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Soundscapes and living communities in coral reefs: temporal and spatial variation

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ABSTRACT: Acoustic landscapes, or soundscapes, can vary due to biological ('biophony'), geophysical ('geophony') and anthropogenic ('anthrophony') components, and in some environments, such as many coral reefs, biophony dominates the soundscape. We compared 126 sound recordings from 3 different times of day (day, dusk and night) at 42 locations with concurrent fish and habitat surveys to investigate the relationships of acoustic parameters with biological and physical characteristics of coral reefs in the Gambier Archipelago, French Polynesia. Principal Component Analysis revealed that most of the variability in soundscapes could be described using only 4 factors: (1) full bandwidth root mean squared sound pressure level (SPL; 0.01 to 22.5 kHz in dB re 1 µPa); SPL of frequencies (2) >0.63 kHz and (3) between 0.16 and 2.5 kHz; and (4) the number of snaps made by snapping shrimp. Number of snaps in a recording and SPL above 0.63 kHz were negatively related to live coral cover, and the density and diversity of adult and juvenile fish, but positively related to dead coral cover and time of day (as the day progressed from day to dusk to night). Full bandwidth SPL and midrange SPL were positively related to sea state, depth, *Porites* coral, the coral forms 'branched' and 'massive' and whether the bottom was coverd by coral (live or dead). Soundscape recordings can contribute to a more complete assessment of ecological landscapes and, in cases where logistical constraints preclude traditional survey methods, passive acoustic monitoring may give valuable information on whether habitats are changing over time.

KEY WORDS: Coral reefs · French Polynesia · Passive-acoustic monitoring · Soundscapes

INTRODUCTION

Soundscapes are composed of biophonic, geophonic and anthropophonic sounds that are altered by propagation through the environment in which they are found (Pijanowski et al. 2011). Thus, soundscapes relate to the composition of species and the physical features of the local habitat. Soundscape cues can be used by animals to find prey, avoid predators and find suitable habitat (e.g. Montgomery et al. 2006, Slabbekoorn & Bouton 2008), but soundscapes also present a valuable but as yet underutilised method for passive ecological monitoring (Tricas & Boyle 2014).

In air, soundscape analysis has proven very useful for determining how habitat structure may predict soundscapes (Pekin et al. 2012) and for assessing species present in habitats where other survey meth-

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*Corresponding author: sophie.nedelec@bristol.ac.uk ods may be logistically difficult (Pijanowski et al. 2011). For example, canopy structure has long been recognised as being strongly correlated with species distributions and diversity (Macarthur & Macarthur 1961), and it has been more recently demonstrated that vertical forest structure attributes, as derived from light detection and ranging (LIDAR) data in a neotropical rainforest in Costa Rica, can also be used to predict acoustic diversity (Pekin et al. 2012). Thus, soundscapes are now considered an important part of landscape ecology (Pijanowski et al. 2011). Underwater, where light attenuates rapidly but sound travels 5 times faster than in air (Bradbury & Vehrencamp 1998), soundscapes offer a wealth of information about habitats and living communities. Yet, although underwater soundscapes have likely driven the evolution of hearing (Fay 2009), our knowledge of underwater soundscapes is still in its infancy. Several authors have investigated the spatial variability of soundscapes across habitats and locations, or temporal variability at one or several locations (see for example Radford et al. 2008, Kennedy et al. 2010, Piercy et al. 2014, Staaterman et al. 2014, Tricas & Boyle 2014). However, spatial and temporal variability have not yet been considered together with replication of locations or habitat types, and there remains much to be learned about the links between soundscapes and communities.

Coral reefs are naturally noisy places: fish and invertebrates produce feeding and territorial biotic sounds ('biophony', Parmentier et al. 2009, 2010, Tricas & Boyle 2014), while wind, waves and currents create geophysical sounds ('geophony', Wenz 1962, Arvedlund & Kavanagh 2009). Many species of fish and invertebrates use these natural sounds for important life-history decisions, as an orientation cue (Tolimieri et al. 2000, Simpson et al. 2004), and for selecting suitable habitat for larval recruitment at the end of the pelagic period (Simpson et al. 2005, Radford et al. 2011, Parmentier et al. 2015). Coral reefs are often highly threatened (Wilkinson 1996) making them high priority for monitoring by conservationists. But monitoring of reefs by SCUBA divers is financially and logistically challenging. Passive acoustic monitoring may offer a fast, non-invasive method for assessing the health of ecosystems because soundscapes contain biotic and abiotic information about habitats that may change over time (Qi et al. 2008).

In this study, we made acoustic recordings around coral reefs in the Gambier Archipelago, French Polynesia. We looked at a set of acoustic parameters derived from recordings and examined how these linked with fish community and benthic habitat data. We present our findings with respect to the potential of acoustic recordings of soundscapes being used for passive acoustic monitoring, paying particular attention to the use of habitats as nursery areas by coral reef fish, as survival through early developmental stages underpins population dynamics (Gosselin & Qian 1997, Gagliano et al. 2007).

MATERIALS AND METHODS

Sampling sites and data collection

This study was carried out in the lagoon surrounding Mangareva Island in the Gambier Archipelago, French Polynesia, in October 2010. The lagoon is founded on a sunken volcano with several islands encircled by a barrier reef atoll that reaches the water surface in some areas. Since tropical bays often provide valuable nursery areas for marine species (Doherty 2002), in this study 7 bays were identified on 3 of the largest islands as representing typical nursery habitats within the lagoon (Fig. 1).

In each of the 7 bays we randomly selected 3 fringing reef and 3 coral pinnacle (coral heads 10 to 30 m in diameter) locations, totaling 42 recording sites (6 per bay). At each recording site we conducted a habitat survey, 3 fish counts and three 3 min acoustic recordings. Habitat surveys were conducted once at each of the 42 locations, while fish counts and acoustic recordings were made during the time intervals 08:00–15:00, 16:00–18:00 and 18:30–21:30 to represent day, dusk and night respectively. This resulted in 126 acoustic recordings and fish surveys.

