evening due to the abundance and feeding activity of the urchin, *Evechinus chloroticus*, within the habitat (Radford et al. 2008a, b).

The present research replayed two recorded habitat sounds, Fringing Reef and Lagoon, which could be distinguished by some fish species. Analyses of recordings of the Fringing Reef sound showed the majority of the acoustic energy was in two distinct bandwidths, 150–400 Hz and 2.5–8 kHz, whereas the Lagoon sound had two peaks of intensity at 400 and 700 Hz. It could be that some fish are distinguishing and orientating to habitats on the basis of the divergence in the gross spectral composition of the habitat sound signatures, which is known as ‘soundscape orientation’ and has been observed in other animal groups, such as frogs and birds (Bogert 1960; Sinsch 2006; Slabbekoorn and Bouton 2008). This may help to explain the differences in the suite of fish species attracted to experimental patch reefs when low- and high-frequency components of coral reef habitat sound were broadcast (Simpson et al. 2008b). In coral reef habitats, the sounds produced by fish are known to dominate the lower frequencies (>700 Hz), with members of the Holocentridae and Pomacentridae producing popping sounds at 400–700 Hz and 350–1,000 Hz, respectively (Myrberg et al. 1986, 1993; Kenyon 1994; Mann and Lobel 1997, 1998; Myrberg 1997; McCauley and Cato 2000). In contrast, the higher frequencies (2.5–15 kHz) are dominated by invertebrate noises, especially the most ubiquitous sound-producing organism in the world’s oceans, snapping shrimp (Fish 1964; Cato 1992; Au and Banks 1998; Versluis et al. 2000; Cato and McCauley 2002; Radford et al. 2010). Alternatively, it could be that some fish are distinguishing and orientating to habitats on the basis of distinctive conspecific or heterospecific acoustic signals, a phenomenon that has also been identified in birds and amphibians (Mönkkönen et al. 1990; Mönkkönen and Forsman 2002; Diego-Rasilla and Luengo 2004, 2007; Fletcher 2007).

Our results suggest that members of some key families of fish are using acoustic orientation to distinguish between habitats in the coral reef environment. This finding raises important management and conservation issues for coral reefs because of rapidly increasing underwater sound pollution, mainly due to increased shipping, but now also due to the increasing development of renewable coastal energy generation, i.e. wind, wave, tidal generation (Jasny 1999;

Jasny et al. 2005; Wahlberg and Westerberg 2005; Madsen et al. 2006). A recent review of the response of animals to acoustic pollution revealed a range of common biological impacts across a wide range of taxa, including interference with acoustic orientation and communication (Laiolo 2010). It has been suggested that the broadcasting of artificial sources of natural underwater sound could be used as a conservation tool for attracting fish in order to restore depleted coral reef habitats (Simpson et al. 2008b); however, a lack of understanding of fish behaviour in relation to underwater acoustic cues may result in unintended outcomes at the community level, as has been shown in avian examples (Fletcher 2008). Therefore, the research challenge now is to distinguish the acoustic orientation cues used by fish for orientation and to identify the breadth of their behavioural and ecological significance.

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## References

- Au WL, Banks K (1998) The acoustics of the snapping shrimp *Synalpheus parneomeris* in Kaneohe Bay. *J Acoust Soc Am* 103:41–44
- Bogert CM (1960) The influence of sounds on the behaviour of amphibians and reptiles. In: Lanyon WE, Tavolga WN (eds) *Animal sounds and communication*. American Institute of Biological Sciences, Washington, D.C., pp 137–320
- Brokovich E, Baranes A, Goren M (2006) Habitat structure determines coral reef fish assemblages at the northern tip of the Red Sea. *Ecological Indicators* 6:494–507
- Cato DH (1992) The biological contribution to the ambient noise in waters near Australia. *Acoust Aust* 20:76–80
- Cato DH, McCauley RD (2002) Australian research in ambient sea noise. *Acoust Aust* 30:13–20
- Choat JH, Bellwood DR (1991) Reef fishes: their history and evolution. In: Sale PF (ed) *The ecology of fishes on coral reefs*. Academic Press, San Diego, pp 39–68
- Cocheret de la Morinière E, Pollux BJA, Nagelkerken I, van der Veldef G (2002) Post-settlement life cycle migration patterns and habitat preference of coral reef fish that use seagrass and mangrove habitats as nurseries. *Estuar Coast Shelf Sci* 55:309–321
- Diego-Rasilla FJ, Luengo RM (2004) Heterospecific call recognition and phonotaxis in the orientation of the marbled newt, *Triturus marmoratus*. *Behav Ecol Sociobiol* 55:556–560
- Diego-Rasilla FJ, Luengo RM (2007) Acoustic orientation in the palmate newt, *Lissotriton helveticus*. *Behav Ecol Sociobiol* 61: 1329–1335
- Egner SA, Mann DA (2005) Auditory sensitivity of sergeant major damselfish *Abudefduf saxatilis* from post-settlement juvenile to adult. *Mar Ecol Prog Ser* 285:213–222

