

Habitat quality affects sound production and likely distance of detection on coral reefs

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ABSTRACT: The interwoven nature of habitats and their acoustic fingerprints (soundscapes) is being increasingly recognized as a key component of animal ecology. Natural soundscapes are crucial for orientation in many different taxa when seeking suitable breeding grounds or settlement habitats. In the marine environment, coral reef noise is an important navigation cue for settling reef fish larvae and is thus a possible driver of reef population dynamics. We explored reef noise across a gradient of reef qualities, tested sound propagation models against field recordings and combined them with fish audiograms to demonstrate the importance of reef quality in determining which reefs larvae are likely to detect. We found that higher-quality reefs were significantly louder and richer in acoustic events (transient content) than degraded reefs, and observed that sound propagated farther with less attenuation than predicted by classic models. We discuss how zones of detection of poor-quality reefs could be reduced by over an order of magnitude compared to healthy reefs. The present study provides new perspectives on the far reaching effects habitat degradation may have on organisms that utilize soundscapes for orientation towards or away from coral reefs, and highlights the value of sound recordings as a cost-effective reef survey and monitoring tool.

KEY WORDS: Underwater soundscape · Anthropogenic impact · Larval fish · Coral reef · Settlement habitat · Passive acoustic monitoring

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INTRODUCTION

The connection between habitats and their soundscape has been recognized for many decades (Carson 1962, Krause 1987), but the true scope of the ecological function of soundscapes and its importance to the fitness of the individual has only emerged over the past 10 yr (e.g. Slabbekoorn & Peet 2003, Simpson et al. 2005). Sound is used as a cue for identifying and locating targets across many taxa, from parasitic flies that lay eggs on singing crickets (Cade 1975) and male mosquitoes in search of mates (Göpfert &

Robert 2000) to penguins locating parents and partners amongst the cacophony of a squawking colony (Aubin & Jouventin 2002). The use of natural soundscapes as an orientation cue to locate breeding grounds and settlement habitats has gained increasing interest over recent years (Slabbekoorn & Bouton 2008). Newts have been found to use the vocalizations of other anurans to guide them to permanent ponds in which to breed (Diego-Rasilla & Luengo 2004, Pupin et al. 2007), and birds select suitable nesting habitats based on the calls of heterospecifics (reviewed by Mönkkönen & Forsman 2002).

Recent research has demonstrated the critical role that coral reef soundscapes play in the recruitment of settlement-stage larval fish, crustaceans and corals (Simpson et al. 2005, Montgomery et al. 2006, Arvedlund & Kavanagh 2009, Vermeij et al. 2010). Eggs and hatchlings of most tropical and temperate reef fish and decapod crustaceans are exported from their coastal habitats and develop as larvae in the open ocean (Montgomery et al. 2001, Kingsford et al. 2002, Leis & McCormick 2002). Species abundance and community structure are largely driven by the supply of these pelagic larvae (Doherty & Fowler 1994, Lee & Bruno 2009), and therefore understanding the environmental factors that regulate the supply of larvae to coral reefs is crucial to conservation and fisheries management. Whilst there are still major gaps in our knowledge concerning the ecology of oceanic larvae, often referred to as the 'pelagic black box' (Leis & McCormick 2002), it is now known that larvae of many species across taxa use noise generated by resident animals as one of the cues to identify settlement areas (Simpson et al. 2004, 2005, 2008, 2011a, Radford et al. 2007, Vermeij et al. 2010). Since reefs and nearby nursery habitats produce unique signature sounds (Kennedy et al. 2010, Huijbers et al. 2012), there is potential for larvae to be able to distinguish between them to select habitat (Stanley et al. 2010, 2012, Radford et al. 2011a). Studies have demonstrated that soundscapes can be used to estimate biodiversity in terrestrial habitats (Sueur et al. 2008, Pijanowski et al. 2011a) which has led to the hypothesis that they can provide information on habitat quality and integrity (Krause 2002, Dumyahn & Pijanowski 2011). However, no studies have specifically looked at sound signatures across a gradient of habitat quality in either terrestrial or marine systems. Defining the relationship between reef quality and acoustic signature would allow researchers to formulate new predictions on the long-term implications of environmental degradation on patterns of recruitment by animals using auditory cues, and validate the use of sound recordings as a cost effective and rapid assessment tool for reef quality.

Many reef organisms are relatively sedentary during their adult life and thus the 'decision' to settle at a specific site for a larva returning from an early pelagic developmental phase has consequences for the success and fitness of the individual. Audition, together with olfaction, has emerged as one of the key senses that provide larvae with the ability to orientate towards a reef (see review by Arvedlund & Kavanagh 2009). The value of audition depends on species' hearing capabilities and characteristics of

the sound source (Montgomery et al. 2006, Mann et al. 2007). Sound can provide information on both the identity and direction of the source over long distances (reefs can be detected up to 15 km away with a hydrophone; Cato & McCauley 2002) and, unlike olfactory cues, is largely unaffected by water currents. Larval fish and decapod crustaceans, however, might detect reefs only over shorter distances (in the range of hundreds of metres; Mann et al. 2007) because of their low sensitivity and because most fish only detect the particle motion component of sound which decays faster than the particle pressure component (Kalmijn 1988, Rogers & Cox 1988). Despite an increase in the number of studies demonstrating the use of sound cues by fish and crustacean larvae for orientation towards reefs (see Simpson et al. 2004, 2005, 2008, 2011a, Radford et al. 2007, Stanley et al. 2010, 2012), the distances over which larvae detect and discriminate between reefs are uncertain (Mann et al. 2007, Wright et al. 2010, 2011, Radford et al. 2011b).

