









RESEARCH ARTICLE

The sound of recovery: Coral reef restoration success is detectable in the soundscape

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Abstract

1. Pantropical degradation of coral reefs is prompting considerable investment in their active restoration. However, current measures of restoration success are based largely on coral cover, which does not fully reflect ecosystem function or reef health.
2. Soundscapes are an important aspect of reef health; loud and diverse soundscapes guide the recruitment of reef organisms, but this process is compromised when degradation denudes soundscapes. As such, acoustic recovery is a functionally important component of ecosystem recovery.
3. Here, we use acoustic recordings taken at one of the world's largest coral reef restoration projects to test whether successful restoration of benthic and fish communities is accompanied by a restored soundscape. We analyse recordings taken simultaneously on healthy, degraded (extensive historic blast fishing) and restored reefs (restoration carried out for 1–3 years on previously degraded reefs). We compare soundscapes using manual counts of biotic sounds (phonic richness), and two commonly used computational analyses (acoustic complexity index [ACI] and sound-pressure level [SPL]).
4. Healthy and restored reef soundscapes exhibited a similar diversity of biotic sounds (phonic richness), which was significantly higher than degraded reef soundscapes. This pattern was replicated in some automated analyses but not others; the ACI exhibited the same qualitative result as phonic richness in a low-frequency, but not a high-frequency bandwidth, and there was no significant difference between SPL values in either frequency bandwidth. Furthermore, the low-frequency ACI and phonic richness scores were only weakly correlated

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despite showing a qualitatively equivalent overall result, suggesting that these metrics are likely to be driven by different aspects of the reef soundscape.

5. *Synthesis and applications.* These data show that coral restoration can lead to soundscape recovery, demonstrating the return of an important ecosystem function. They also suggest that passive acoustic monitoring (PAM) might provide functionally important measures of ecosystem-level recovery—but only some PAM metrics reflect ecological status, and those that did are likely to be driven by different communities of soniferous animals. Recording soundscapes represents a potentially valuable tool for evaluating restoration success across ecosystems, but caution must be exercised when choosing metrics and interpreting results.

KEYWORDS

bioacoustics, coral reef, ecoacoustics, ecosystem monitoring, passive acoustic monitoring, restoration, soundscape

1 | INTRODUCTION

A suite of global and local anthropogenic stressors are causing unprecedented damage to tropical coral reefs around the planet (Harborne et al., 2017). This imperils biodiversity and jeopardises the livelihoods of hundreds of millions of people who rely on reefs for food, income and storm protection (Cinner, 2014). In response, hundreds of conservation programmes worldwide are implementing a range of active physical interventions aimed at restoring heavily degraded reef systems (Boström-Einarsson et al., 2020; Duarte et al., 2020). These interventions are primarily focussed on increasing coral cover, by using different methods to enhance asexual reproduction (e.g. collecting and replanting coral fragments; Williams et al., 2019), sexual reproduction (e.g. releasing fertilised coral larvae into the water; de la Cruz and Harrison (2017)) and larval settlement (e.g. stabilising loose substrate; Ceccarelli et al. (2020)). However, while many such restoration programmes are effective at growing corals, very few attempt to measure the wider ecosystem health of restored reefs (Hein et al., 2017). For example, healthy fish and invertebrate populations are essential components of ecosystem functioning and service provision on reefs (Graham et al., 2015; Sato et al., 2020), but their recovery remains inadequately tested by the majority of reef restoration programmes (Boström-Einarsson et al., 2020).

Soundscapes represent a functionally important measure of a reef's ecological status. On healthy reefs, a wide range of soniferous fishes and invertebrates contribute to a loud and diverse soundscape that plays an important role in ecosystem functioning; acoustic cues in the soundscape guide the recruitment and settlement behaviour of many reef organisms (Montgomery et al., 2006; Simpson et al., 2008). In turn, reef degradation causes changes to the soundscape that reduce its attractiveness to settlement-stage fishes and invertebrates (Gordon et al., 2018; Lillis et al., 2016). Furthermore, many of the organisms contributing to reef soundscapes are

nocturnal and/or cryptic, meaning that soundscapes reflect a component of the biological community that is not measured by traditional visual surveys. As such, reef soundscapes contain information about the presence, diversity, abundance and behaviour of organisms that are difficult to survey visually and underpin important functional processes central to population replenishment.

Recent technological developments in sound-recording hardware (microphones, hydrophones and digital recorders) and software (computational approaches to store and process large acoustic datasets) have led to increasing use of passive acoustic monitoring (PAM) to produce rapid, objective, cost-effective assessments of ecosystem health (Gibb et al., 2019; Merchant et al., 2015). Several studies have used PAM to measure the recovery of populations of bats, birds and sponge communities in the wake of habitat restoration (Borker et al., 2020; Butler et al., 2016; Helms et al., 2018; Smith & Gehrt, 2010). Several approaches to PAM have been used to measure different aspects of coral reef ecosystem health. Some studies have analysed the frequency and time of occurrence of individual biotic sounds; for example, McWilliam et al. (2017) described spatial and temporal variation in the choruses of unidentified fishes on the Great Barrier Reef. Other studies have applied automated computational metrics that produce single values describing particular aspects of the whole soundscape. A recent systematic review revealed that the two most commonly used of these computational metrics are sound-pressure level (SPL) and the acoustic complexity index (ACI), which between them appeared in nearly two-thirds of all studies using sound to monitor marine ecosystems (Pieretti & Danovaro, 2020). SPL is a root-mean-square average of the amplitude of a soundscape within a given time and frequency range; it measures the total acoustic energy produced by the reef ecosystem. Several studies have found that higher SPL values are associated with marine-protected areas and high densities of reef fishes, suggesting that SPL may be driven by the abundance of soniferous animals (Kaplan et al., 2015; Piercy et al., 2014). The ACI is an algorithm

designed to quantify variation in biotic sound by summing the differences between sound levels in adjacent frequency bandwidths and time steps (Pieretti et al., 2011). Some studies have found that reefs with high fish diversity had higher ACI values than low-diversity reefs (Bertucci et al., 2016; Harris et al., 2016); suggesting that the ACI may be driven by the diversity of soniferous animals. Furthermore, severe cyclones and bleaching caused changes across both SPL and ACI on the Great Barrier Reef (Gordon et al., 2018), suggesting that both of these metrics are altered by habitat degradation. Despite these promising applications of PAM, however, doubts remain concerning the generality of findings across different biogeographical contexts and seasons, and the extent to which computational metrics can describe biological variability without being affected by anthropogenic and geophysical background noise (Bohnenstiehl et al., 2018; Kaplan et al., 2018; Staaterman et al., 2017). If these challenges can be overcome, there is hope that PAM could offer quantitative, objective, easy-to-collect measures of reef health in both natural and actively restored reef systems (Obura et al., 2019).