- Faunce CH, Serafy JE (2007) Nearshore habitat use by gray snapper (*Lutjanus griseus*) and bluestriped grunt (*Haemulon sciurus*): environmental gradients and ontogenetic shifts. *Bull Mar Sci* 80:473–495
- Fish MP (1964) Biological sources of sustained ambient sea noise. In: Tavolga WN (ed) *Marine bio-acoustics*. Pergamon Press, New York, pp 175–194
- Fletcher RJ (2007) Species interactions and population density mediate the use of social cues for habitat selection. *J Anim Ecol* 76:598–606
- Fletcher RJ (2008) Social information and community dynamics: nontarget effects from simulating social cues for management. *Ecol Appl* 18:1764–1773
- Hobson ES (1965) Diurnal-nocturnal activity of some inshore fishes in the Gulf of California. *Copeia* 1965:291–302
- Hobson ES (1973) Diel feeding migrations in tropical reef fishes. *Helgol Wiss Meeresunters* 24:361–370
- Holm S (1979) A simple sequentially rejective multiple test procedure. *Scand J Stat* 6:65–70
- Jasny M (1999) *Sounding the depths: supertankers, sonar, and the rise of undersea noise*. Natural Resources Defense Council, New York
- Jasny M, Reynolds J, Horowitz C, Wetzler A (2005) *Sounding the depths II: the rising toll of sonar, shipping, and industrial ocean noise on marine life*. Natural Resources Defense Council, New York
- Kennedy EV, Guzman HM, Holderied MW, Mair JM, Simpson SD (2010) Reef-generated noise provides reliable information about habitats and communities: evidence from a Panamanian case study. *J Exp Mar Biol Ecol* 395:85–92
- Kenyon TN (1994) The significance of sound interception to males of the bicolor damselfish, *Pomacentrus partitus*, during courtship. *Environ Biol Fish* 40:391–405
- Kenyon TN (1996) Ontogenetic changes in the auditory sensitivity of damselfishes (Pomacentridae). *J Comp Physiol A* 179:553–561
- Kingsford MJ, Leis JM, Shanks A, Lindeman KC, Morgan SG, Pineda J (2002) Sensory environments, larval abilities and local self recruitment. *Bull Mar Sci* 70:309–340
- Knudby A, LeDrew E, Brenning A (2010) Predictive mapping of reef fish species richness, diversity and biomass in Zanzibar using IKONOS imagery and machine-learning techniques. *Remote Sens Environ* 114:1230–1241
- Kolm N, Hoffman EA, Olsson J, Berglund A, Jones AG (2005) Group stability and homing behavior but no kin group structures in a coral reef fish. *Behav Ecol* 16:521–527
- Kopp D, Bouchon-Navaro Y, Louis M, Bouchon C (2007) Diel differences in the seagrass fish assemblages of a Caribbean island in relation to adjacent habitat types. *Aquat Bot* 87:31–37
- Laiolo P (2010) The emerging significance of bioacoustics in animal species conservation. *Biol Conserv*. doi:10.1016/j.biocon.2010.03.025
- Leis JM, Carson-Ewart BM, Cato DH (2002) Sound detection in situ by the larvae of a coral-reef damselfish (Pomacentridae). *Mar Ecol Prog Ser* 232:259–268
- Lubell Laboratories (2010) Lubell Laboratories LL9642T underwater acoustic transducer—specifications and operation manual. Lubell Laboratories, Columbus, Ohio
- Luo J, Serafy JE, Sponaugle S, Teare PB, Kieckbusch D (2009) Movement of gray snapper *Lutjanus griseus* among subtropical seagrass, mangrove, and coral reef habitats. *Mar Ecol Prog Ser* 380:255–269
- Madsen PT, Wahlberg M, Tougaard J, Lucke K, Tyack P (2006) Wind turbine underwater noise and marine mammals: Implications of current knowledge and data needs. *Mar Ecol Prog Ser* 309:279–295
- Mann DA, Lobel PS (1997) Propagation of damselfish (Pomacentridae) courtship sounds. *J Acoust Soc Am* 101:3783–3791