On each pinnacle and fringing reef location, three 20 m transects were placed parallel to the shore, 2.5 m apart, so that the centre of the central transect was at the location of the acoustic recording. For habitat surveys, substrate was recorded every metre (line intercept transect method) defining coral genus, form, state (dead or alive), macro-algae, rubble, sand or rock. These point observations were used to calculate percentage coverage of each type of substrate.

Acoustic recordings were taken 50 cm above the substrate from an anchored inflatable kayak to avoid the sound of waves slapping on the hull. Recordings were made with an omnidirectional hydrophone (HiTech HTI-90, flat frequency response 0.1–30 kHz, sensitivity −165 dB re 1 V μPa^{-1}) and a fully calibrated solid state recorder in wav format (Edirol R-09, 44.1 kHz sampling rate, 16 bit rate, calibrated by calculating the ratio between recorded voltage and

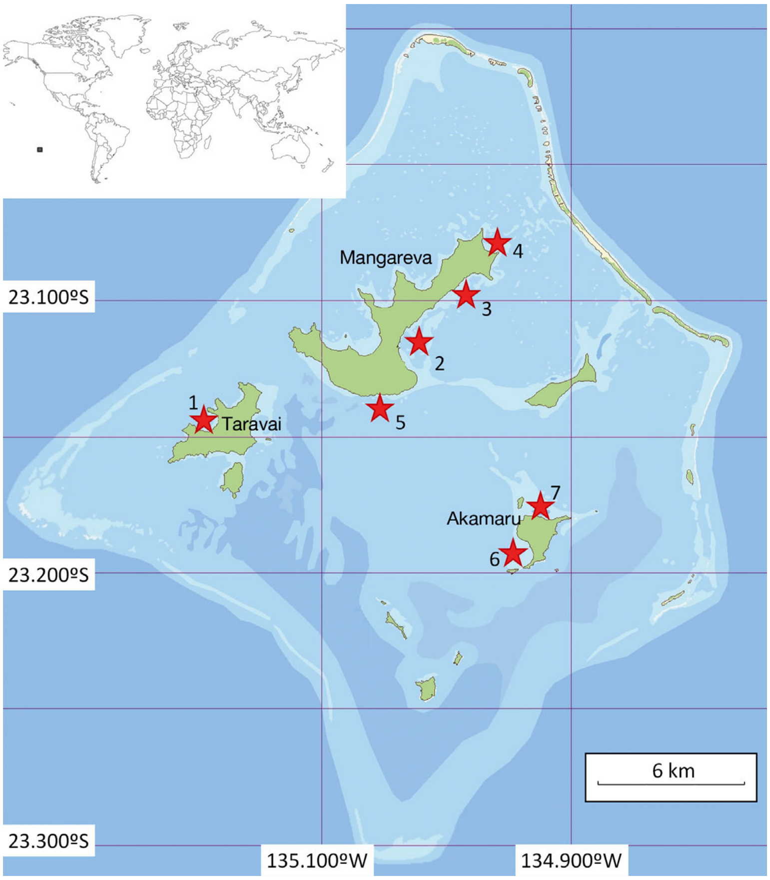

Fig. 1. Location of the 7 bays (stars; Numbers correspond to the order in which they were sampled) in the Gambier Islands (black square in map inset) where acoustic recordings at fringing reefs and pinnacles were made. (Copyright ©2006 Mr. Minton. Licence notice and disclaimer of warranties: http://creativecommons.org/licences/by/4.0/legalcode. Modified from http://www.flickr.com/photos/evsmap/200349227)

known input voltage of a sine wave). Sea state was 0 to 4 on the Beaufort scale, and acoustic recordings were not made during rain. Water depth, measured with a weighted tape measure, was between 0.6 and 4.5 m. Maximum tidal range in the area is only 1.1 m; thus tidal noise was not a concern.

Fish surveys were conducted along the same transects as the habitat surveys with a width of 1 m and were conducted immediately after the acoustic recordings. Active (not hiding in coral at rest) juvenile and adult fishes were recorded to species level (except for Gobiidae and Blenniidae families, in which counts and species-level identification by underwater visual census are difficult, and thus were excluded to avoid potential unreliable data; as in Lecchini & Galzin 2005). Fish surveys were conducted by the same diver during 2 passes over each transect. On the first pass, the diver swam quickly (>5 m min^{-1}) to record mobile fishes that swam within the transects but usually fled with the divers' approach. On the second pass, the diver swam more slowly (<1 m min^{-1}) to record site-attached species. At night a dive torch was used, which is a limited method, as visibility is reduced to the area illuminated and some fish may be attracted or repelled by the light (Lecchini et al. 2007). Survey data were used to calculate fish density and Shannon-Wiener index of diversity for all fishes, as well as juveniles and adults separately.

Acoustic analysis

Acoustic recordings were analysed in MATLAB (version 7.10.0 2010a, MathWorks). Each 3 min recording was subsampled to provide 5 clean 5 s subsamples from each recording; each subsample was >5 s apart from another subsample and was inspected aurally and visually via spectrograms (which show the distribution of energy in a recording across frequencies and time) to ensure there was no human-introduced sound (any subsamples containing anthrophony such as boat engine or wave slap noises were excluded). Several parameters were calculated for each subsample: root mean squared (RMS) full bandwidth (0.01 to 22.05 kHz) sound pressure level (SPL; dB re 1 µPa); RMS SPL at 1/3 octave bands centred at 0.025 to 16 kHz; and the number of snaps produced by snapping shrimp (*Alpheus* sp. and *Synalpheus* sp.) in each recording. The number of snaps was calculated by setting a threshold level on the raw data; any transient spike that was less than 0.2 s and above the threshold was counted as a snap by a shrimp. The detection threshold was set by visually inspecting the waveform for each period of the day. The level was then set above the background noise where snapping shrimp clicks could easily be discriminated from background chatter (Radford et al. 2008). Note that whenever averages of SPLs were calculated in our study, they were converted into the linear scale before the mean was calculated; the resulting mean was then translated back into the dB scale.