In this study, we use PAM to assess whether coral restoration leads to the recovery of reef soundscapes. Using recordings taken on naturally healthy, degraded and actively restored patches of

habitat within one of the world's largest coral reef restoration programmes, we compare soundscapes using both manual identification of biotic sounds and automated computational metrics. These approaches allow us to evaluate the success of ecosystem restoration in a novel manner that is complementary to existing metrics of success. By measuring the soundscape as an emergent property of a restored ecosystem, we can evaluate the impact of restoration on a taxonomically broad and functionally important aspect of ecosystem health.

2 | MATERIALS AND METHODS

2.1 | Study site

This study uses acoustic recordings taken in August–September 2018 and June–July 2019 as part of the monitoring programme of the Mars Coral Reef Restoration Project (www.buildingcoral.com) at Badi and Bontosua Islands, in the Spermonde Archipelago (South Sulawesi, Central Indonesia; 4°56.9'S, 119°18.1'E; Figure 1). Reefs in South-East Asia are heavily threatened by local anthropogenic

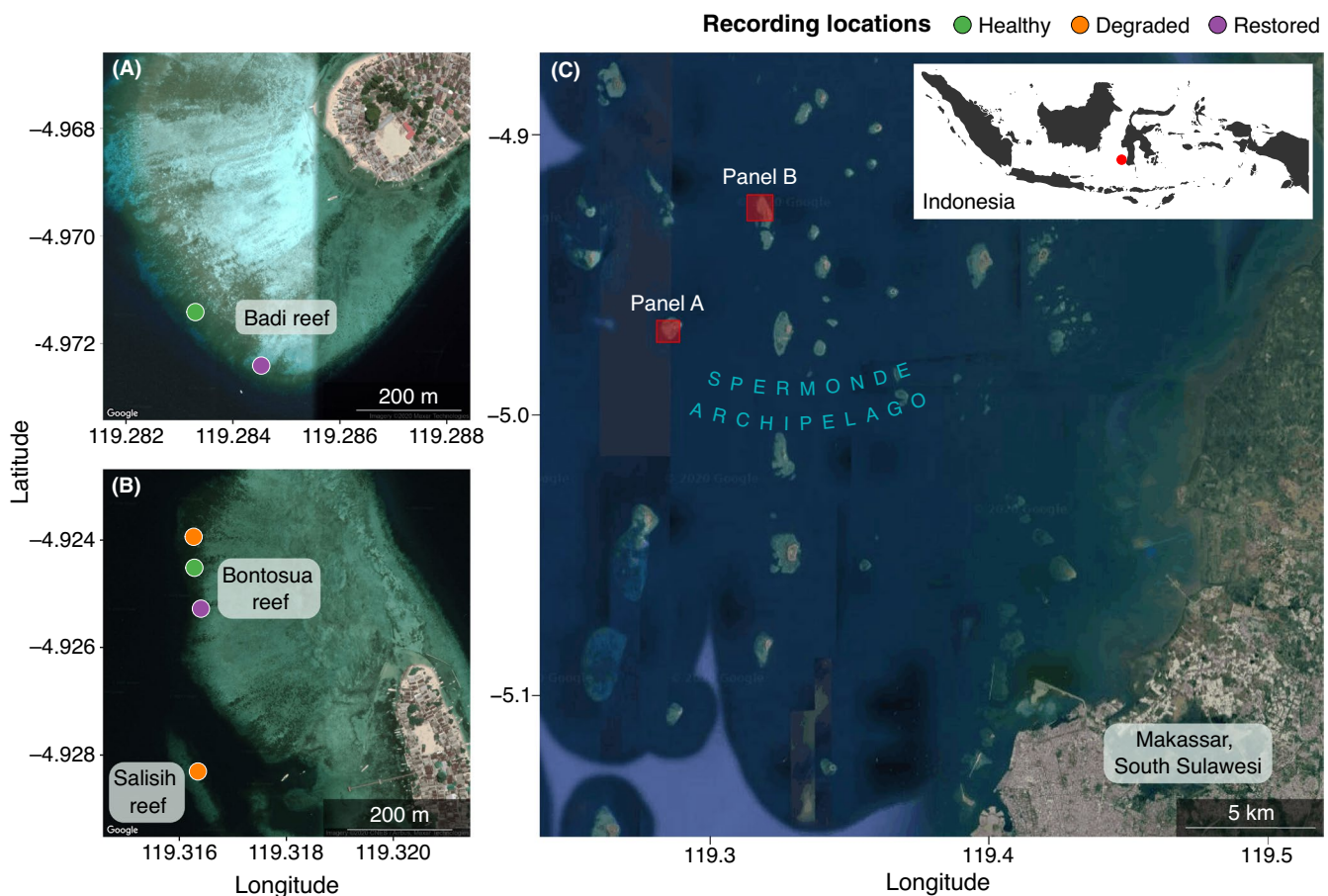


FIGURE 1 Map of the study sites and their location in Indonesia. Shown are the locations of recording sites (healthy, degraded and restored) at (A) Badi reef and (B) Bontosua and Salisih reefs; and (C) the location of the study site within Indonesia. Satellite images obtained from Google Maps, available at <https://goo.gl/maps/sQrMPoAJQp2d4QHL6> (last accessed on 15/7/2020; map data from Google, CNES/Airbus, Landsat/Copernicus and Maxar Technologies)

stressors including overfishing, destructive fishing practices, coastal development, and sediment and nutrient runoff associated with deforestation, agriculture and construction (Burke et al., 2012). Reefs in the Spermonde Archipelago are particularly threatened by widely practised blast fishing, which causes extensive ecosystem damage with slow natural recovery rates (Ceccarelli et al., 2020; Fox et al., 2003).

2.2 | Site selection and classification

For several years preceding this study, the Mars Coral Reef Restoration Project (www.buildingcoral.com) carried out rubble stabilisation and coral gardening on several hectares of reef historically damaged by blast fishing. Fragments of live coral were attached to networks of modular metal frames ('Reef Stars'; called 'spiders' in previous studies) and deployed in degraded rubble fields; this stabilised rubble and accelerated coral regrowth, leading to substantial increases in live coral cover (see Williams et al., 2019 for full details of the restoration technique and its impacts on coral cover). After deployment, all restored reefs were regularly maintained by manual cleaning, repairs of physical damage and active management of disease outbreaks and algal-farming damselfish. The reefs recorded in this study therefore consisted of a patchy matrix of three different habitat types: naturally healthy reefs (no evidence of damage from blast fishing), degraded rubble fields (highly damaged by blast fishing) and restored reefs (Reef Stars of 1–3 years age facilitating ecosystem recovery).

