Adjacent coral reef habitats produce different underwater sound signatures

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ABSTRACT: The underwater sound generated by the organisms on a reef has been shown to provide an important orientation cue for a wide range of larval, juvenile and adult marine organisms. There is some preliminary evidence that some organisms can discriminate among different benthic habitats using sound cues over relatively short spatial ranges (i.e. within hundreds of metres); however, the divergence in the sound emitted from different habitats, often in close proximity to one another, is poorly described. Therefore, the sound emitted from single locations within 3 adjacent habitats, Fringing Reef, Back Reef and Lagoon, at Lizard Island on the Great Barrier Reef, Australia, were recorded during the new moon phase in early summer. Analyses of the sound recordings revealed differences among these 3 habitats in the temporal and frequency composition and in sound levels. Most of the spectral variability among the 3 habitats was observed below 800 Hz, where the duration of the dusk chorus differed between the 3 habitats. Some of these observed differences were due to the acoustic output of some key soniferous organisms dwelling in these habitats, especially snapping shrimp and fish species producing a pop sound. It is possible that these habitat-related differences in underwater sound are being used to remotely guide the movement of coastal organisms in relation to these habitats.

KEY WORDS: Reef sound · Fish sound · Habitat · Great Barrier Reef · Acoustic orientation

INTRODUCTION

Ambient underwater sound in the sea is composed of a combination of biotic and abiotic acoustic sources (Acosta et al. 1997, Cato & McCauley 2002). Abiotic sources of ambient underwater sound in the nearshore environment are mostly due to the effect of the wind and waves, and tend to produce sound of frequencies above 150 Hz. In contrast, sound from biotic sources covers a wide range of frequencies and is generated by a variety of marine life involved in activities such as feeding, reproductive displays, territorial defence and echolocation (Knudson et al. 1948, Tait 1962, Wenz 1962, Cato 1978, 1992, McCauley & Cato 2000, Radford et al. 2008a,b).

The fact that ambient underwater sound varies among locations in the marine environment has been known for many years (Urick 1983). For example, the spatial variability of underwater sound due to surf and ice movement (Wilson et al. 1985, Yang et al. 1987, Deane 2000) has been described, but there are limited data describing the acoustic environment in shallow-water coastal environments in tropical or temperate waters (Kennedy et al. 2010, Radford et al. 2010, Staaterman et al. 2013). Only 2 published studies have examined differences in the underwater acoustic environment in shallow coastal waters over small spatial scales (within kilometres) in typical temperate (Radford et al. 2010) and tropical reefs and associated habitats (Kennedy et al. 2010). Marked differences were found over relatively short spatial scales in the spectral and temporal composition of ambient sound associated with different coastal habitat types along a coastline in the temperate waters of New Zealand (Radford et al. 2010). Similarly, the frequency characteristics of the daytime sound pro-
duced by tropical reefs around a small island group were found to be closely associated with the number of fish present, as well as coral and benthic diversity (Kennedy et al. 2010).

Previous studies have also shown that sound produced by reefs exhibits marked temporal changes in acoustic characteristics, especially from dusk until dawn, when a wide range of nocturnal marine organisms is emergent (Cato 1978, McCauley & Cato 2000). For example, many of the differences in the sound produced by different habitats on a temperate coast become more apparent at dusk compared with at noon, and with overall sound levels most often being at their lowest when the sun is at its height during the day (Radford et al. 2010).

Underwater sound is emerging as an important environmental parameter for influencing the spatial distribution of many groups of animals around reefs. For example, a wide range of nocturnally active pelagic crustacean taxa, including copepods, ostracods, mysids, caridean shrimp, gammarid and hyperiid amphipods actively avoid replayed coral reef sound, presumably due to the increasing risk of predation with closer proximity to a reef (Simpson et al. 2011). Also, differences in underwater sound that appear to be associated with habitat influence the nocturnal movements of juvenile and adult fish in a tropical reef environment (Simpson et al. 2008a, Radford et al. 2011). Perhaps most importantly, ambient underwater sound also appears to be guiding a wide range of pelagic larval reef fish and invertebrates to settlement habitats on coastal reefs, and triggering behavioural and morphological changes associated with settlement (Tolimieri et al. 2000, 2002, 2004, Jeffs et al. 2003, Simpson et al. 2004, 2005, 2008a,b, 2011, Montgomery et al. 2006, Radford et al. 2007, Stanley et al. 2010, 2012, Vermeij et al. 2010, Holles et al. 2013). For example, Simpson et al. (2005) showed that the nocturnal settlement of different species of larval fish on experimental patch reefs was affected by the presence and frequency range of underwater sound broadcast from these reefs. Likewise, the behaviour and morphological changes required for settlement of pelagic megalopae of a number of reef-dwelling crab species are significantly expedited when they are exposed to underwater reef sound (Stanley et al. 2010). Furthermore, the settlement response of pelagic megalopae of some reef-dwelling crabs appears to be ‘tuned’ to sounds emanating from preferred benthic settlement habitats (Stanley et al. 2010).