The importance of distance of detection was first highlighted in models of larval recruitment, where simulations demonstrated that the size of the 'sensory halo' around reefs and the differential sensory abilities of larvae strongly affected simulated fish recruitment to a stylized reef (Armstrong 2000, Codling et al. 2004, Leis 2007, Staaterman et al. 2012). Several studies have since focused on characterizing reef sound propagation (Mann et al. 2007, Radford et al. 2011b) and have explored interspecific differences in the auditory thresholds of fish larvae (Wright et al. 2010, 2011). Recent studies have shown identifiable differences in the sound produced by different temperate (Radford et al. 2010) and tropical (Huijbers et al. 2012) coastal environments. However, as yet, little attention has been paid towards characterizing sound produced within reef habitat, although a study by Kennedy et al. (2010) revealed that particular components of the soundscape could be utilized to discriminate broad reef characteristics. Those authors found that high-frequency sound correlated with coral diversity at 11 Panamanian reefs surveyed in the same year, likely due to increased numbers of snapping shrimp, which are known to associate with both coral and coral rubble (Hultgren & Duffy 2010, Enochs et al. 2011). Their findings also supported significant correlations between broad-spectrum root mean square (RMS) levels and density of the soniferous damselfish *Stegastes flavilatus*, one of the most abundant fish on the reefs studied. Comparisons of recordings taken in 2007 with a further 30 sites surveyed 3 yr earlier confirmed these findings and

revealed some additional associations between the reef community and the soundscape.

We investigated the importance of reef quality in shaping the surrounding soundscape with 2 key objectives in mind: (1) to characterize sound at reefs across a gradient of habitat quality utilizing short 'snapshot' recordings and (2) to evaluate models of underwater sound propagation using acoustic recordings taken at different distances from coral reefs. Considering the role of sound in recruitment, we assumed that larvae attempting to locate reefs are unlikely to rely on sound intensity alone to gauge their distance from a reef or to distinguish between reefs if other acoustic information is available. We therefore considered sound intensity combined with transient content, a measure of the rate of short energy bursts in the sound, characteristic of the clicks produced by snapping shrimp that dominate many reef soundscapes. Our findings suggest that reef quality substantially modifies the intensity and transient content of the reef's soundscape, with the magnitude of this effect possibly large enough to greatly undermine potential distance over which recruitment-stage larvae can detect impacted reefs. We suggest that the 'snapshot' approach to sound recordings could be useful as an objective and cost-effective tool to assess and monitor reef condition.

MATERIALS AND METHODS

Sites

Recordings across a gradient of habitat quality were taken around 7 small islands off Bohol in the central Philippines (see Fig. S1 in Supplement 1, available at www.int-res.com/articles/suppl/m516p035_supp.pdf), where reefs with a range of habitat qualities, from coral- to algae-dominated reefs, were studied. The sites consisted of (1) 3 healthy reefs in marine protected areas (MPAs; CCEF 2007, UPMSI 2007): Balicasag Island (BCBF), Pamilacan Island (PMSY) and Bilang-bilangan (BB); (2) 1 recovering reef recently designated as an MPA: Pangapasan Island (PG); and (3) 3 impacted reefs dominated by macroalgae or urchins: BHIN, BHOUT and CBIN (S. Green pers. comm.; see Table 1 for site abbreviations and descriptions). Further details including coral cover and fish density are provided in Table 1.

Our study of sound propagation focused on reefs in Oman and Indonesia representing extremes in biodiversity and bathymetry. The Omani reefs are located on shallow shelving coastlines in the Masirah Chan-

nel (depth <20 m; Fig. S2 in Supplement 1) and are characterized by high coral cover dominated by a single coral species, *Montipora foliosa* (Claereboudt 2006). In contrast, the fringing reefs of Hoga Island, in the Wakatobi Marine National Park, south-east Sulawesi, Indonesia, are surrounded by waters >100 m deep and are located in the centre of the Coral Triangle, one of the most biodiverse regions in the world (Veron 1995, McMellor & Smith 2010; Fig. S3 in Supplement 1).

Sound recordings

Recordings were made in February 2005 (Oman), June 2007 (Philippines) and June 2009 (Indonesia) using a calibrated omnidirectional hydrophone (HiTech HTI-96-MIN with inbuilt preamplifier, High Tech) and either a calibrated Edirol R-1 recorder (Roland Systems Group; Oman recordings) or Zoom H4 recorder (Zoom Corporation; Philippines and Indonesia recordings), both at 24-bit, 44.1 kHz sampling rate. The hydrophone was suspended from the boat, with the cable held by the person making the recording to dampen out any movements caused by the boat bobbing (which was negligible due to working in calm conditions). Depth was measured by weighted rope when less than 20 m, but otherwise taken from charts (e.g. Hoga Island). Recordings were made 5 m below the surface, as this escapes the very different conditions of the 1 m closest to the surface, and is where fish are likely to swim when seeking habitat (e.g. Leis et al. 1996). For the study on soundscapes across a gradient of different quality reefs, two 1 min recordings separated by >1 h were taken for each of the 7 sites (20 m from the reef) in the central Philippines (between 09:00 and 13:00 h). The daytime 'snapshot' approach (two 1 min recordings 1 h apart) was adopted so that meaningful comparisons with other widely adopted census methods, such as underwater visual censuses (UVCs), could be made at these sites.

In the second part of this study where propagation models were compared with real sound recordings, 3 seaward transects up to 1.5 km away from the reef, each consisting of up to 5 recording points, were completed in Oman (Fig. S2a in Supplement 1): one East of Barr al Hickmann (BAHE; Fig. S2b in Supplement 1) and 2 south of Masirah Island (MIS1 and MIS2; Fig. S2c in Supplement 1) and 2 seaward transects were taken at Hoga (Fig. S3a in Supplement 1): Front Beach (FB) and Pak Kasim's (PK; Fig. S3b in Supplement 1). One minute recordings were taken

Table 1. Geographical location, Marine Protected Area (MPA) status and description of sites used for recording sound for habitat comparisons and sound propagation models