Two examples each of healthy, degraded and restored habitat were selected as recording sites (all sites between 2.0 and 3.3 m depth at low tide with a total tidal range of 0.7 m; site map in Figure 1; representative photos of each habitat type in Figure 2A–C). Ecological differences between the habitat types were classified using surveys of benthic cover (60 photo quadrats per habitat type) and resident fish communities (six transects per habitat type). The healthy and restored habitats were ecologically very similar to each other, and both were distinct from the degraded habitat. Healthy and restored sites exhibited 60%–85% live coral cover, constituting mainly branching *Acropora*; by contrast, degraded habitat exhibited less than 10% live coral cover and contained no branching *Acropora* (Figure 2D). There was slightly more massive and foliose coral in healthy sites than restored sites, but overall there was a high degree of overlap between healthy and restored habitat, which were both distinctly separated from degraded habitat, on a non-metric multidimensional scaling plot of benthic cover (Figure 2E). There were significantly fewer resident fishes in the degraded habitat than the healthy habitat, with the restored habitat exhibiting an intermediate abundance that was not significantly different to either of the other habitat types (Figure 2F). In the most populous trophic group (planktivores; 65% of all resident fishes), healthy and restored habitats both contained a significantly higher abundance than degraded habitat. Herbivores (10% of all resident fishes) exhibited no difference in abundance between habitat types, and corallivores (5% of all resident fishes) trended towards

lower abundance in degraded habitat than healthy and restored habitat, although this comparison was limited by small sample size and did not exhibit a statistically significant difference. The small differences between benthic and fish communities in healthy and restored habitat may be due to the fact that restored reefs were still relatively young (1–3 years since restoration interventions started). Full details of the ecological surveys are reported in Supporting Information Methods and Table S1.

2.3 | Acoustic recordings

Soundscape recordings were taken at each site using hydrophones with inbuilt recorders (SoundTrap 300 STD; Ocean Instruments, NZ; sampling rate 48 kHz; manufacturer-calibrated; all SoundTraps set at 'high gain' for all recordings), suspended 0.5 m above the seabed on vertical ropes held between weights and sub-surface floats. Hydrophones were placed at the centre of the 10 × 10 m grid used for coral-cover measurements; a small piece of flagging tape was fixed to this location at each site to ensure that repeat deployments were always in the same place. At least 10 min before the scheduled start time of a recording, the hydrophone was placed in position by a snorkeler, who then retreated at least 500 m away. Hydrophones were retrieved after the hour-long recording had finished.

Multiple 1-hr recordings were taken at each site in 2018 and 2019. The recording schedule was designed to span full and new moon periods, at five different time points within the day, because soundscapes are known to vary with both lunar phase and time of day (Bertucci et al., 2016; Kaplan et al., 2018). The five daily time points were sunrise (half an hour either side of sunrise), morning (1 hr between 09:00 and 12:00), afternoon (1 hr between 12:00 and 15:00), sunset (half an hour either side of sunset) and night (half an hour either side of midnight). Recording schedules were organised with counterbalanced blocking designs, such that there was a similar number of recordings taken of each habitat type, comprising an approximately even spread of time points and lunar phases (for full details of the recording schedule, see Table S2). Three different hydrophones were used to facilitate simultaneous recording of different sites; hydrophone ID was also factored into the blocking design such that each site was recorded a similar number of times by each hydrophone. The requirement to compare multiple habitat types with adequate spatial replication and a balanced recording schedule meant that multiple repeats of short-term, hour-long recordings at each site were preferred to longer-term recordings in a single location.

One-minute samples were taken from each of the 91 hr-long recordings, for acoustic analysis. Each sample was checked by visual and auditory examination to ensure that it contained no anthropogenic noise. Where anthropogenic noise was detected (from small-boat engine noise, distant shipping noise, blast fishing explosions and noises associated with boats docking and anchoring), samples were replaced with alternatives from the same hour-long recording. There were no discernible differences in environmental sounds (wind, rain, currents or sediment movement) between sites, and all recordings took place in calm weather and