Statistical analysis

Principal Component Analysis (PCA) is a statistical procedure that uses orthogonal transformation to convert a set of observations of possibly correlated variables into a set of linearly uncorrelated variables called principal components (PCs). We used 3 separate PCAs on acoustic, habitat survey and coral form data to reduce the number of variables we were handling. We describe the results of these PCAs in the methods because the variables which were created were then used for the final Multi Factorial Analysis (MFA).

Third octave band SPLs (in dB re 1 µPa) were log transformed and normalized to meet the assumptions of the PCA analysis before they were reduced to the primary axes of variation using PCA. PC1 (53.5% of variance; see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m524p125_supp.pdf) indicated that all octave bands were correlated in the same way and could thus be considered loudness and be represented by full bandwidth SPL. PC2 (26.3% of variance; Figs. S1 & S2 in the Supplement) indicated that patterns in amplitude of third octave bands above 0.63 kHz were different from those below 0.63 kHz and could give some information on dominant pitch in the soundscape. PC3 (8.5% of variance; Fig. S2 in the Supplement) indicated that third octave bands between 0.16 and 2.5 kHz were characteristically different from frequencies above and below and could thus be considered loudness in mid frequency range (henceforth referred to as midrange SPL). Acoustic parameters were thus reduced to those described by the PCs, plus the count of number of snaps (see Table 1 for detailed descriptions).

A second PCA of habitat survey data (live coral, dead coral, macroalgae, rubble or sand) revealed that benthos was best described according to whether the substrate was coral-based or not coral-based (PC1 = 56.9% of variance separated live and dead coral from macroalgae, rubble and sand; see Fig. S3 in the Supplement), and then whether the substrate was live coral or not (PC2 = 28.0% of variance separated live coral from all other factors; see Fig. S3 in the Supplement). A third PCA based on coral form (massive, branched, tabular and encrusting) revealed that PC1 (49.0% of variance) was driven by whether coral was massive and PC2 (26.9%) by whether coral was branched (see Fig. S4 in the Supplement). Habitat survey data were thus reduced to those described by PCs (see Table 1 for detailed descriptions, including physical and fish community factors).

Table 1. Acoustic, physical, fish and habitat factors used in the Multiple Factor Analysis (MFA). SPL: sound pressure level; PCA: Principal Component (PC) Analysis

Factors	Description
Acoustic	
Fullband	Full bandwidth SPL: 0.01–22.05 kHz
Pitch	PC2 of acoustic PCA
Midrange	PC3 of acoustic PCA
Snaps	Threshold analysis
Physical	
Bay	Bay ID
Location in bay	Individual location ID
Habitat type	Pinnacle or fringing reef
Time of day	Morning, evening, night
Depth	Water depth
Sea state	Beaufort wind scale
Fish	
Adult density	Fish m^{-2}
Juvenile density	Fish m^{-2}
All fish density	Fish m^{-2}
Adult diversity	Shannon-Wiener index
Juvenile diversity	Shannon-Wiener index
All fish diversity	Shannon-Wiener index
Habitat	
Coral cover	PC1 of habitat PCA
Dead vs. live coral	PC2 of habitat PCA
Porites	% cover
Pocillopora	% cover
Acropora	% cover
Montipora	% cover
Massive	% cover
Branched	% cover

The factors in the 4 categories in Table 1 (and described below) were then subjected to an MFA (Escofier & Pagès 1994). MFA extracts the main factors or components that account for interrelations in observed data, thereby reducing correlational data to a smaller number of explanatory dimensions or factors. Factors were grouped into acoustic (Aco), physical (Phys), fish (Fish) and habitat (Hab). Acoustic factors included PCs from the acoustics PCA: PC1 — full bandwidth SPL (Fullband); PC2 — higher values at higher frequencies, positive above 0.63 kHz (Pitch; PC2); PC3 — higher values closer to 1.6 kHz, positive between 0.16 and 2.5 kHz (Midrange; PC3) and the number of snaps (Snaps). Physical factors were habitat type (fringing or pinnacle; HAB), time of day (ToD), Bay, Sea state, Depth and individual location within a habitat type (Id). Fish factors were adult density (ADe), juvenile density (JDe), all fish density (AllDe), adult Shannon-Wiener diversity (ADi), juvenile S-W diversity (JDi) and all fish diversity (AllDi). Habitat factors were percentage cover of coral types, and PC1 (Coral) and PC2 (DeadCoral) from the habitat PCA.

RESULTS

Benthos

The most prevalent benthos type across all locations was dead coral (Fig. 2a). The dominant genus of live and dead coral was *Porites*, followed by *Acropora* (Fig. 2b). The dominant form of coral was branched (Fig. 2c). Bay 1 stood out with high macroalgae cover (Fig. 2a), while Bay 5 had very low live coral cover but very high dead coral cover (Fig. 2a).