While the overall extent to which reef sound influences the scale of the natural settlement of reef organisms is unknown, it is possible that spatial variation in ambient underwater sound could be an important contributor to the large amount of spatial variability observed in larval settlement and recruitment (Doherty 1991, Caselle & Warner 1996). It would be advantageous for pelagic larval settlers to be able to remotely detect and respond to differences in underwater sound if the sound reliably represented differences in the coastal settlement habitat at the sound source. Radford et al. (2010) provide the only published evidence that identifiably different nocturnal sounds are produced by different habitats that could be encountered over the active swimming range of a nocturnally active settling larval reef fish (i.e. kilometers; Stobutzki & Bellwood 1994, Stobutzki 1998). However, this previous study was undertaken in temperate coastal waters.

While there have been a few previous studies of spatial variation in ambient underwater sound in shallow tropical waters (as noted above), none to our knowledge have determined whether tropical coastal habitats on the spatial scale encountered by a larval settler (i.e. kilometres) are producing distinct sounds, especially at night, when larval settlers are active in the water column and seeking out suitable settlement habitats. Therefore, the aim of the present study was to describe the spatial differences in underwater sound emanating from a typical coral reef environment that a larval settler may encounter during migration to appropriate settlement habitat. Specifically, we determined the temporal variability, spectral composition and differences in noise-producing animals at a single location within 3 habitats, coral reef, back reef and lagoon.

**MATERIALS AND METHODS**

### Study site and recording

To assess the spatial variation and habitat differences in ambient underwater sound, recordings were made at a single location within 3 different habitats during a new moon period (3 d either side of the new moon—a total of 2 full recording days) in summer (December 2008) around Lizard Island, a small midshelf island group on the Great Barrier Reef, Australia (Fig. 1). The habitats consisted of: (1) Fringing Reef, at Coconut Beach, which has an extensive fringing reef on the seaward side of Lizard Island, with a sandy/reef interface, (2) Back Reef, which is a series of small isolated patch reefs on the leeward side of Lizard Island, with sand separating each reef, and (3) Lagoon, an ex-
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A remote recording system was fixed 1 m off the sandy seafloor in 5−6 m of water depth for Fringing Reef and Back Reef, and 1 m off the sandy seafloor at 12−13 m depth for the Lagoon at low water spring tide. The recording hydrophone was a calibrated High Tech Inc. HTI96-MIN omnidirectional hydrophone (10 Hz−30 kHz flat response) connected to an automated recording system contained in an underwater housing. The system had a Unidata Micrologger timing and relay unit operating a Sony TCD-D8 digital recorder with a sampling rate of 48 kHz, which took a 5 min recording every hour, on the hour. The digital recordings were transferred to a PC and analysed using MATLAB software with codes specifically written for these recordings. No extraneous anthropogenic sources of underwater noise, such as ships, power boats or nearby coastal building activities, were present in the recordings. All recordings were conducted in calm or near-calm conditions (<10 km h⁻¹ wind speed, 0.25 m wave height).

Each 5 min recording was examined for uniformity, and then acoustic power spectra were generated by analyses of 5 randomly selected 30 s sub-samples of the 5 min recording. Data were band-pass filtered (100−20000 Hz) to remove any effect of surface waves. To compare the distribution of acoustic energy throughout time and between the 3 sites, the 30 s band filtered spectral data were compiled into 100 Hz bins.