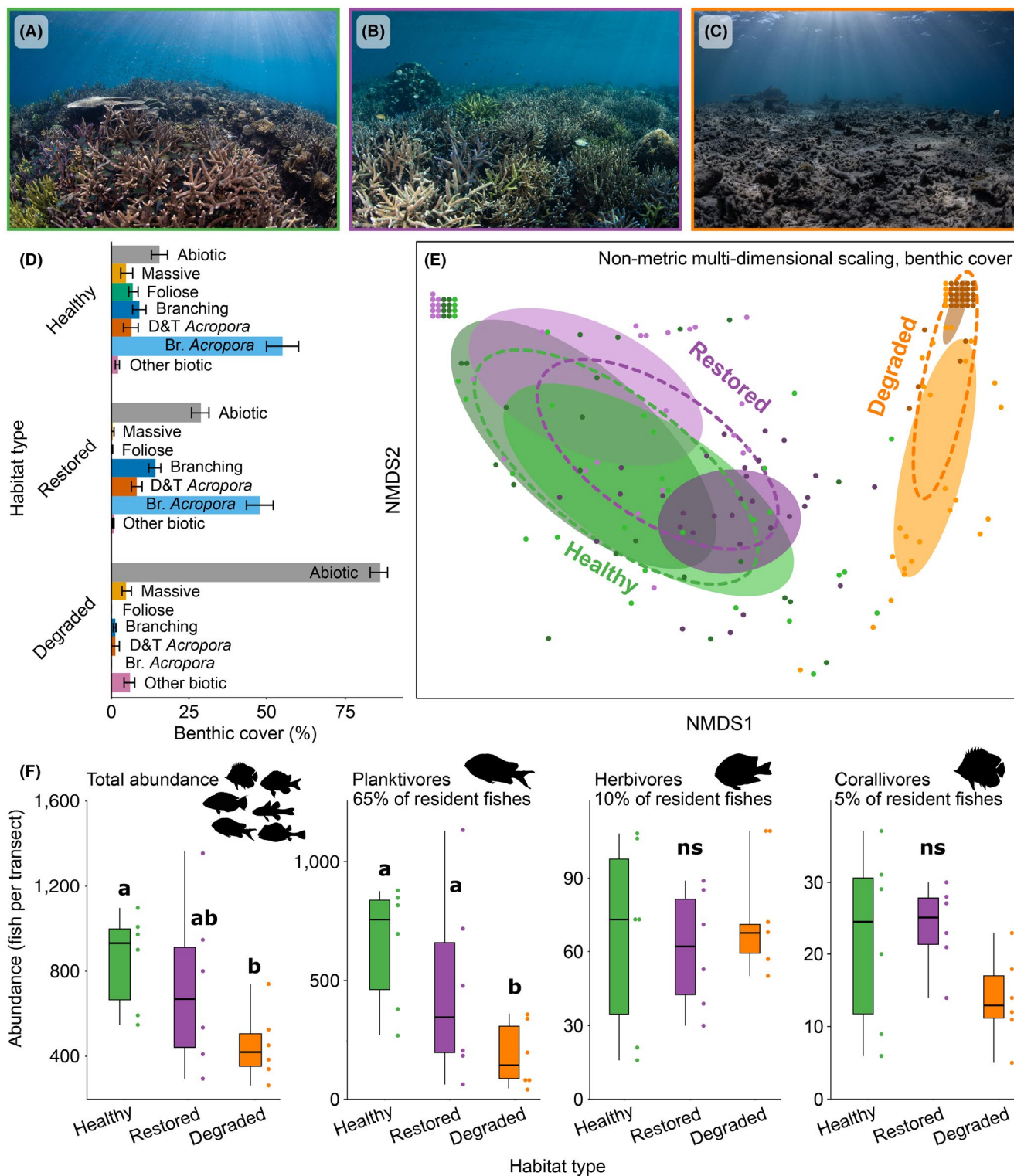


FIGURE 2 Characterisation of habitat types. (A–C) Examples of healthy (A), restored (B) and degraded (C) habitat measured in this study. (D) Average benthic cover in each habitat type, split by growth form. (E) Non-metric multi-dimensional scaling plot of benthic cover in each of the six sites (dashed-line ellipses) and with sites combined by habitat type (filled ellipses). Each point represents one quadrat (30 per site); ellipses represent standard deviations. (F) Total abundance of fishes and abundances of the three most populous trophic groups. Each point represents one transect (six per habitat type); boxplots represent the median (centre line), interquartile range (boxes) and full range (whiskers). Different letters represent significant differences in Tukey's HSD post-hoc testing, following a significant effect of habitat type in Poisson-distributed generalised linear mixed models; 'n.s.' indicates there was no significant effect of habitat type in the model. The significance threshold in all cases was 0.05; for full models and post-hoc comparisons, see Table S1

benign conditions. In total, each habitat type (healthy, degraded and restored) was represented by at least 28 samples and each time point (sunrise, morning, afternoon, sunset and night) was represented by at least 10 samples. Full details of the sampling procedure are provided in Supporting Information.

2.4 | Calculation of phonic richness

Audio inspection of each of the 91 samples was carried out in a single-blind analysis, with the same observer (T.A.C.L.) noting down the presence of distinct biophonic sounds in each recording. A total of 10 distinct sounds were identified as biophonic, based on having very similar spectral characteristics to fish sounds documented on coral reefs by previous studies (McWilliam et al., 2017; Parmentier & Frederich, 2016; Tricas & Boyle, 2014). A conservative approach was taken to describing distinct sound types, that is, sounds were only included if there was a very high degree of confidence that they were characteristically different from other sounds. As such, the 10 sound types are likely to be a considerable underestimate of the total acoustic diversity in the ecosystem; these represent just those sounds that could be confidently described as particularly distinctive. The sounds of coral reef fishes are not well documented, meaning that we cannot confidently ascribe any of these sounds to an individual species; however, full qualitative and quantitative descriptions of each sound type are given in Table 1 and Figure 3, and representative audio recordings of each sound type are included in Supporting Information.

The number of distinct sound types present in each sample was defined as its phonic richness. Rates of sound production for each sound type were not quantified, as there were many instances where group calling made the start and end of individual calls difficult to identify. To ensure repeatability of the results, 20 samples were selected at random to be listened to again. The same observer scored the recordings again several months after first listening to the sounds; the observer was blind to both the identity of the recording and its original score, and had no recollection of any of the recordings from the first time listening. On all 20 occasions, the result was the same on both scorings.

2.5 | Calculation of computational metrics

The ACI and SPL were calculated for each sample, as the two most commonly used computational metrics in marine soundscape research (Pieretti & Danovaro, 2020). Both metrics were calculated across the duration of the whole sample, in both a low-frequency (50–800 Hz) and a high-frequency (2,000–7,000 Hz) bandwidth. These two bandwidths are likely to contain different ecological information, because fish vocalisations are predominantly pitched lower than 800 Hz (Tricas & Boyle, 2014); the higher-frequency band is therefore likely to have been dominated by invertebrate sounds. ACI was calculated using *seewave* (Sueur et al., 2008) in R v3.6.2 (<https://www.r-project.org/>) and SPL was calculated using *paPAM* (Nedelec et al., 2016). In both cases, a Hamming Fast-Fourier Transform (FFT) window of 512 samples and a 50% overlap was

TABLE 1 Qualitative and quantitative descriptions of each of the 10 distinct biophonic sound types present in recordings, and their frequency of occurrence (the number of recordings each sound appeared in)

Name	Dominant frequency (Hz)	Duration (s)	Type	Description	Frequency of occurrence (out of 91)	Most frequent time of occurrence
Scrape	Broadband	0.1	Percussive	Crunching sound, commonly heard when excavating grazers take bites on hard substrate	37	Morning and afternoon
Knock	800	0.02	Percussive	Short, sharp percussive sound, often repeated several times	22	Sunset
Purr	400	0.5	Pulse train	Very slow pulse train with a very gentle rise and decay, often repeated continuously for several seconds	17	Night
Raspberry	320	0.2	Pulse train	Very fast pulse train with a sharp rise and decay, often repeated in groups	15	Night
Croak	700	0.15	Pulse train	Fast pulse train with a sharp rise and decay, often repeated in groups	14	Sunset and night
Growl	300	0.4	Pulse train	Slow pulse train with a gentle rise and decay	13	Sunrise
Grunt	150	0.35	Tonal	Single deep tonal sound with a gentle rise and decay	14	Sunset
Foghorn	200	2.0	Tonal	Long tonal sound that rises in frequency through the call	10	Afternoon
Whoop	650	0.1	Tonal	Short tonal sound with a fast rise and decay, often repeated two or three times	7	Sunrise
Laugh	150	0.1	Tonal	Short tonal sound, repeated four or five times, with each repetition slightly quieter than the previous	2	Sunrise