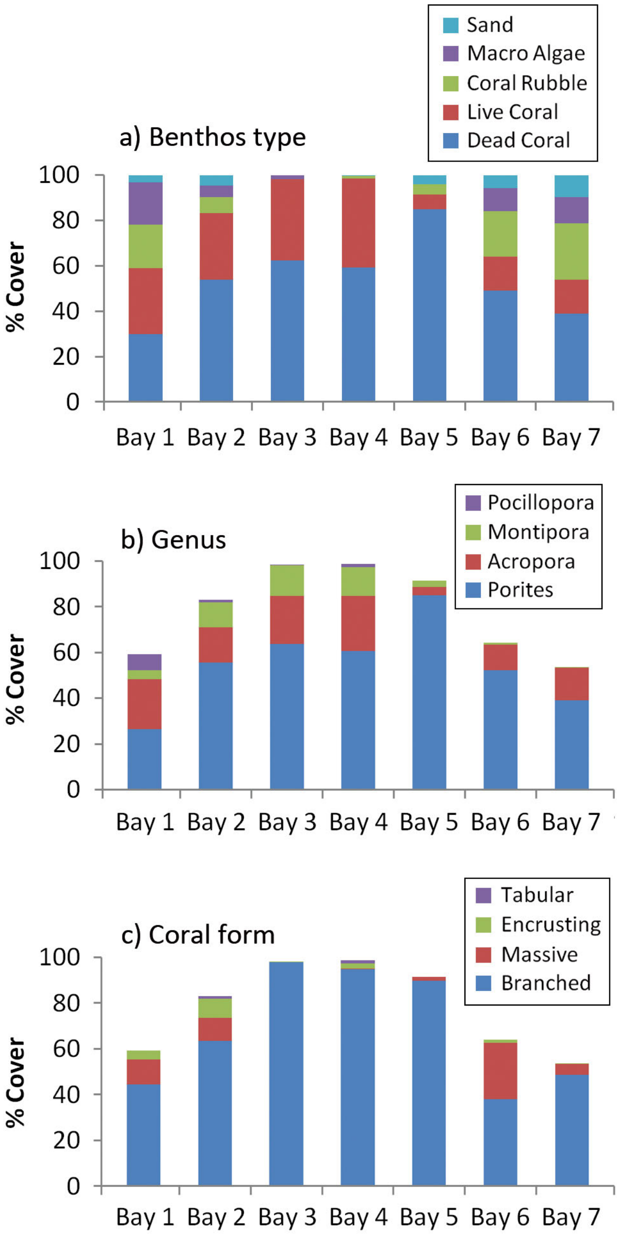

Fig. 2. Percent cover from habitat surveys

Fish community

Fish density and diversity of juveniles and adults varied in similar ways across bays and times of day. Fish were least dense and diverse in Bay 5 (Fig. 3a,b). Active adult and juvenile fish were less numerous and less diverse at night than during the day or dusk (Fig. 3c,d).