Site	Location	MPA status	Site description
Philippines			
Balicasag Island 'Black Forest' Fish Sanctuary (BCBF)	9° 30' 48" N, 123° 41' 19" E	MPA and no-take zone; established 1986	High coral cover (70%) and fish density (7208.5 fish 500 m ⁻²); Management Level 2 rating (established), low fishing beyond boundary (White et al. 2007)
Bilang-bilangan Marine Sanctuary (BB)	9° 59' 31" N, 123° 52' 48" E	MPA and no-take zone; established 1999	Fair coral cover (55.3%), medium fish density (1396.6 ± 290.1 fish 500 m ⁻²); Management Level 4 rating (sustained), high fishing pressure outside protected zone (CCEF 2007)
Pamilacan Island Fish Sanctuary (PMSY)	9° 29' 16" N, 123° 55' 58" E	MPA and no-take zone; established 1985	Fair coral cover (36.8%), medium fish density (1285 ± 218.7 fish 500 m ⁻²); Management Level 4 rating (sustained), medium fishing pressure outside protected zone (White et al. 2007)
Pangapasan Island Fish Sanctuary (PG)	9° 59' 52" N, 123° 56' 37" E	MPA and no-take zone; established 1998	Poor coral cover (18.4%), fair fish density (428.55 ± 71.7 fish 500 m ⁻²); Management Level 3 (enforced); regular boundary breaching by fishermen (CCEF 2007)
Reef in the Bohol-Cebu Channel (BHIN)	10° 0' 43" N, 123° 55' 40" E	No official management or protection status	Low coral cover, low fish density, macroalgae-dominated reef; historically overfished through destructive methods; no active management (S. Green pers. comm.)
Reef in the Bohol-Cebu Channel (BHOUT)	10° 1' 10" N, 123° 56' 15" E	No official management or protection status	Low coral cover, low fish density, macroalgae-dominated reef; historically overfished through destructive methods; no active management (S. Green pers. comm.)
Reef in the Bohol-Cebu Channel (CBIN)	10° 1' 25" N, 123° 55' 49" E	No official management or protection status	Low coral cover, low fish density, urchin-dominated reef; historically overfished through destructive methods; no active management (S. Green pers. comm.)
Oman			
Barr al Hickmann (BAHE)	20° 20' 53" N, 58° 27' 2" E	No official management or protection status	High coral cover (70–100%), high fish density; monospecific coral reef consisting of tabulate <i>Montipora foliosa</i> ; commercial fishing prohibited by local fishing right holders of the Hickmani tribe (Salm 1993, Claereboudt 2006)
Masirah Island 1 (MIS1)	20° 9' 52" N, 58° 37' 55" E	No official management or protection status	High coral cover (50–100%), high fish density; offshore monospecific <i>Pocillopora</i> reef with high densities of urchins and parrotfish; low fishing activity (Salm 1993, MRME 1996, Claereboudt 2006)
Masirah Island 2 (MIS2)	20° 9' 52" N, 58° 37' 31" E	No official management or protection status	High coral cover (50–100%), high fish density, coral reef dominated by tabulate <i>Montipora foliosa</i> with some monospecific <i>Pocillopora</i> stands and <i>Acropora</i> thickets; low fishing activity with hook and line method (Salm 1993, MRME 1996, Claereboudt 2006)
Indonesia			
Pak Kasim (PK)	5° 27' 50" S, 123° 45' 18" E	Marine National Park	Fair coral cover (27–42%), fair fish density (~875 fish 500 m ⁻²); high diversity of coral and fish; 2001–2012 no active management (Smith & Jompa 2009, McMellor & Smith 2010)
Front Beach (FB)	5° 28' 20" S, 123° 45' 25" E	Marine National Park	Fair coral cover (45–55%), medium fish density (~1020 fish 500 m ⁻²); high diversity of coral and fish; 2001–2007 no-take zone; 2008–2012 no active management (Smith & Jompa 2009, McMellor & Smith 2010)

for each transect point (Oman and Hoga) at 4 m below the sea surface, and all recordings were made between 13:00 and 15:00 h during the dry season (WMO 2013). Distance from the reef was measured using a handheld GPS navigator (Garmin GPSMAP 60CSx), and satellite images were used to ensure that no charted reefs were present within 1.5 km from the sampled reef point. However, at the 2 farthest transect points taken from MIS3 (1.2 to 1.5 km), a reef was clearly audible in the vicinity and so these were removed from the analyses.

All samples considered in this study were carried out in Force 1 or 2 conditions (Beaufort scale, wind speeds $<11 \text{ km h}^{-1}$), which cause no wave break and have negligible effects on background noise (Stewart 2004). However, this meant that the most distant sampling point for BAHE had to be removed due to wave break, likely caused by the site having less protection from the wind and/or local currents. Since temporal variability in reef sound is predictable ($<2 \text{ dB re } 1 \text{ } \mu\text{Pa}$ during the daytime; Lammers et al. 2008), standardized sampling times of between 09:00 and 15:00 h were used to limit within-site variation (i.e. excluding dawn, dusk and night; Cato 1978, McCauley & Cato 2000, Cato & McCauley 2002, Lammers et al. 2008).

Acoustic analyses

Recordings were divided into subsamples (10 s), and those with obvious anthropogenic noise (passing boats, waves slapping on the hull of the boat) were removed from the analyses (as per Kennedy et al. 2010). The remaining recording samples were high-pass (0.1 kHz) and low-pass (5 kHz) filtered in Adobe Audition (CS5.5 V4, Adobe Systems) to remove electrical noise from the recording equipment (high-pass filter) and to limit the analysis to the upper hearing ranges of coral reef fish (Wright et al. 2010, 2011). RMS sound intensity and power spectra of each recording were calculated in Adobe Audition and calibrated according to the full dynamic range measured in Avisoft SASLab Pro (Avisoft Bioacoustics). Transient content, an indicator of the rate of high-intensity broadband impulsive sounds in the recording, was calculated using a custom designed algorithm in Matlab (v R2010a, The MathWorks; more details in Supplement 2). The transient content is independent of the RMS sound intensity and effectively excludes the possible effect of stochastic fish vocalizations by considering only short broadband signals.