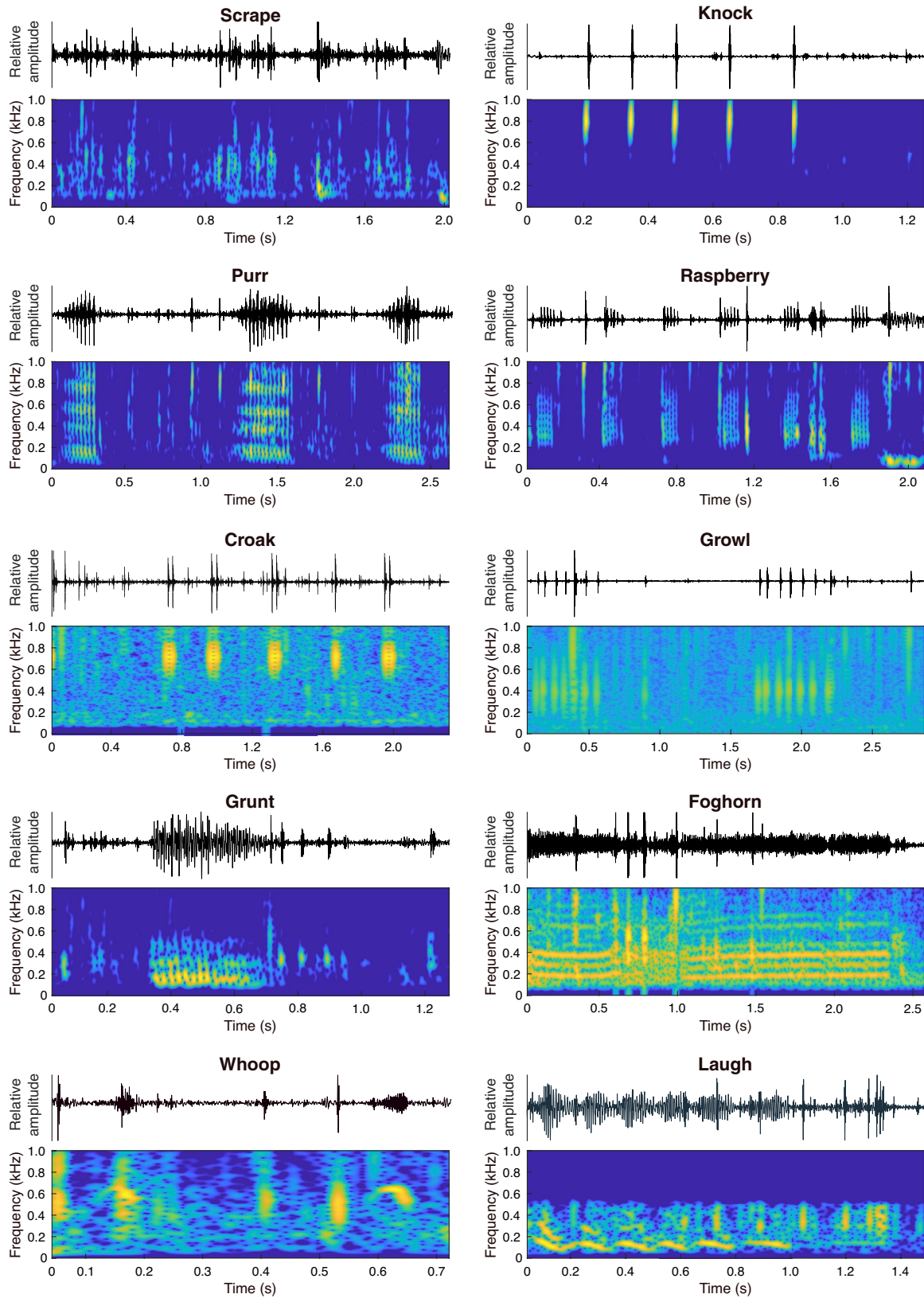


FIGURE 3 Illustrative waveforms and spectrograms of each of the 10 distinct biophonic sound types, generated by selectively amplifying and filtering representative recordings using a custom-made script in MATLAB (<https://www.mathworks.com/products/matlab.html>). In spectrograms, higher power is indicated by brighter yellow and lower power by darker blue; however, the absolute levels of these spectrograms are not directly comparable with each other because the source fish in each exemplar was an unknown distance from the recorder, and the sound files were independently modified by differential amplification and filtering to highlight the qualitative structure of individual calls. Raw recordings are available in Supporting Information

used, resulting in a 93.75 Hz frequency resolution and a 10.6 ms temporal resolution.

2.6 | Statistical analysis

Each of the computational metrics (ACI and SPL in high- and low-frequency bandwidths, respectively, and phonic richness) were compared across the healthy, degraded and restored sites using a linear mixed model (LMM) if data were normally distributed, or a Poisson-distributed generalised linear mixed model (GLMM) if correction for positive skew was required. Visual examination of histograms and normal quantile plots of model residuals was used to confirm model goodness-of-fit. In all models, habitat type (healthy, degraded or restored) was included as a fixed effect, and time of day (sunrise, morning, afternoon, sunset or night), lunar phase (new or full), date, hydrophone ID (one of the three hydrophones) and reef location (Badi, Bontosua or Salisih) were included as categorical random effects. All models were optimised by stepwise deletion of random terms with variance of less than 0.001, starting with the term with lowest variance, in order to minimise risk of over-fitting. The overall effect of habitat type on the dependent variable was tested using ANOVA comparisons to null models that were identical except for the omission of the fixed term. If this comparison was statistically significant ($p < 0.05$), post-hoc Tukey's HSD testing followed to provide between-habitat comparisons. Canonical correspondence analysis was also used to visualise the groupings of different sound types present in each habitat type; habitat type, time point, lunar phase and reef location were used as constraining environmental variables.

Finally, correlation tests were carried out between ecoacoustic metrics that displayed significant effects of habitat type. Two correlation tests were used: the Pearson's linear correlation test, which identifies variables that covary at constant rates; and the Spearman's rank monotonic correlation test, which identifies variables that covary in consistent directions but not necessarily at constant rates. A correlogram was used to assess pairwise comparisons between variables for each sample, and Pearson's (linear) and Spearman's rank (monotonic) correlation tests were calculated for each individual comparison. All model residuals met assumptions of normality and homoscedasticity, and a Bonferroni adjustment for multiple testing was applied when considering the statistical significance of the multiple pairwise comparisons.

All statistical analyses and figure creation were carried out in R v3.6.2 (www.r-project.org); specific package information is available in Supporting Information.