- Mann DA, Lobel PS (1998) Acoustic behavior of the damselfish *Dascyllus albisella*: behavioral and geographic variation. *Environ Biol Fish* 51:421–428
- Marnane MJ (2000) Site fidelity and homing behaviour in coral reef cardinalfishes. *J Fish Biol* 57:1590–1600
- Mazeroll AI, Montgomery WL (1995) Structure and organisation of local migrations in brown surgeonfish (*Acanthurus nigrofuscus*). *Ethology* 99:89–106
- Mazeroll AI, Montgomery WL (1998) Daily migrations of a coral reef fish in the Red Sea (Gulf of Aqaba, Israel): initiation and orientation. *Copeia* 4:893–905
- McCauley RD, Cato DH (2000) Patterns of fish calling in a nearshore environment in the Great Barrier Reef. *Philos Trans R Soc Lond B* 355:1289–1293
- McFarland WN, Ogden JC, Lythgoe JN (1979) The influence of light on the twilight migrations of grunts. *Environ Biol Fish* 4:9–22
- Mellin C, Kulbicki M, Ponton D (2007) Seasonal and ontogenetic patterns of habitat use in coral reef fish juveniles. *Estuar Coast Shelf Sci* 75:481–491
- Mönkkönen M, Forsman JT (2002) Heterospecific attraction among forest birds: a review. *Ornith Sci* 1:41–51
- Mönkkönen M, Helle P, Soppela K (1990) Numerical and behavioural responses of migrant passerines to experimental manipulation of resident tits (*Parus* spp.): heterospecific attraction in northern breeding bird communities? *Oecologia* 85:218–225
- Montgomery JC, Jeffs AG, Simpson SD, Meekan MG, Tindle CT (2006) Sound as an orientation cue for the pelagic larvae of reef fish and crustaceans. *Adv Mar Biol* 51:143–196
- Myrberg AA (1997) Sound production by a coral reef fish (*Pomacentrus partitus*): evidence for a vocal, territorial “keep-out” signal. *Bull Mar Sci* 60:1017–1025
- Myrberg AA, Mohler M, Catala JD (1986) Sound production by males of a coral reef fish (*Pomacentrus partitus*): its significance to females. *Anim Behav* 34:913–923
- Myrberg AA, Ha SJ, Shablott MJ (1993) The sounds of bicolor damselfish (*Pomacentrus partitus*): predictors of body size and a spectral basis for individual recognition and assessment. *J Acoust Soc Am* 94:3067–3070
- Nagelkerken I, Dorenbosch M, Verberk WCEP, Cocheret de la Morinière E, van der Velde G (2000) Day-night shifts of fishes between shallow-water biotopes of a Caribbean bay, with emphasis on the nocturnal feeding of Haemulidae and Lutjanidae. *Mar Ecol Prog Ser* 194:55–64
- Odling-Smee L, Simpson SD, Braithwaite VA (2006) The role of learning in fish orientation. In: Brown C, Laland K, Krause J (eds) *Fish cognition and behavior*. Blackwell Publishing, Oxford, pp 119–138
- Ogden JC, Buckman NS (1973) Movements, foraging groups, and diurnal migrations of the striped parrotfish *Scarus croicensis* Bloch (Scaridae). *Ecology* 54:589–596
- Ogden JC, Quinn TP (1984) Migration in coral reef fishes: ecological significance and orientation mechanisms. In: McCleave JD, Arnold GP, Dodson JJ, Neill WH (eds) *Mechanisms of migration in fishes*. Plenum Press, New York, pp 293–308
- Ouzts AC, Szedlmayer ST (2003) Diel feeding patterns of red snapper on artificial reefs in the north-central Gulf of Mexico. *Trans Am Fish Soc* 132:1186–1193
- Radford CA, Jeffs AG, Tindle CT, Montgomery JC (2008a) Resonating sea urchin skeletons create coastal choruses. *Mar Ecol Prog Ser* 362:37–43
- Radford CA, Jeffs AG, Tindle CT, Montgomery JC (2008b) Temporal patterns in ambient noise of biological origin from a shallow water temperate reef. *Oecologia* 156:921–929