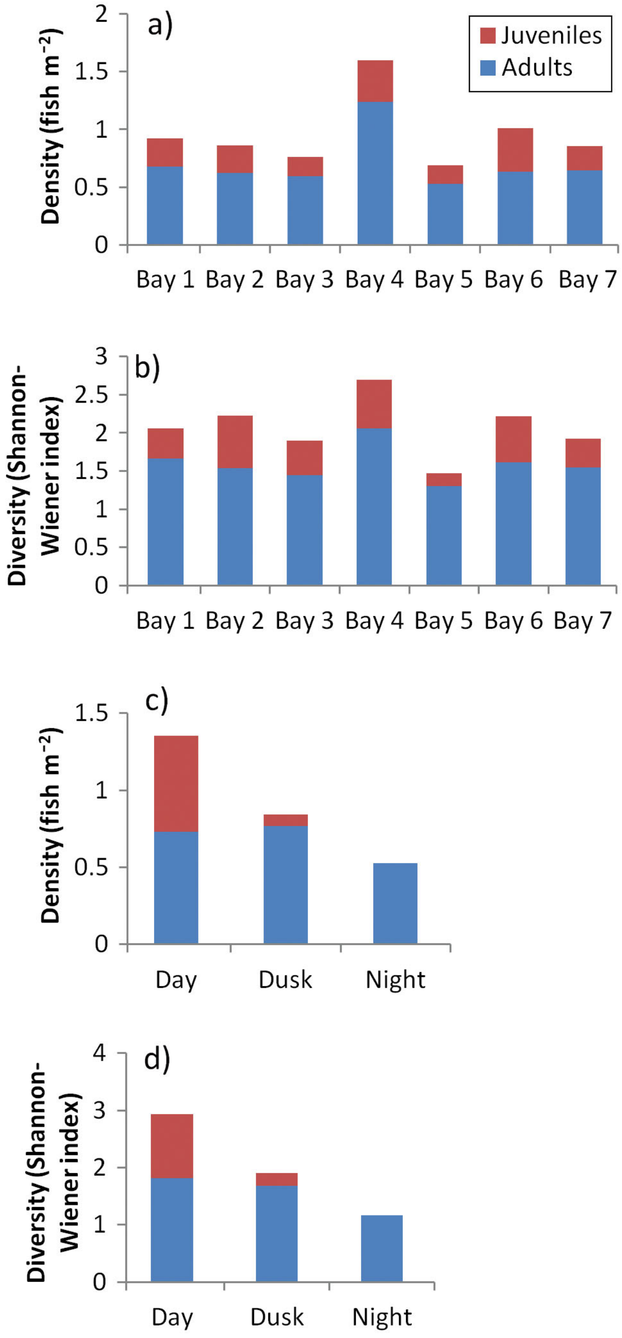

Fig. 3. Fish survey data for adults and juveniles for each bay and time of day

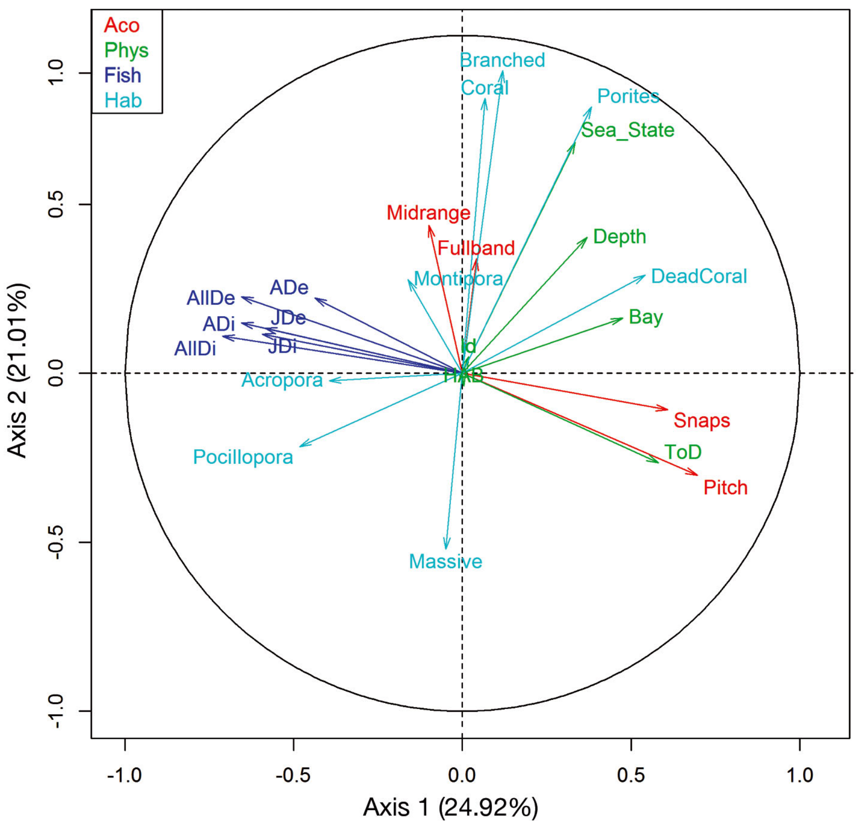

Fig. 4. Correlation circle for the 2 primary axes (Axis 1 and Axis 2) from the Multiple Factor Analysis (MFA) on the 4 factors: acoustic (Aco), physical (Phys), fish (Fish) and habitat (Hab). Variables far from the centre and close to each other are significantly and positively correlated (r close to 1). Length of arrows: strength of the link between raw data and derived primary axes. Acoustic factors: full bandwidth (Fullband) sound pressure level (SPL), frequency bands >0.63 kz (Pitch), between 0.16–2.5 kHz (Midrange), and number of snaps (Snaps) (see Table 1 for more details). Physical factors: habitat type (HAB; fringing or pinnacle), time of day (ToD) and individual location within a habitat type (id). Fish factors: adult density (ADe), juvenile density (JDe), all fish density (AllDe), adult Shannon-Wiener (S-W) diversity (ADi), juvenile S-W diversity (JDi) and all fish diversity (AllDi). Habitat factors: percentage coverage of coral types, Coral and DeadCoral. For details see 'Materials and methods: Statistical analysis'

MFA: primary axes

The results from the MFA revealed correlations between qualitatively different factors (acoustic, physical, fish and habitat factors; Fig. 4). The 2 first axes of the MFA described 24.9 and 21.0% of the variance within the data respectively. Only the first 2 axes are discussed here as the acoustic factors did not make a large contribution to the third axis (see Tables S1–S4 in the Supplement for more detailed results of MFA). Axis 1 was influenced by predominantly biological factors (fish, snapping shrimp, coral genus, whether coral was alive or dead, but also time of day). Axis 2 was influenced by predominantly physical factors (sea state, depth, benthos, but also coral form). These 2 axes of the MFA also separated the acoustic factors (number of snaps and SPL at frequencies above 0.63 kHz along Axis 1; full bandwidth SPL and midrange SPL along Axis 2).

Table 2. Correlations between acoustic factors and biological factors that contributed strongly to Multiple Factor Analysis (MFA) Axis 1. Pitch = frequency bands >0.63 kz; Snaps = shrimp snaps; Adult/juvenile: fish factors

	Pitch	Snaps
Snaps	0.56	
Bay	0.14	0.16
Time of day (ToD)	0.28	0.44
Adult density	−0.16	−0.24
Juvenile density	−0.27	−0.31
All density	−0.28	−0.35
Adult diversity	−0.28	−0.33
Juvenile diversity	−0.19	−0.22
All diversity	−0.29	−0.34

MFA Axis 1: linking snaps and high frequency SPL with biological factors

The factors which contributed the most to MFA Axis 1 were Pitch, Snaps, ToD, Bay and all fish-based measures (Fig. 4, see Table S3 in the Supplement). ToD and DeadCoral were positively correlated with Pitch and Snaps, while fish-based measures correlated negatively with Pitch and Snaps (Table 2). The overall mean number of snaps from all 586 subsamples was 85.3. The number of snaps was lowest in Bays 1 (mean = 47.1) and 5 (35.8), and highest in Bay 7 (150.7), as well as lowest during the day and highest at night (day = 46.1; dusk = 61.3; night = 159.3). The MFA revealed that habitat type (pinnacle or