Modelling sound propagation

Four models of sound propagation were used to generate predictions that were compared with the seaward transect recordings (Oman and Indonesia) taken from the reef up to 1500 m away. Differences in frequency-dependent propagation loss due to absorption were not considered since they are negligible ($<0.3 \text{ dB km}^{-1}$) within the frequencies (0.1 to 5 kHz) and the distances ($<1500 \text{ m}$) considered (calculations obtained using absorption equation described by Ainslie & McColm 1998). The models used were (1) spherical spreading and (2) cylindrical spreading of sound in water (see Mann et al. 2007 for a description of both of these models); (3) 'extended reef' model (Radford et al. 2011b), which considers reefs as extended sources of sound rather than point sources; and (4) geometric spreading parameterized by our transect recordings: this model is based on geometric spreading, where 2 parameters, α and β , are estimated from the best fit to each of our recordings and then averaged between reefs (see Supplement 3).

RESULTS

Spectral analysis of reef noise

Descriptive characterization of the sound across different frequencies was performed by visual inspection of the sound spectrograms for all sites (Fig. 1 and see Fig. S6 in Supplement 4). All sites in the Philippines had a broadband peak in the range 1.5 to 4 kHz dominated by invertebrate noise, most likely the 'clicking' of snapping shrimp, but each site also had distinctive power spectra (Fig. 1a). The reef with highest coral cover and fish abundance (BCBF) had the highest intensity of sound across all frequencies including those $<1 \text{ kHz}$, which consisted of a variety of fish vocalizations ('pops', 'grunts', 'croaks' and 'drums') audible throughout the recordings. The other 2 healthy sites (BB and PMSY) also had high levels of higher-frequency invertebrate 'clicking' noise (broad peak between 1 and 5 kHz centred on $\sim 3.8 \text{ kHz}$), but relatively lower power in the frequencies associated with fish vocalizations ($<1 \text{ kHz}$). The broad peak in the 0.2 to 0.8 kHz range at PG resulted from multiple high-energy 'pops' and 'grunts', indicating a high abundance of vocalizing fish. The 3 historically overfished and now depauperate sites generally had much lower power across all frequencies, although BHOUT (one of the macroalgae-dominated

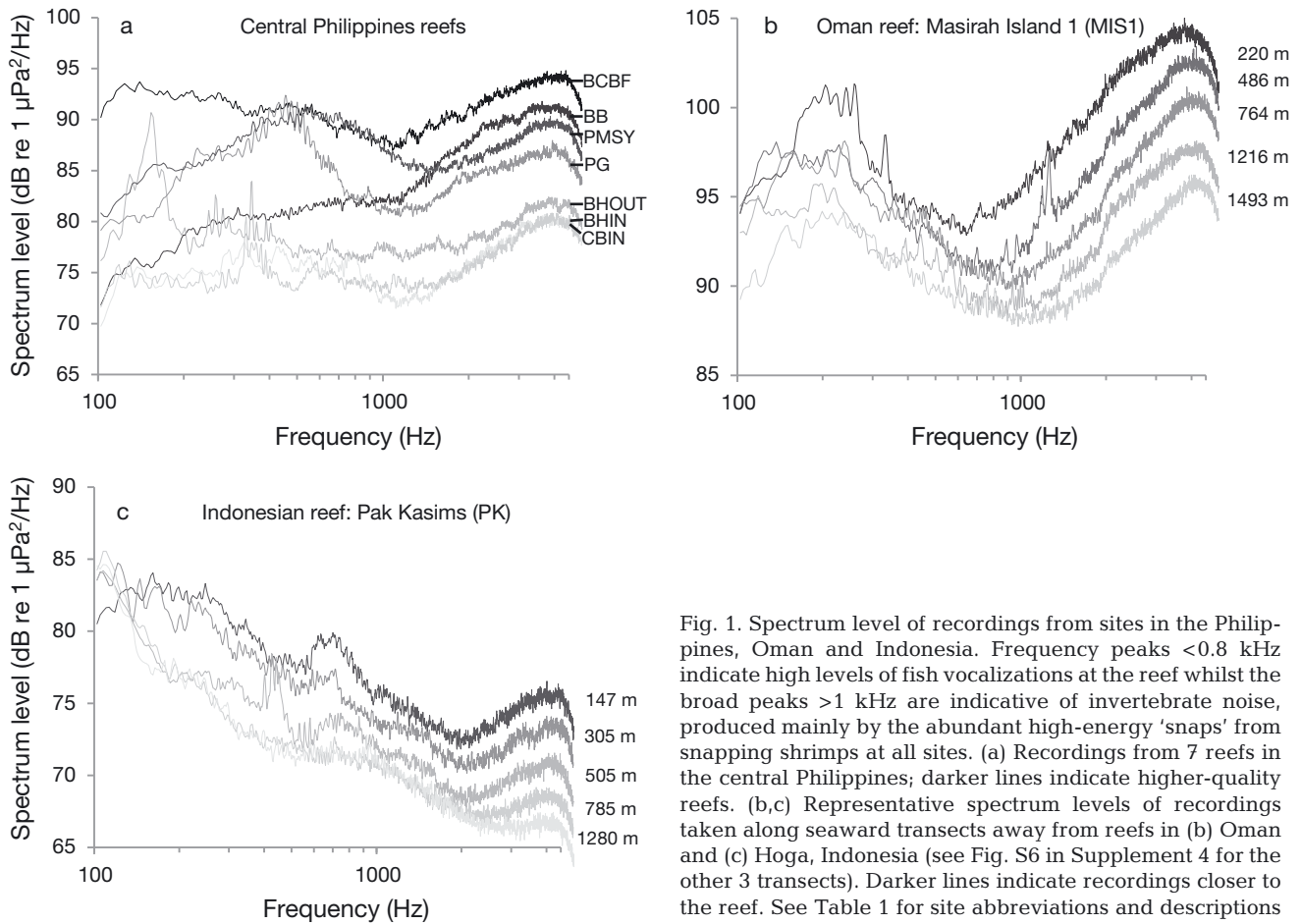


Fig. 1. Spectrum level of recordings from sites in the Philippines, Oman and Indonesia. Frequency peaks <0.8 kHz indicate high levels of fish vocalizations at the reef whilst the broad peaks >1 kHz are indicative of invertebrate noise, produced mainly by the abundant high-energy 'snaps' from snapping shrimps at all sites. (a) Recordings from 7 reefs in the central Philippines; darker lines indicate higher-quality reefs. (b,c) Representative spectrum levels of recordings taken along seaward transects away from reefs in (b) Oman and (c) Hoga, Indonesia (see Fig. S6 in Supplement 4 for the other 3 transects). Darker lines indicate recordings closer to the reef. See Table 1 for site abbreviations and descriptions

reefs) had a sharp peak between 0.1 and 0.2 kHz, unlikely to be of natural origin and possibly caused by a distant anthropogenic source.