Octave analysis

Octave analyses were used to analyse the frequency composition of fish vocalisation in relation to background habitat sound. Only the most dominant category of fish vocalisation present in the recordings, known as a ‘pop’, was selected for analyses because there were numerous types of fish vocalisation present in the recordings. Pop sounds have previously been found to be a dominant fish call in underwater recordings on the Great Barrier Reef and consist of a single pulse lasting for <10 ms with the dominant frequency of 400−700 Hz due to swim bladder resonance (McCauley & Cato 2000). Due to the inconsistency of fish-to-hydrophone distances, comparison of the relative rather than absolute sound level amongst octave bands were considered for all vocalisations pooled across time of day. By measuring sound power in respective octave bands (octave band level; dB re 1 µPa), the spectral contribution of fish vocalisation to the overall habitat sound can be evaluated. The octave analyses are also useful for gauging the audibility of a sound/signal in the presence of ambient background sound within octave bands because masking of sound occurs within and not between octave bands (Clark et al. 2009). Sounds from the temporal recordings from the 3 habitats were separated into 5 octave bands (i.e. nominally bands 1−5 with their centre frequencies [Fₜ] at 125, 250, 500, 1000 and 2000 Hz, respectively) with MATLAB using digital octave band filters. These bands were selected because they corresponded to the frequency range (bandwidth) of the majority of fish vocalisations. Although the precise bandwidths of the auditory filters for fish are unknown, they have been reported as being slightly larger than those found in other vertebrates (one-third octave band filters) (Fay 1988) and are approximated by the octave band filter banks. Therefore,
representing noise in octave bands was considered more meaningful and suitable to gauge audibility of a signal in the presence of other background noise. For each habitat, the octave band levels $\text{rms}$ of 10 sound segments containing an individual fish vocalisation (i.e. a ‘pop’) (also including background habitat sound) were measured from averaging the time equal to the duration of the vocalisation (approximately 10 ms). Next, the octave band levels of sound samples containing only background ambient sound of a similar duration were sampled either before or after the fish call from the same recording. The difference in sound levels between these 2 sound samples was measured for each octave band and then compared. The differences in sound levels amongst octave bands were compared using Kruskal-Wallis tests within each habitat for sampled sound, both with and without fish vocalisation present. Where significant differences were identified, Dunn’s multiple comparison tests were used to identify which octave bands were significantly different.

**Snapping shrimp**

For the noon (12:00 h) and dusk (18:00 h) 5 min recordings, 5 randomly selected 30 s sub-samples were taken and the number of snaps produced by snapping shrimp was estimated by setting a threshold level on the raw data and any transient spike that was of $<0.2$ s duration and above a preset threshold level was counted as a snap by a shrimp. Preliminary manual analyses confirmed that this automated method, run in MATLAB, provided a reliable count of snapping shrimp snaps ($\pm 15$ snaps per minute). The mean number of snaps for each recording site was compared with a 2-way ANOVA after assumptions of data normality and heterogeneity of variance had been confirmed. The ANOVA enabled comparisons to be made among time of day (noon and dusk) and site. Significant differences between individual pairs of means were determined using Tukey’s tests (Zar 1999). All data were analysed using SAS and are presented as statistical means $\pm$ SEM.

**RESULTS**

**Spectra**

The temporal patterns seen at the 3 sites on Lizard Island are typical of underwater bioacoustic activity (Fig. 2). At sunset, there were significant increases in acoustic energy between 100 and 800 Hz, which lasted for a few hours and is typical of chorusing of fish at dusk. During the night there was also a rise in acoustic energy between 2 and 20 kHz, which can be attributed to snapping shrimp activity. However, the duration of these choruses varied between the 3 sites, with the Lagoon site having a shorter in duration and lower in frequency chorus than the Fringing Reef. There was an unusual pattern observed in acoustic energy: at 980, 1200 and 1800 Hz there were decreases in acoustic energy, which was similar between the 3 sites. The main difference between the 3 sites was sound intensity, with the Fringing Reef (Coconut Beach) being typically 2–5 dB louder during the same time of day compared with the other 2 sites (Lagoon and Back Reef). The Lagoon site also had a higher intensity dusk chorus compared with Back Reef. However, the snapping shrimp frequency band (2–20 kHz) was less intense in the Lagoon compared with the Back Reef. Such comparisons in sound intensity among the habitat locations can only be generalised because overall sound intensity varies in relation to the source receiver distance and the total extent of the source habitat, which are difficult to directly quantify.

**Octave analysis**

There were noticeable relative increases in sound intensity in Octave bands 1, 2 and 3 ($F_c = 125, 250, 500$ Hz) for pop vocalisations from each of the 3 habitats (Fig. 3). In general, the pop vocalisations were significantly louder (Kruskal-Wallis $H_s = 367.98$, $p < 0.001$) than ambient background noise during every time of the day except 21:00, 00:00 and 03:00 h for all habitats (Fig. 3). The exception was at 21:00 h in the Back Reef habitat (Fig. 3). The greatest difference between the bands was observed in Band 2 ($F_c = 250$ Hz) for all habitats, which signifies the majority of the sound energy of the pop vocalisations is in this bandwidth. For all the habitats and times of day, octave band levels between the pop vocalisation and ambient background sound for Bands 4 ($F_c = 1000$ Hz) and 5 ($F_c = 2000$ Hz) were similar, which indicates there was no sound energy from the pop vocalisations in these bandwidths.