3 | RESULTS

The presence or absence of different biotic sounds was affected by both time of day and habitat type. Of the 10 sound types present in recordings (Table 1), two occurred most frequently in day-time recordings (morning and afternoon), five occurred most frequently in

crepuscular recordings (sunrise and sunset) and three occurred most frequently at night (Figure 4A). Seven of these 10 sound types occurred at least 50% more often in healthy and restored habitat than in degraded habitat (Figure 4B). This led to a significant effect of habitat type on phonic richness (GLMM: $\chi^2 = 8.82$, $df = 2$, $p = 0.012$; Figure 4C); healthy and restored habitat had a significantly higher phonic richness than degraded habitat, with no significant difference between the healthy and restored habitat (Figure 4C; full model and post-hoc comparisons in Table S3). Canonical correspondence analysis on all recordings with a phonic richness >0 ($n = 71$) revealed that the distributions of sound types present in healthy and restored habitat were similar to each other, and both differed from those present in degraded habitat (Figure 5).

There was a significant effect of habitat type on the ACI (LMMs, low frequency: $\chi^2 = 13.08$, $df = 2$, $p = 0.002$; high frequency: $\chi^2 = 40.46$, $df = 2$, $p < 0.001$), although the between-group results were not consistent across the two frequency bandwidths. Degraded habitat had significantly lower ACI scores than both healthy and restored habitat in both frequency bandwidths. However, although there was no significant difference between the ACI values of healthy and restored habitat in the low-frequency bandwidth, restored habitat had significantly higher ACI values than healthy habitat in the high-frequency bandwidth (Figure 6A; full model and post-hoc comparisons in Table S3). There was no significant effect of habitat type on SPL in either frequency bandwidth (Figure 6B; low frequency: $\chi^2 = 0.69$, $df = 2$, $p = 0.708$; high frequency: $\chi^2 = 2.31$, $df = 2$, $p = 0.315$; full model and post-hoc comparisons in Table S3).

Of the ecoacoustic metrics that were significantly affected by habitat type (phonic richness and low- and high-frequency ACI), only the low- and high-frequency ACI values shared a strong positive correlation when using a Bonferroni-adjusted significance threshold of 0.012 (Figure 7; $n = 91$ for all comparisons). This relationship was significant for both linear Pearson's correlation ($\rho = 0.33$, $p < 0.01$) and monotonic Spearman's rank correlation ($r = 0.39$, $p < 0.01$). By contrast, phonic richness had weak monotonic correlations with both low-frequency ACI ($r = 0.26$, $p = 0.01$) and high-frequency ACI ($r = 0.21$, $p = 0.04$), and no linear correlation with ACI in either frequency bandwidth (low frequency: $\rho = 0.19$, $p = 0.07$; high frequency: $\rho = 0.12$, $p = 0.25$).

4 | DISCUSSION

This study tests whether ecosystem recovery at one of the world's largest coral reef restoration projects is accompanied by recovery of the soundscape. Restored habitats (1–3 years since restoration began) were quantitatively similar to healthy habitat in both benthic cover and fish populations, albeit with lower benthic cover of massive and foliose coral and lower populations of planktivores (Figure 2). In turn, restored habitat also had similar levels of phonic richness to healthy habitat, with degraded habitat displaying significantly lower phonic richness than both healthy and restored habitat (Figure 4). Different sound types dominated at different times of