Transect recordings from Oman had distinct power spectra in both the higher (>1 kHz) and lower (<1 kHz) frequency regions compared to sites in Indonesia (Fig. 1b,c). Despite similarities in the frequency composition between sites located in similar geographical regions, the power spectra for each site was distinct both for the high-frequency and low-frequency components, suggesting different fish and invertebrate assemblages at each site (Fig. 1b,c and see Fig. S6 in Supplement 4). For each site, the power spectra were similar across all ranges for frequencies >1 kHz, decreasing reliably in power as range increased. There was greater variability in the pattern of the power spectra at frequencies <1 kHz, due to a combination of background noise and vocalizations from non-reef dwelling fish. However, overall there was a decrease in power over distance across most of the lower frequencies as well (Fig. 1b,c and see Fig. S6 in Supplement 4).

Sound intensity and transient content across a habitat gradient

To quantitatively investigate differences in sound between reefs across a gradient of habitat qualities, we adopted 2 simple measures: sound intensity and transient content. Average RMS sound intensity between 0.1 and 5 kHz obtained from 10 s subsamples ($n = 5$, randomly selected from two 1 min recordings taken 1 h apart) from the recordings of the 7 Philippine reefs was consistently different between some sites (1-way ANOVA, $F = 350.37$, $p < 0.001$, Fig. 2a). Two of the high-quality MPAs (BB and PMSY) and the 2 lowest-quality reefs (BHIN and CBIN) were each grouped together, while the other 3 sites were significantly isolated from all other groups ($BCBF > BB = PMSY > PG > BHOUT > BHIN = CBIN$, Tukey's test, $p < 0.05$).

Transient content decreased significantly (Kruskal-Wallis [K-W], $H = 31.1$, $p < 0.001$) with decreasing habitat quality (Fig. 2b). Post hoc tests revealed that the transient contents of the 3 low-quality reefs did not differ significantly from one another but were

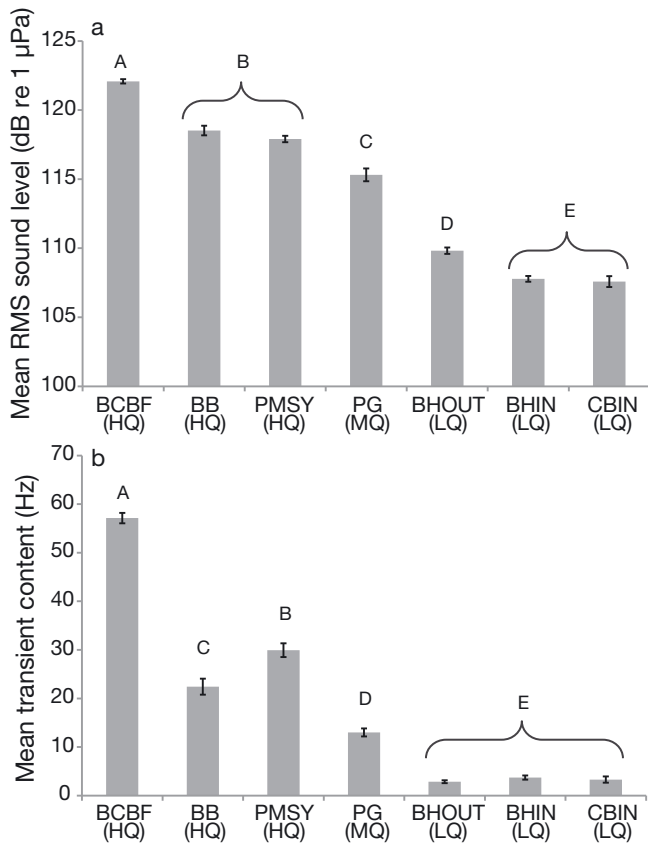


Fig. 2. Mean \pm SD of (a) root mean square (RMS) sound intensity and (b) transient content at sites of different quality in the Philippines. SDs are representative of 10 s subsamples ($n = 5$) randomly selected from two 1 min recordings taken 1 h apart. Sites are denoted as high quality (HQ), medium quality (MQ) or low quality (LQ) based on marine protected area (MPA) status and habitat type (see Table 1). Groupings A–E denote ranks of reefs by (a) broadband RMS sound intensity and (b) transient content. Reefs grouped by letter were not significantly different (panel a: Tukey's tests; panel b: Mann-Whitney U -tests). Site abbreviations as in Table 1

significantly lower than 2 of the high-quality reefs (BCBF and PMSY > BHIN, CBIN and BHOUT, K-W all pairwise comparisons by site, $p < 0.01$; Fig. 2b). With the exception of one high-quality site (BB), ranking by transient content was the same as that by sound intensity. In further investigations, ranking of reefs by transient content varied little when a range of window bin sizes and thresholds were applied (see Figs. S4 & S5 in Supplement 2).