**Snapping shrimp**

The number of snaps produced by snapping shrimp exhibited significant differences for site ($F_{2,2} = 1.73$, $p < 0.05$), time of day ($F_{1,1} = 3.45$, $p < 0.05$) and
Fig. 2. The power spectral density of 100 Hz bands is plotted across the duration of the recording for both locations; colour bars also indicate power spectral density. (A) Fringing Reef, (B) Back Reef, (C) Lagoon
Fig. 3. Comparison of sound levels for 5 octave bands for Fringing Reef (red), Lagoon (black) and Back Reef (blue) habitat sound with pop vocalisations present (solid circles) and without pop vocalisations (open circles) measured at 3 hourly intervals over a 24 h period.
their interaction ($F_{2,2} = 4.78$, $p < 0.05$; Fig. 4). There were significantly more snaps produced during the hours of darkness (18:00–06:00 h) compared with during the daylight hours (06:00–18:00 h). However, overall, the Fringing Reef habitat had significantly more snaps produced during both the night and noon periods compared with the Lagoon and Back Reef sites. Both the Back Reef and Lagoon habitats had similar number of snaps produced during the noon periods.

**DISCUSSION**

The aim of the present study was to describe differences in the spectral composition of underwater sound emanating from recordings at single locations in 3 distinct habitats around a small tropical island (Fringing Reef, Back Reef and Lagoon) that were located only a few kilometres apart. These 3 types of habitat are typical of many tropical coastal ecosystems. Analyses of representative samples of underwater sound from each habitat revealed marked differences in their spectral and temporal acoustic characteristics, as well as overall sound intensity. Most of the spectral variability among the 3 habitats was observed below 800 Hz, where the dusk chorus varied in its duration. All 3 habitats exhibited a marked nocturnal increase in spectral levels in the frequency band 2–20 kHz during the night.

Two studies have described the spatial and temporal patterns of ambient underwater sound around Australia, but on a spatial scale several orders of magnitude larger than the present study (Cato 1976, 1978). Both studies reported diurnal patterns in ambient sound production similar to those of the present study, including the occurrence of evening choruses, with a rise in the lower frequencies of 300–800 Hz. They also reported higher intensity sounds in the higher frequencies (2–10 kHz) during the night. These patterns in sound activity are consistent with the present study and have been attributed to the same biological sources, chorusing fish and snapping shrimp, respectively.

There are only 3 other published studies of localised spatial differences in the underwater sound emanating from coastal reefs (Kennedy et al. 2010, Radford et al. 2010, Huijbers et al. 2012). These studies had limited temporal sampling of underwater sound, with Radford et al. (2010) only taking recordings during noon and at dusk, while Kennedy et al. (2010) and Huijbers et al. (2012) took recordings at various times during the daytime in order to make inferences about habitat differences in sound production or to use the sounds in behavioural experiments. However, the present study sampled underwater sound at regular hourly intervals over a 48 h period during the new moon and found significant variation in the underwater sound, often within only a few hours. Radford et al. (2010) showed that there was extensive spatial variation in underwater sound in shallow-water habitats in a temperate marine environment that was mostly attributed to the abundance of noisy grazing urchins on reefs (Radford et al. 2008b). Kennedy et al. (2010) showed that there is considerable spatial variation in underwater sound on a broad-scale around a tropical island archipelago during daytime due to various biological factors, such as fish abundance and coral cover. For example, coral cover explained 38% of the variation in noise among the 40 reef sites sampled. This could be a likely explanation of the broad-scale patterns observed in the present study, where the habitats that were examined ranged from extensive coral cover (Fringing Reef) to little or no coral cover (Lagoon) and were characterised by visually obvious marked differences in abundances of resident fish.