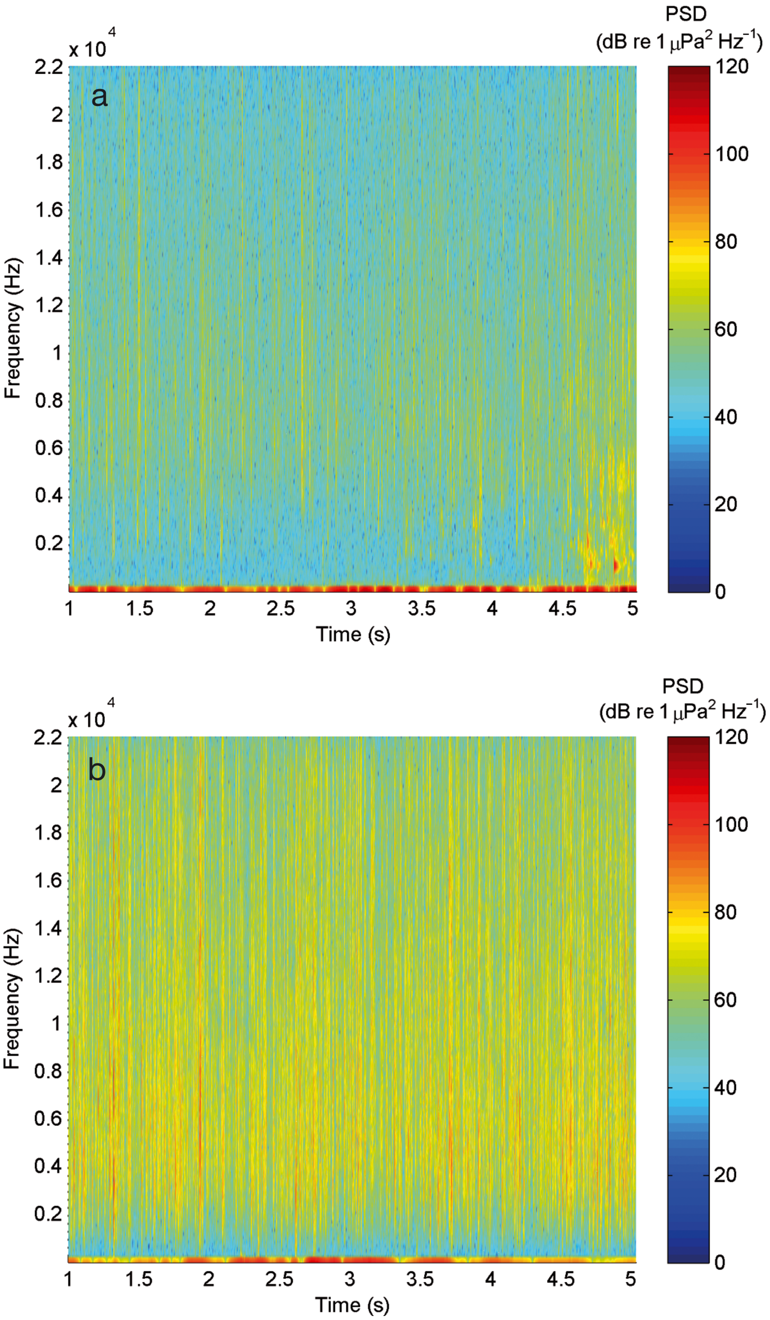

Fig. 5. Example spectrograms of 2 recordings with the highest and lowest number of snaps from snapping shrimp. (a) Snaps detected = 0: This was a morning recording, the location had 36.6 % live coral cover, fish Shannon-Wiener (S-W) diversity was 1.35, fish density was 1.95 fish m^{-2}, cover of *Acropora* and *Pocillopora* corals were 15 and 11.67 % respectively. Some geophony (wave noise) can be seen in the spectrogram between 4.5 and 5 s. (b) Snaps detected = 717 (yellow vertical lines): This was a night recording, the location had 3.33 % live coral cover, fish S-W diversity was 1.01, fish density 0.32 fish m^{-2}, cover of *Acropora* and *Pocillopora* corals were 20 and 0 % respectively. Spectrograms were created in MATLAB 7.10.0 (2010a). Fast Fourier transform (FFT) length = 256, Hamming window, overlap = 50 %

fringing reef) was not correlated with any of the acoustic factors. This was evident in the number of snaps: the mean (± SD) was lower on pinnacles (80.2 ± 75.9) than on fringing reef (90.4 ± 101.3), showing that the variability was very high. Fig. 5 shows the recordings that had the highest and lowest number of snaps. Bay 5 had very low live coral cover (6.3 %) but very high dead coral cover (85 %), which linked to a high mean number of snaps (Bay 5 = 89.6, all bays = 85.3) and SPL above 0.63 kHz (Bay 5 = 90.4 dB, all bays = 89.9 dB).

MFA Axis 2: linking full bandwidth and midrange SPL with physical factors

The factors which contributed the most to MFA Axis 2 were Fullband, Midrange, Sea state, Depth, *Porites* coral and the coral forms Branched and Massive (Fig. 4, see Table S3 in the Supplement). Except for massive coral, all of these physical factors, as well as a coral cover, were correlated positively with the acoustic factors (Table 3). Adult fish density was also positively correlated with Midrange (Fig. 4, Table 3). For example, the lowest Fullband was 100.89 dB re 1 μPa from a location where percentage cover of live and dead coral was 55 %, branched coral was 37 %, massive coral was 18 %, sea state was 1 and depth was 1.1 m. Conversely, the highest Fullband was 137.73 dB re 1 μPa from a location with cover of 100 % live and dead coral, 100 % branched coral, 0 % massive coral, a sea state of 4 and depth of 1.9 m. Fig. 6 shows the correlation between sea state and Fullband. Fig. 7

Table 3. Correlations between acoustic and biological factors that contributed to Multiple Factor Analysis (MFA) Axis 2

	Fullband (0.01–22.5 kHz)	Midrange (0.16–2.5 kHz)
Midrange	0.28	
Coral	0.29	0.39
Sea state	0.34	0.17
Depth	0.15	0.25
Porites	0.28	0.23
Massive coral	−0.09	−0.23
Branched coral	0.27	0.39
Adult density	−0.04	−0.2