Evaluation of propagation models using transect sound recordings

All 5 transects performed across Oman and Indonesia displayed characteristic non-linear declines in broadband (0.1 to 5 kHz) RMS sound intensity with

increasing distance from the reef (Fig. 3). Source intensities were higher at Omani reefs (mean RMS at the sites ranged from 123 dB re 1 μ Pa at BAHE to 133 dB re 1 μ Pa at MIS1) compared to Indonesian reefs (mean RMS of 110 and 111 dB re 1 μ Pa at PK and FB, respectively) and attenuated more gradually with distance at Omani reefs (attenuation of mean RMS at the sites ranged between 5.6 and 8.0 dB re 1 μ Pa over \sim 800 m) compared to Indonesian reefs (9.6 to 10.5 dB re 1 μ Pa over the same distance; Table S1 in Supplement 3). For each site, predictions of sound propagation based on spherical spreading, cylindrical spreading, the 'extended reef' and best fit recording-parameterized geometric spreading models were compared to measured intensities (Fig. 3). No significant difference was found between cylindrical spreading, extended reef or recording-parameterized geometrical spreading models in their goodness of fit to sound intensities at different sites but spherical spreading had a significantly poorer fit for all sites (2-way ANOVA, $F = 64.4$, $p < 0.001$).

Spherical and cylindrical spreading both underestimated sound propagation, most likely due to the simplifying assumption that sound is propagating from a point source. The extended reef model explained propagation well for the smallest coral reef in this study (MIS1, 600 m in length), but underestimated sound intensity at the source for all other sites and would consequently overestimate sound intensity over distance if propagated from measured source levels. The exception to this would be BAHE, where the sound intensity at 300 m was underestimated by all 4 models, possibly due to noise from uncharted reefs. The mean \pm SD $\alpha\beta$ coefficient calculated for the geometric spreading model was 8.28 ± 1.70 . This coefficient indicates a lower attenuation in sound intensity compared to cylindrical spreading (coefficient of 10), but a greater attenuation than predicted by the extended reef model except at MIS1 for the distances examined. There was a significant decrease in transient content levels with distance for all reefs (2-way ANOVA; MIS1, $F = 72.6$, $R^2 = 0.76$, $p < 0.001$; MIS 3, $F = 37.3$, $R^2 = 0.84$, $p < 0.001$; FB, $F = 96.1$, $R^2 = 0.89$, $p < 0.001$; PK, $F = 88.0$, $R^2 = 0.87$, $p < 0.001$; Fig. 4) with the exception of 1 reef in Oman (BAHE), where the level of transient content did not change significantly.

DISCUSSION

The present study demonstrates the influence of habitat quality on acoustic output in coral reef environments. Controlling for abiotic sound sources (e.g.

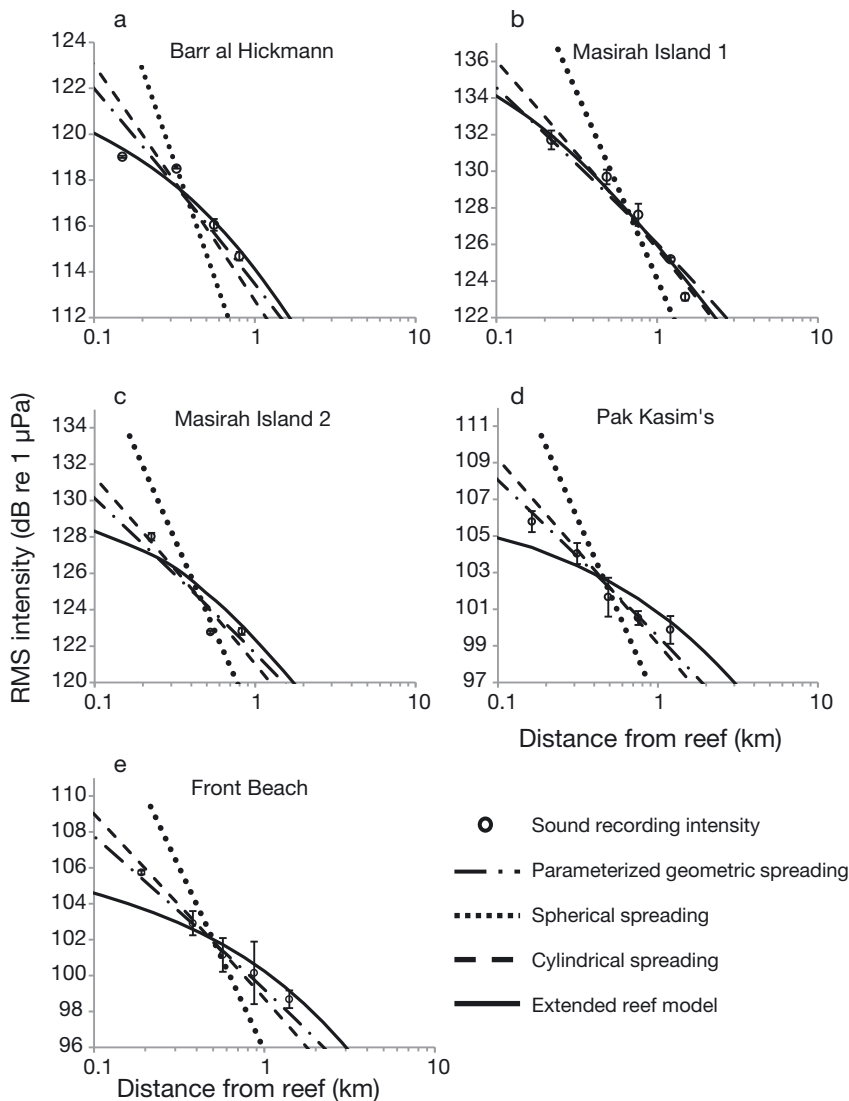


Fig. 3. Mean \pm SD RMS sound intensity at different distances from the reef at 5 sites in (a–c) Oman and (d,e) Indonesia. SDs are representative of 10 s sub-samples ($n = 5$) randomly selected from two 1 min recordings. Fits of 4 propagation models (spherical, cylindrical, extended reef and geometric spreading parameterized using the mean $\alpha\beta$ coefficient) are also displayed for each site. The source sound is not represented due to geographical complexities which arise in proximity to the reef (Radford et al. 2011b), and the first recordings are taken at 150 to 200 m

waves and wind Force 1–2 on the Beaufort scale, wind speed $<11 \text{ km h}^{-1}$; Stewart 2004), reefs of higher quality had higher sound intensity and were richer in transient content during the daytime (between 09:00 and 15:00 h). We also evaluated the validity of different propagation models in 2 different biogeographic regions. We report that classical models of sound propagation (spherical and cylindrical spreading) underestimate the distance over which sound is broadcast, probably due to the simplifying assumption that reefs are point sources of sound, as

previously suggested by Radford et al. (2011b) for temperate reefs.