In the present study, the majority of the variation in underwater sound found among the habitats was below 800 Hz, which is the frequency range within which the majority of fish vocalisation occurs (Amorim 2006). For example, 8 out of the 29 genera of damselfish are known to be highly vocal, producing a range of chirps, pops or grunts during agonistic or reproductive displays (Amorim 2006), with sounds in the frequency range 90–1000 Hz (Myrberg et al. 2006).
Pomacentridae, with over 100 species recorded as present in Panama. At Lizard Island, there is a great diversity of Stegastes flavilatus. Kennedy et al. (2010) found that the variation in spectral levels observed below 1000 Hz was significantly correlated with the abundance of the commonly occurring pomacentrid species. Kennedy et al. (2010) also showed that the differences observed in both the spectra and the proportion of total sound intensity within the frequency range of 2–20 kHz. Other studies have also shown that there is considerable spatial (Radford et al. 2010) and temporal (Radford et al. 2008b) variation among the number of snaps produced by snapping shrimp, suggesting that habitat type is an important determinant of the abundance of resident snapping shrimp, and that the extent of their sound production can be used as a habitat quality monitoring tool (Watanabe et al. 2002). Therefore, the results of the present research also highlight the potential use of passive acoustics as a tool for monitoring habitat quality, by remotely surveying habitat type and determining the abundance of some sound-producing organisms, such as snapping shrimp or soniferous fishes.

Acoustic cues that convey directional as well as habitat quality information would potentially be of immense value to the pelagic larval stage of a reef organism attempting to remotely locate a suitable habitat in which to settle. Four studies provide some support for this proposition. Settlement-stage reef fish Chromis atripectoralis were shown to be able to discriminate and respond to natural reef sound versus artificial pure tones replayed by underwater speakers (Leis et al. 2002). The arrival of some species of settlement-stage fish on experimental patch reefs were affected by differences in the frequency range of underwater sound broadcast from the reefs, with pomacentrid fish species responding preferentially to the high-frequency treatment (natural reef sound filtered into high frequency >570 Hz), while other fishes, such as apogonids, showed no preference between the high-frequency or the low-frequency treatments (natural reef sound filtered into low frequency <570 Hz) (Simpson et al. 2005). Likewise, broadcasting high-frequency (570–2000 Hz) and low-frequency (<570 Hz) components of natural reef sound in conjunction with light traps resulted in greater numbers of settlement-stage Pomacentridae, Apogonidae, Lethrinidae and Gobiidae in the high-frequency traps than either the low-frequency or the silent traps (Simpson et al. 2008b). In contrast, settlement-stage fish of the Syngnathidae preferred high- to low-frequency traps. Simpson et al. (2008b) concluded that most settlement-stage fish were selecting the higher-frequency reef noise because it was produced mainly by marine invertebrates associated with the preferred settlement habitat for these species. The results from the present study confirm that for snapping shrimp at least, they are producing greater numbers of snaps in the higher frequencies as the coral reef habitats become more complex. Stanley et al. (2012) used laboratory- and field-based experiments to demonstrate that settlement behaviour and time to metamorphosis in the settlement-stage larvae of common coastal crab species varied in response to different underwater sound signatures produced by different habitat types. The megalopae...
of 5 species of both temperate and tropical crabs showed a significant decrease in time to metamorphosis, by almost half in some species, when exposed to sound from their optimal settlement habitat type compared with sound from other habitat types. Overall, the results of these 4 studies tend to indicate that sounds emanating from specific underwater habitats may play a major role in determining spatial patterns of recruitment in an important range of coastal reef species.

To date, the large majority of studies of ambient habitat sound has focused on measuring the pressure versus particle velocity component of underwater sound primarily because it is difficult to measure ambient particle motions in field situations with readily available technology. However, for organisms using underwater sound cues for orientating among habitats 100s of metres apart, the particle velocities can generally be expected to be directly related to the propagating pressure wave (i.e. operating in the far field) (Rogers & Cox 1988, Montgomery et al. 2006).

In conclusion, our results show that locations within different tropical coastal habitats that are geographically separated by distances of only 100s of metres show marked spectral and temporal variation in the underwater sound they generate. This variation appears to be due in large part to differences in the acoustic output of the soniferous organisms dwelling in these habitats. For example, the magnitude of the most common types of fish call and shrimp snapping sounds were found to be important contributors to the differences that characterised the sound emitted from these habitats, both temporally and spatially. Overall, the measured fish vocalisations tended to be a greater contributor to the sound in all habitats during daylight hours compared with shrimp snaps, which generally were more frequent during the hours of darkness. These habitat-related differences in underwater sound in tropical coastal environments appear to play a role in the orientation and movements of juvenile and adult fishes. There is some evidence that they may be used for the remote selection of target settlement habitats by pelagic larval fish and crabs. Further research is required to determine specifically which elements of the differences in the acoustic output of coastal habitats are being used for orientation by migrating fish.

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LITERATURE CITED

- Maruska KP, Boyle KS, Dewan LR, Tricas TC (2007) Sound production and spectral hearing sensitivity in the Hawai-


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