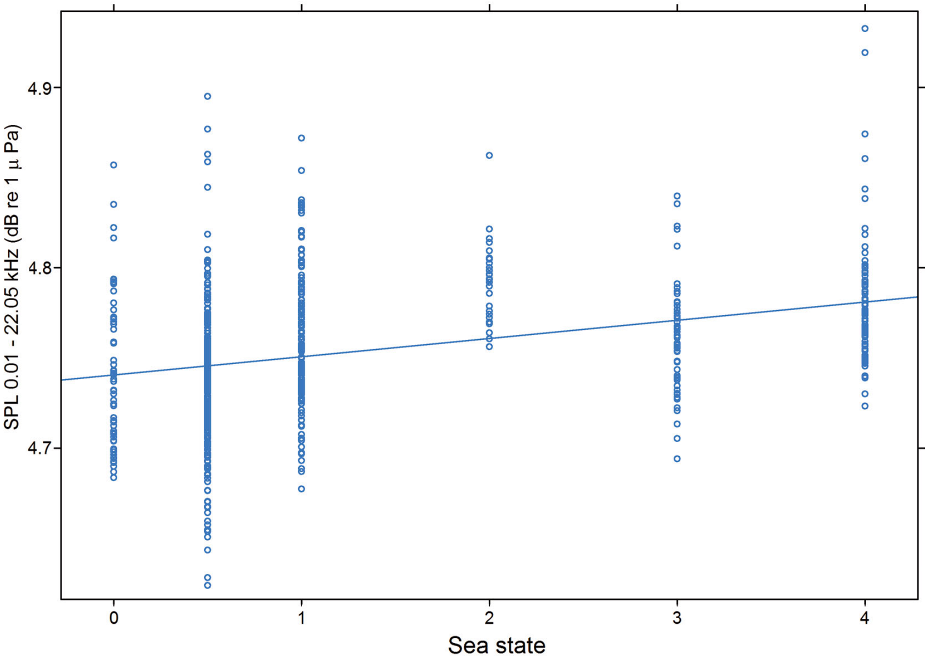

Fig. 6. Correlation between sea state and full bandwidth (Fullband; 0.01–22.5 kHz) sound pressure level (SPL)

shows the relationship between coral cover and full bandwidth SPL at each sea state. Bay 1 stood out with high macroalgae cover (mean: Bay 1: 18.6%; all bays: 7.0%), and low coral cover, which linked to low Fullband (Bay 1 = 115.0 dB; all bays = 116.7 dB) and Midrange (Bay 1 = 88.8 dB; all bays = 92.2 dB).

Acoustic and fish factors contribute almost equally to MFA Axis 1 (Fig. 8). Acoustic factors are closer to physical factors on MFA Axis 2. Acoustic factors and habitat factors are not close on the groups representation plot, but they are closer on Axis 1 than 2. Habitat factors contribute the most to MFA Axis 2 (Fig. 8).

DISCUSSION

Our analyses of soundscapes revealed that acoustic recordings could be reduced to 4 parameters with associations to the biological and physical characteristics of the surveyed coral reefs. The number of snaps in a recording and the sound pressure level (SPL) above 0.63 kHz were negatively related to live coral cover and the density and diversity of adult and juvenile fish, but positively related to dead coral cover; number of snaps and SPL above 0.63 kHz increased from day to dusk to night. Full bandwidth

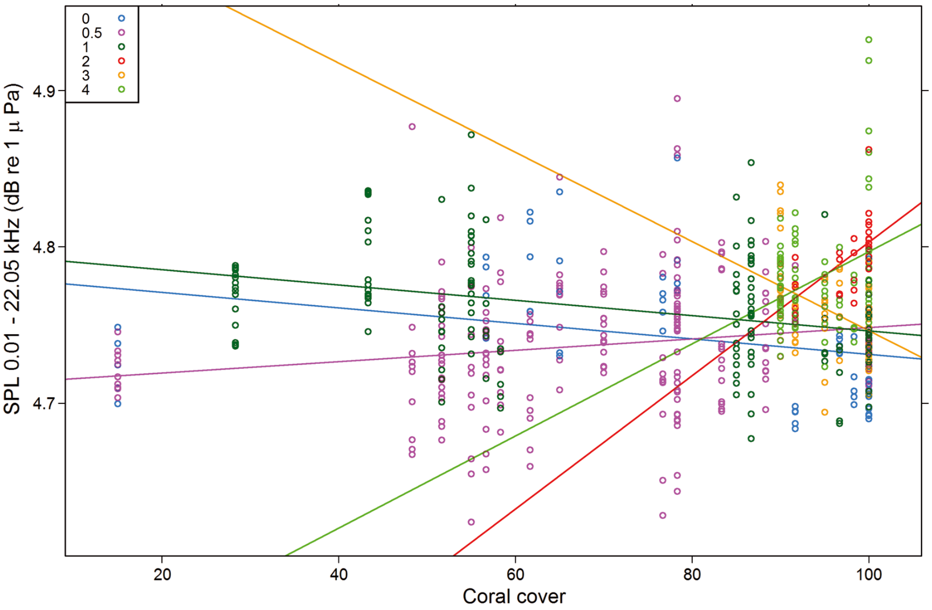

Fig. 7. Correlation between percentage coral cover and full bandwidth (0.01–22.5 kHz) sound pressure level (SPL) at each sea state (0–4)

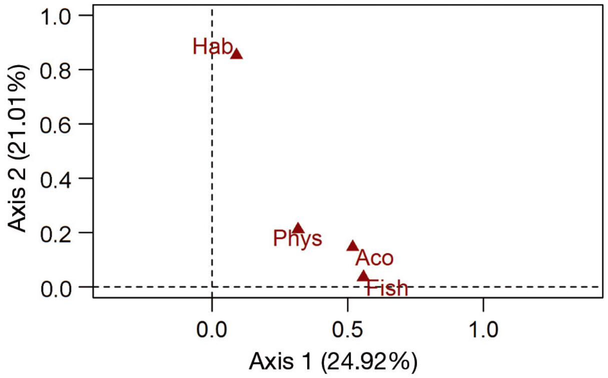

Fig. 8. Groups representation: relative strength of the 4 groups of factors (Aco: acoustic, Phys: physical, Fish: fish, Hab: habitat) in contributing towards the 2 primary axes from the Multiple Factor Analysis (MFA)

and midrange SPL (0.16 to 2.5 kHz) were positively related to sea state, depth, *Porites* coral, coral forms branched and massive and whether the benthos was coral (live or dead). Our findings are consistent with previous studies in this area (Radford et al. 2008, Kennedy et al. 2010, McWilliam & Hawkins 2013, Staaterman et al. 2013) in that we found temporal variability in soundscapes and correlations between some sound parameters and assessments of fish and benthic habitat. Thus, passive acoustic monitoring is a useful tool for monitoring the health of coral reef ecosystems. This must be taken with the caveat that acoustic monitoring cannot replace traditional visual survey methods (Staaterman et al. 2013), but in cases where logistical constraints preclude extensive traditional survey methods, such as short sampling windows, limited trained personnel, dangerous conditions or wildlife, or financial limitations, passive acoustic monitoring gives indications about habitat change over time.