Soundscapes across habitat quality

Meaningful heterogeneity in reef noise found in this study supports the idea of using ‘snapshot’ sound recordings for rapid and cost-effective reef quality assessment and monitoring (Simpson 2008). Sound has already been used in terrestrial environments to gather biodiversity and abundance estimates (Sueur et al. 2008, Pijanowski et al. 2011a). This method has surpassed other sampling methods of assessing individual occurrence in birds and amphibians for locations where visibility is poor (e.g. rainforest) and also because of its potential for continuous monitoring (Acevedo & Villanueva-Rivera 2006, Celis-Murillo et al. 2009, 2012, Marques et al. 2013). Considering the close correlation found between certain environmental characteristics and acoustic fingerprints of reefs (Kennedy et al. 2010), it is likely that specific biological indicators of reef quality could also be estimated from acoustic recordings. This concept has been applied previously to monitor the presence/absence of specific fish populations (Lobel 2001, Mann 2012).

More recently, Staaterman et al. (2013) recognized the need to consider acoustic monitoring alongside other assessment methods since the soundscape plays an important role in larval recruitment and in other important ecological functions such as mating and territorial defence. Similar to Staaterman et al. (2013), we do not advocate that acoustic assessment should replace classical assessment methods. However, we suggest that ‘snapshot’ soundscape measurements could be used as a means to sample a large number of sites in a cost- and time-efficient manner. This could help identify priority locations where more detailed and long-term assessments might be necessary (i.e. to assess fish species populations which vocalize at specific times of day) in an unbiased manner.

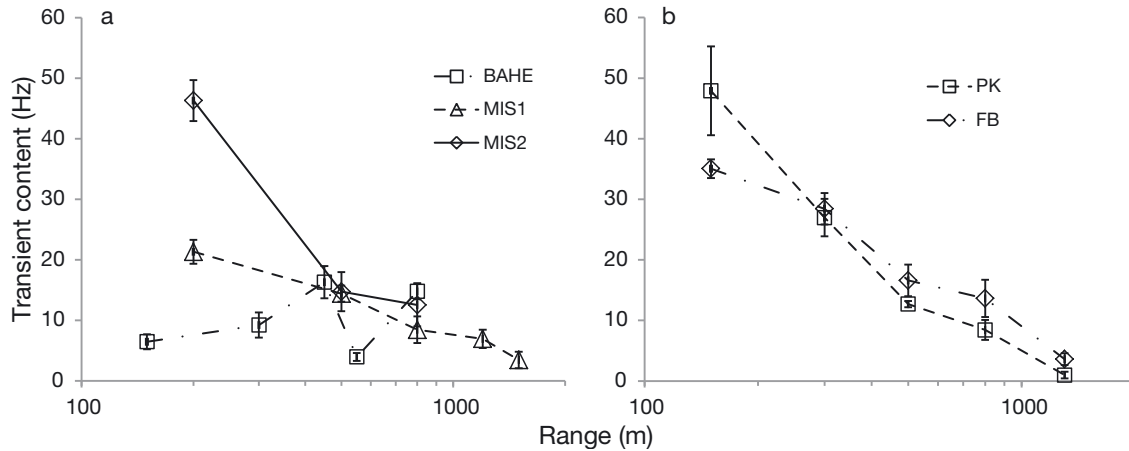


Fig. 4. Mean \pm SD transient content values for recordings on seaward transects away from coral reefs in (a) Oman and (b) Indonesia. The decline in transient content with increasing distance likely indicates homogenization of sound with distance and a lower signal to noise ratio, with fewer distinguishable transient events due to interference between sound waves. Site abbreviations as in Table 1

It is worth noting that although this study does provide a valuable indication of the relationship between a reef's soundscape and its habitat, future studies would benefit greatly from more detailed visual assessments. This includes fish biomass and benthic cover, but also assessments of the cryptobenthos which may contribute significantly towards the reef soundscapes through the snaps of cryptic snapping shrimp and vocalizations of cryptic fish (e.g. gobies; Tavolga 1956). It would also be of great value for future acoustic assessments to investigate how the soundscape changes before and after disturbances which greatly affect the reef's assemblage, such as tropical cyclones or crown-of-thorns starfish *Acanthaster planci* outbreaks (Wolanski 1994). In this context, it is possible to envisage acoustic monitoring of the reef as an early warning system for *A. planci* outbreaks or as a rapid assessment tool for reef damage following cyclones.

Lastly, acoustic monitoring may prove to be a useful tool in assessing nighttime assemblages of fish and invertebrates where visual censuses are challenging due to the low light conditions and would likely disturb the wildlife through the use of flashlights. The approach of nighttime acoustic monitoring was recently validated by Freeman et al. (2014), who coupled acoustic recordings with infrared cameras to monitor the activity of invertebrate species on coral reefs at night. Further studies, however, are needed to validate its use as an estimator of nighttime fish communities, as acoustic cues are likely to play a greater role in nocturnal fish than in daytime fish, when visual cues also play a role in communication.