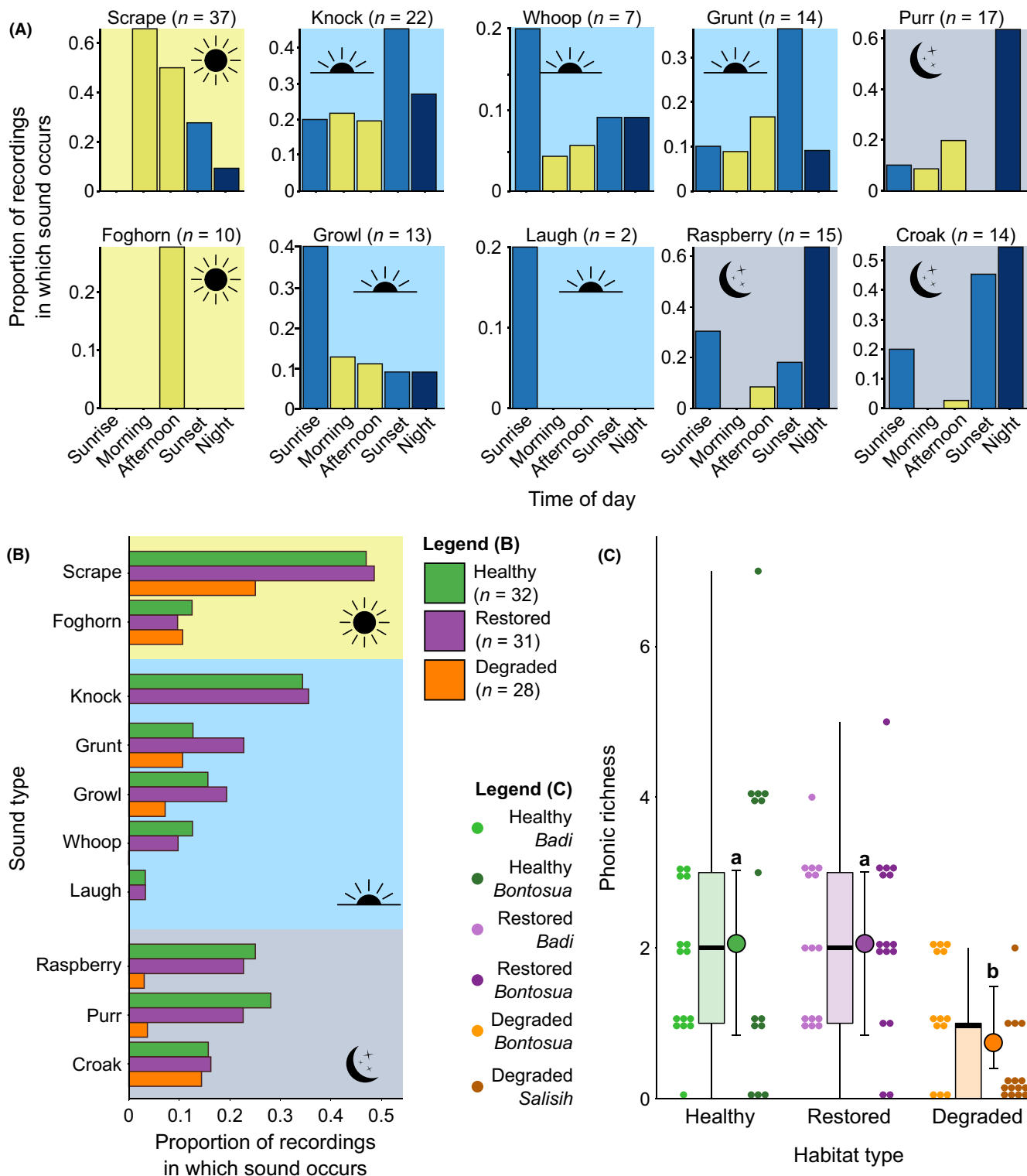


FIGURE 4 Phonic richness of healthy, degraded and restored habitat. (A and B) The proportion of recordings in which each sound type occurred, by time of day (A) and habitat type (B). Sample sizes (n) in A indicate the total number of recordings in which the sounds occurred. Bars in A correspond to broader time categories, with yellow representing day-time (morning or afternoon), blue representing crepuscular (sunrise or sunset) and grey representing nocturnal (night) recordings. Background colours in A and B indicate which of these time categories each sound occurred most frequently in, using the same colour code. (C) The effect of habitat type on phonic richness. Shown are raw data from each site (small points, jittered such that directly overlaid points appear adjacent to one another), and model estimates and 95% confidence intervals (large points and error bars) from a Poisson-distributed generalised linear mixed model (GLMM). Boxplots combine raw data from each habitat type; thick lines indicate the median, boxes indicate 25% and 75% quartiles, and whiskers indicate the full range of the data. Different letters represent significant differences in Tukey's HSD post-hoc testing ($p < 0.05$), following a significant effect of habitat type in the GLMM (for full model and post-hoc comparisons, see Table S3)

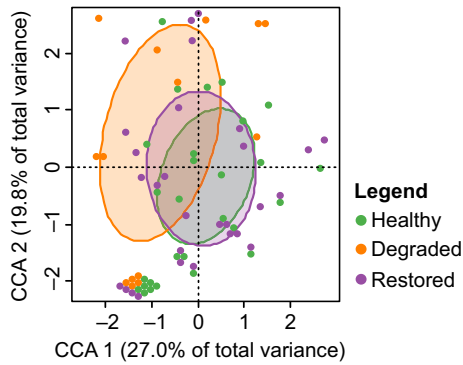


FIGURE 5 Canonical correspondence analysis (CCA) plot of phonic richness in recordings of healthy (green), degraded (orange) and restored (purple) reefs. Each point represents a single recording; points are jittered such that directly overlaid points appear adjacent to one another. Recordings with no individual sounds detected (phonic richness = 0) were removed from the dataset prior to this analysis. The clustering of 16 points in the bottom left represents recordings in which only scraping sounds occurred (phonic richness = 1), which was the most common result in the dataset. Ellipses represent the area encompassing the standard deviation of all points within each group

day (Figure 4A), but the relative differences between habitat type were consistent between time periods (Figure 4B), suggesting that differences in phonic richness are robust to within-day variation. A qualitatively similar pattern to this was found in the ACI values (Figure 6A), despite only weak correlations between the ACI and phonic richness values for each recording (Figure 7). There was no effect of habitat type on SPL (Figure 6B). Taken together, these results suggest that restoration success can be detected in the soundscape, but that computational metrics such as the ACI and SPL are not driven by changes in phonic richness of audible biotic sound types. As such, PAM may represent a valuable tool for measuring functionally important aspects of reef ecosystem recovery, but caution must be exercised in the interpretation of different metrics and their biological relevance.

The observed patterns in phonic richness might be explained by various different mechanisms. Greater phonic richness may reflect a more abundant and/or diverse community of soniferous organisms; indeed, despite limited sample size in the visual surveys of fish communities (fivefold lower sample size in visual surveys compared to acoustic surveys), there were significantly more resident fishes present in healthy and restored habitat than in degraded habitat (Figure 2). Alternatively, differences in phonic richness might be a result of different behaviours exhibited by soniferous organisms in different habitats; or a combination of both abundance and behaviour effects. The specific organisms responsible for making the sounds driving these patterns are unknown. Some of the sound types described in this study (Table 1; Figure 3) have been previously described; for example, a range of percussive and pulse-train sounds have been associated with triggerfish (family Balistidae), damselfish (Pomacentridae) and butterflyfish (Chaetodontidae); growl and grunt sounds have been associated with soldierfish (Holocentridae); scraping sounds have

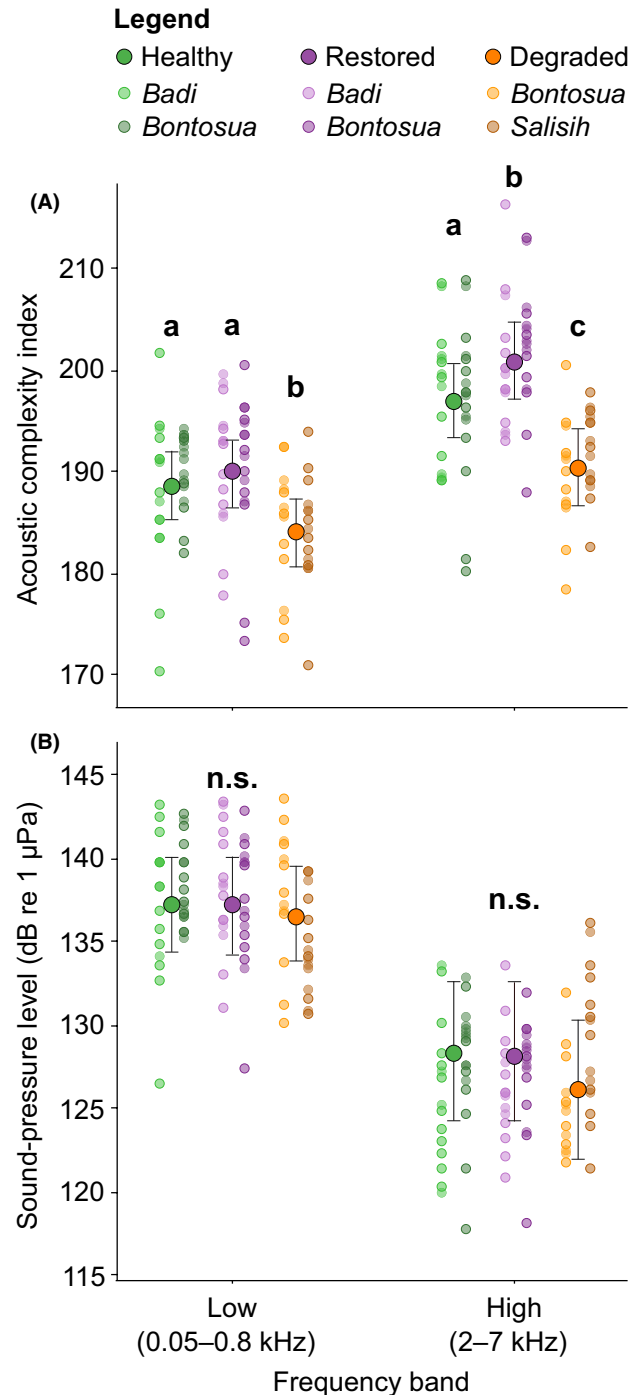


FIGURE 6 (A) Acoustic complexity index and (B) sound-pressure level of recordings of healthy, degraded and restored reefs. Shown are model estimates (large points) and associated 95% confidence intervals (error bars) from linear mixed models (LMMs), overlaid on top of raw data (small points, separated by reef location). Different letters represent significant differences in Tukey's HSD post-hoc testing, following a significant effect of habitat type in the LMMs; 'n.s.' indicates there was no significant effect of habitat type in the LMMs. The significance threshold in all cases was 0.05; for full models and post-hoc comparisons, see Table S3