- Radford CA, Stanley J, Tindle CT, Montgomery JC, Jeffs AG (2010) Localised coastal habitats have distinct underwater sound signature. *Mar Ecol Prog Ser* 401:21–29
- Rickel S, Genin A (2005) Twilight transitions in coral reef fish: the input of light-induced changes in foraging behaviour. *Anim Behav* 70:133–144
- Robblee MB, Zieman JC (1984) Diel variation in the fish fauna of a tropical seagrass feeding ground. *Bull Mar Sci* 34:335–345
- Roberts CM, Ormond RFG (1987) Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. *Mar Ecol Prog Ser* 41:1–8
- Rooker JR, Dennis GD (1991) Diel, lunar and seasonal changes in a mangrove fish assemblage off southwestern Puerto Rico. *Bull Mar Sci* 49:684–698
- Sheridan P, Hays C (2003) Are mangroves nursery habitat for transient fishes and decapods? *Wetlands* 23:449–458
- Simpson SD, Meekan MG, McCauley RD, Jeffs AG (2004) Attraction of settlement-stage coral reef fishes to reef noise. *Mar Ecol Prog Ser* 276:263–268
- Simpson SD, Meekan MG, Montgomery JC, McCauley RD, Jeffs AG (2005) Homeward sound. *Science* 308:221
- Simpson SD, Meekan MG, Jeffs AG, Montgomery JC, McCauley RD (2008a) Settlement-stage coral reef fishes prefer the higher frequency invertebrate-generated audible component of reef noise. *Anim Behav* 75:1861–1868
- Simpson SD, Jeffs AG, Montgomery JC, McCauley RD, Meekan MG (2008b) Nocturnal relocation of adult and juvenile coral reef fishes in response to reef noise. *Coral Reefs* 27:97–104
- Sinsch U (2006) Orientation and navigation in Amphibia. *Mar Freshw Behav Physiol* 39:65–71
- Slabbekoorn H, Bouton N (2008) Soundscape orientation: a new field in need of sound investigation. *Anim Behav* 76:e5–e8
- Stanley JA, Radford CA, Jeffs AG (2010) Induction of settlement in crab megalopae by ambient underwater reef sound. *Behav Ecol* 21:113–120
- Tolimieri N, Jeffs AG, Montgomery JC (2000) Ambient sound as a cue for navigation by the pelagic larvae of reef fishes. *Mar Ecol Prog Ser* 207:219–224
- Tolimieri N, Haine O, Montgomery JC, Jeffs AG (2002) Ambient sound as a navigational cue for larval reef fish. *Bioacoustics* 12:214–217
- Tolimieri N, Haine O, Jeffs AG, McCauley R, Montgomery JC (2004) Directional orientation of pomacentrid larvae to ambient reef sounds. *Coral Reefs* 23:184–191
- Urick RJ (1983) Principles of underwater sound. McGraw-Hill, New York
- Versluis M, Schmitz B, von der Heydt A, Lohse D (2000) How snapping shrimp snap: through cavitating bubbles. *Science* 289:2114–2117
- Wahlberg M, Westerberg H (2005) Hearing in fish and their reactions to sounds from offshore wind farms. *Mar Ecol Prog Ser* 288:295–309
- Williams DM (1991) Patterns and processes in the distribution of coral reef fishes. In: Sale PF (ed) *The ecology of fishes on coral reefs*. Academic Press, San Diego, pp 437–474
- Wright KJ, Higgs DM, Belanger AJ, Leis JM (2005) Auditory and olfactory abilities of pre-settlement larvae and post-settlement juveniles of a coral reef damselfish (Pisces: Pomacentridae). *Mar Biol* 147:1425–1434
- Zar JH (1999) Biostatistical analysis. Prentice-Hall, Upper Saddle River