Some of the differences we observed in different bays related to fundamental differences in community structure that would be of concern in a monitoring programme are the following: Bay 1 stood out with a high macroalgae cover suggesting a shift from coral to algae, while Bay 5 had very low live coral cover but very high dead coral cover, suggesting recent disturbance. If these sites had been monitored over time, we would expect the full bandwidth and midrange SPLs to have diminished with the reduction in coral cover associated with increased macroalgae cover in Bay 1, while in Bay 5 the number of snaps and SPL above 0.63 kHz would have increased with a shift from live to dead coral cover. This was reflected in the differences from the means we observed for each respective acoustic factor. In both cases (recent disturbance or long-term shift), if passive acoustic monitoring were implemented, changes from previously observed patterns in these acoustic parameters could point to the type of environmental change that was occurring, and thus potentially help to direct further observations and focus conservation efforts.

The number of snaps correlated negatively with live coral cover, although higher frequency sounds of snapping shrimp have previously been linked with high coral cover and diversity (Kennedy et al. 2010). This is the first time that live coral cover has been linked with the number of snaps, rather than only the bandwidth in which snaps are usually found. A potential explanation for our finding is that snapping shrimp can be highly abundant in dead or fragmented reefs or rubble (Enochs et al. 2011). In our study, a positive correlation was found between dead coral cover and the number of snaps. Considering that settlement-stage larval fish are attracted to the higher frequency component of reef noise encompassed in snapping shrimp sounds (Simpson et al. 2008), dead coral habitats harbouring snapping shrimp may be larval population sinks. Higher full bandwidth SPLs were also recorded over coral (live and dead), particularly during high sea states (Fig. 7); a reason for this, other than presence of snapping shrimp, may be that hard substrates reflect sound better, and thus sounds are likely to travel further across such landscapes.

Although different habitats experience different geophony and this can affect the biophonic elements of the soundscape, we did not find that sea state was correlated with the number of snaps counted in a recording (and therefore is unlikely to affect this type of invertebrate abundance estimate). Sea state affected the full bandwidth SPL in a predictable way (higher sea states led to higher SPLs; as per Wenz 1962, their Fig. 6). However, various other physical characteristics of the coral reef locations surveyed covaried with full bandwidth SPL despite variability in sea state.

Acoustic recordings could not be used to predict the density or diversity of juvenile fish differentially to adults; thus this style of passive monitoring does not seem suited to assessing nursery habitats. An acoustic parameter that was positively linked with adult fish density was midrange SPL (0.16 to 2.5 kHz). This frequency range encompasses the greatest sensitivity of fish hearing (see for example Ladich 1999, 2000, Horodysky et al. 2008, Wright et al. 2010). While we accept that there are limitations to auditory brainstem response measures of fish hearing in tanks due to the inability to establish absolute hearing thresholds, we acknowledge that these studies do reveal that most fish have a U-shaped audiogram. All fish studied so far can hear, and fish may be listening to many different sounds which make up 'acoustic daylight' (Buckingham et al. 1992). Salient sound sources which fall in this range include fish vocalisations, which many reef species emit, particularly damselfish (Kihslinger & Klimley 2002).

For our short-term, rapid assessment, we monitored each reef location at 3 times of the day (day, dusk, night) and found that time of day had a strong influence on the number of snaps, which also correlated negatively with measures of the fish community. It is possible that the negative relationship between snaps and fish was driven by the low overlap in active periods of most fish and snapping shrimp (more fish were active during the day, while more snaps were counted at night). However, time of day was not strongly correlated with full bandwidth or midrange SPLs (0.16 to 2.5 kHz), sound characteristics that were more strongly linked with unchanging physical characteristics such as benthos and coral form (as well as sea state). While clear relationships between acoustic and environmental surveys were found in this study, the presence of diel, lunar, seasonal and annual patterns would need to be taken into account when designing comprehensive long-term acoustical monitoring programmes and when drawing conclusions from data (Radford et al. 2008).

One understudied aspect of underwater soundscapes from the perspective of the fish and invertebrates that use this noise for orientation is the particle motion component of sound. Particle motion is detected by all fish and many invertebrates (Popper & Fay 1993), and can be measured using an accelerometer, particle velocity sensor, or pair of hydrophones (Mann 2006). This aspect of sound is important for determining the spatial scale over which acoustic cues can be used, because particle motion attenuates more rapidly than pressure, with attenuation varying according to frequency and bathymetry (Mann 2006).

In addition to sound pressure level there are several soundscape indices that have been developed such as 'Entropy and Acoustic Complexity Index', which can be computed in *seewave*, or 'Acoustic Diversity', Acoustic Evenness', 'Bioacoustic Index' and the 'Normalized Difference Soundscape Index' in *sound ecology*, using R software. Future work will determine if these indices provide insight into the reef system. It would be interesting to produce predictive models using acoustic factors as response variables, and measured habitat and fish variables as predictors.

Overall, our findings reveal that simple parameters derived from acoustic recordings can be used to predict certain aspects of coral reef communities and their physical characteristics. While a recording of a soundscape is not a full assessment of a habitat, it is a tool for monitoring long term changes or large scale spatial differences, provided diel, lunar and seasonal patterns are taken into account (Radford et al. 2008, Staaterman et al. 2013). Climate change, coastal development and overfishing are threatening reefs worldwide (Harley et al. 2006, Bruno & Selig 2007); thus passive acoustic monitoring may be particularly useful where time and money restrict the number of visual assessments. Although diel variation must be considered, we suggest that passive acoustic monitoring is a less invasive, and perhaps more effective, method for monitoring at night than visual methods, which require the use of torches or flashlights. Thus, acoustic monitoring may contribute to more comprehensive habitat assessments.

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