Comparison of propagation models for coral reefs

In evaluating the fit of different propagation models to measured sound intensities, the spherical spreading model (used by Mann et al. 2007) is least supported as a useful model for predicting reef sound propagation, and is possibly too conservative, overestimating attenuation for extended-source sounds and shallow water environments. The concept of an 'extended reef' (Radford et al. 2011b) for modelling sound propagation is supported in the present study above models that assume reefs are a point source. However, the 'extended reef' model only explained sound propagation from transect recordings most accurately in the smallest reef (MIS1), of a similar size to the reef used to test the original model (500 m; Radford et al. 2011b). Different parameterization to the extended reef model may be required to characterize the acoustics of reefs >500 m long. The geometric spreading model parameterized using the recordings in the present study explained sound propagation well for 2 geographically distinct reef systems with very different bathymetries (a shallow shelving coastline in depths <20 m for Omani reefs and a fringing reef surrounded by waters >100 m deep for Indonesian reefs) and communities (low fish and coral diversity in Omani reefs compared to some of the highest diversity in coral and fish in the oceans for Indonesian reefs; Claereboudt 2006, McMellor & Smith 2010). By combining the extended reef model with the parameterization approach from the present study, it might be possible to obtain an improved propagation model for future studies on reef soundscapes.

The present study made use of a single hydrophone to measure the sound at different distances from the reef, but it cannot account for the natural variability in sound at the source. Previously Radford et al. (2011b) coupled the acoustic measurements from different distances from a temperate reef with a fixed hydrophone at the reef. By doing so, they were able to obtain both spatial and temporal information on the changes in reef sound during a period of high temporal variation in sound production (dusk chorus). In addition to this, promising recent developments have made use of L-shaped hydrophone arrays to gain directional information on invertebrate sound sources on coral reefs in the Eastern Pacific (Freeman et al. 2013). Combined with topographical mapping of the sea floor, these techniques would provide us with the clearest picture yet on how sound propagates from the reef and on what acoustical information is available to larvae approaching the reef.

Effects of reduced detection zones on reef animals

Finding an appropriate settlement site is a crucial step in the life history of reef fish and decapod crustaceans (Leis & McCormick 2002, Montgomery et al. 2006). Self-recruitment, the process by which fish return to their natal reefs, plays a central role in maintaining supply of larval fish to reefs in MPA networks (Berumen et al. 2012, Harrison et al. 2012). Self-recruitment of larvae may depend on their ability to detect and orient towards a reef early on in development or at the time when they become competent to settle (Fisher 2005, Staaterman et al. 2012). Consequently, smaller detection zones in degraded reefs could significantly reduce the ability of reef fish populations to self-sustain and, therefore, compromise the reef's chances of recovery. If one considers a propagation loss of 10 dB in sound intensity for every 10-fold increase in distance from the reef, as predicted by the cylindrical spreading propagation model, a difference of 14 dB sound intensity at the source, observed between the highest- and lowest-quality reef in the present study, would result in a reduction of the detection zone by over an order of magnitude. A larger detection zone means that high-quality reefs may receive higher rates of larval supply, effectively recruiting more fish from the surrounding ocean, potentially at the expense of nearby degraded reefs.

Furthermore, differential hearing abilities of larvae could result in community shifts away from species

with lower hearing sensitivity at degraded sites, further decreasing diversity, abundance and resilience of fish assemblages. This also calls for new research into the absolute hearing abilities of fish larvae, which are currently confined to comparative studies using auditory brainstem responses which are measured in tanks where the sound field is very complex (Parvulescu 1967; but see also Akamatsu et al. 2002 for possible solutions to the complexities). The influence that habitat quality has on biogenic noise generated on reefs and thus on the likely ability of larvae to detect settlement sites (Kennedy et al. 2010, present study) should be a key consideration when designing and implementing conservation strategies for degraded sites.

Our study highlights the fact that the acoustic environment is richer in information than simple quantitative variations in sound intensity. Transient content is also a good descriptor of reef quality and shows a meaningful decrease with distance from reefs. Both sound intensity and transient content generally showed similar trends with the exception of 1 Omani reef (BAHE), where transient content was variable over distance whilst sound intensity decreased in a predictable fashion. The reason for this is currently unclear since the homogenization of the transient signals is likely to increase with distance, resulting in a lower measured value of transient content. However, the fact that in this case the 2 measures do not appear to be directly related to one another highlights the potential for them to be de-coupled and possibly provide orienting larvae with more information than simple directional gradients. As long as the rate of change between transient content and sound intensity is independent, larvae could use the transient content to sound intensity ratio to tease apart the distance and quality of a reef (e.g. discern between close but poor quality, and far but good quality reefs with similar received sound intensities but contrasting transient content). This theory warrants further investigation to explore the potential for integrating different types of acoustic information in animal orientation.

It would be of great value and interest for future investigations to explore both the geographical (as per Staaterman et al. 2013 for the Caribbean) and seasonal variation in soundscapes for these regions. These investigations could be coupled with UVCs, studies on larval recruitment patterns and experiments on larval attraction to site- and time-specific soundscapes. It is worth noting that if different patterns of diel variation in reef noise between

sites were present (as found between different geographical regions by Staaterman et al. 2013), this could also affect the distance from which fish can detect different habitats. Different patterns of diel variation in reef noise could potentially exacerbate (if sound intensity increases at a higher rate for high-quality sites at night) or dampen (if sound intensity increases at a lower rate or decreases at a higher rate in high-quality sites at night) the effect of habitat quality on the distance larval recruits can detect a reef. This is especially relevant in the context of larval recruitment to reefs since studies to date have shown that fish larvae may respond negatively (i.e. swim away) to reef sound during the daytime but are attracted towards it at night (Leis et al. 2003, Tolimieri et al. 2004). How these factors interplay and the effect they may have on recruitment and avoidance of reef noise remains to be explored. Together with threats from ocean acidification (Simpson et al. 2011b) and rising temperature (O'Connor et al. 2007), our findings add to an increasing number of studies highlighting anthropogenic effects on larval recruitment, and support the need to consider and preserve the intrinsic value of soundscapes (Pijanowski et al. 2011b).

Finally, in the present study, sound intensity and transient content were found to be reliable indicators of reef quality and distance. By combining quantitative measures (e.g. sound intensity) with qualitative information of the signal (e.g. transient content) it should be possible for larvae to exploit sound not only for detecting settlement sites but also for choosing between them and thus maximizing their success in later life stages. Investigating the level to which larvae can detect and integrate this complex array of information presents some exciting new directions to explore in our quest to shine light on the 'pelagic black box'.

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