been associated with the feeding of macroherbivores such as parrotfish (Scaridae) and triggerfish (Balistidae); and whooping sounds have been associated with the Ambon damselfish *Pomacentrus amboinensis*

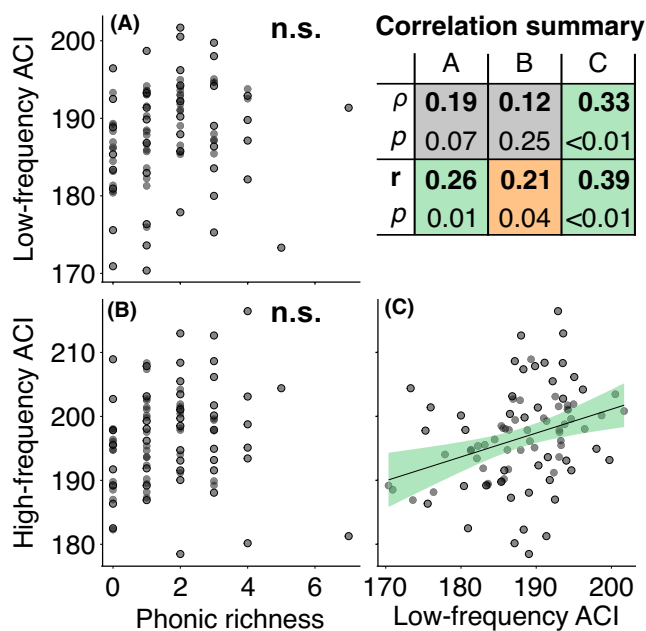


FIGURE 7 Correlations between ecoacoustic metrics that demonstrated a significant effect of habitat type. Shown in (A–C) is a correlogram of all pairwise relationships between phonic richness and high- and low-frequency ACI (acoustic complexity index). The correlation summary gives the Pearson's ρ (linear; top row) and Spearman's rank r (monotonic; bottom row) correlation coefficient for each pairwise comparison, along with its associated p -value; values highlighted in grey are non-significant ($p > 0.05$), those in orange are significant individually but not when Bonferroni adjustment for multiple testing is included ($0.012 < p < 0.05$), and those in green are significant when Bonferroni adjustment is included ($p < 0.012$). In panels (A and B), 'n.s.' indicates no significant linear correlation. In panel (C) (the only relationship with a significant linear correlation), the solid line and green ribbon represents the linear model output and associated standard error, respectively

(Parmentier & Frederich, 2016; Tricas & Boyle, 2014). However, other sound types are less familiar; for example, we are not aware of any previous descriptions of the 'laugh' sound (Table 1; Figure 3). Each individual sound type does not necessarily correspond to a single sound-producing species; some fishes are capable of multiple phonation types (Parmentier et al., 2010, 2019), and may be making more than one of the sounds described in this study. Conversely, there is a high degree of overlap in the spectral characteristics of sounds produced by different fishes (Tricas & Boyle, 2014), and some of these sound types may be produced by more than one species. As such, phonic richness is not a precise count of individuals or species, but is better considered as a measure of the presence or absence of certain soniferous animals, which may be an indirect reflection of the diversity of the whole community.

Results from the two computational metrics (ACI and SPL) were not qualitatively equivalent to each other (Figure 6) and did not correlate well with phonic richness (Figure 7). The low-frequency bandwidth ACI followed a qualitatively equivalent pattern to that observed in phonic richness, but this pattern was different to

that in the high-frequency bandwidth ACI. In contrast, there was no effect of habitat type on SPL in either frequency bandwidth. Despite the qualitative equivalence of the pattern observed in low-frequency ACI and phonic richness scores, there was only a weak Spearman's rank monotonic correlation between these two metrics, and no significant Pearson's linear correlation (Figure 7). It is clear that the results given by different computational metrics are not equivalent, and it is likely that the results of different metrics are driven by different aspects of the soundscape. For instance, all of the biotic sounds driving phonic richness have peak frequencies between 150 and 800 Hz (Table 1), and therefore cannot have been driving the results of computational metrics in the high-frequency bandwidth; this explains the lack of correlation between phonic richness and the high-frequency ACI values. By contrast, the low-frequency ACI values correlate strongly with the high-frequency ACI values, suggesting a common driver across both frequency bands. Invertebrate snapping sounds cover a broadband spectrum (i.e. they occupy both low- and high-frequency bandwidths), suggesting that they are more likely to be driving the observed patterns in ACI values than the low-frequency fish sounds. Indeed, previous work has demonstrated that ACI values correlate better with levels of invertebrate snapping sound than with fish vocalisation rates (Bohnenstiehl et al., 2018). Therefore, although habitat type had a qualitatively equivalent effect on both phonic richness and the low-frequency ACI, it is likely that this was driven by different aspects of the soundscape in each case; fish vocalisations are driving phonic richness, but invertebrate snapping sounds are likely to be driving the ACI.

The documented acoustic recovery described here is important for three main reasons. First, it demonstrates the return of an important functional property of restored reef ecosystems. On healthy reefs, a loud and diverse soundscape guides the orientation and settlement behaviours of many juvenile reef organisms that spend their larval stage in the open ocean (Leis et al., 2011; Lillis et al., 2018; Montgomery et al., 2006; Simpson et al., 2008). When reefs degrade, their denuded soundscapes are less attractive to young fishes and invertebrates, potentially jeopardising this acoustically guided settlement behaviour (Gordon et al., 2018; Lillis et al., 2016, 2018). The recovery of soundscapes suggests that restored reefs have the potential to regain their attractiveness to settlement-stage organisms; this is encouraging as it means that restored reefs may have the capacity to attract future generations of reef organisms, improving the prospects of long-term ecosystem stability.

Second, these results are important because they demonstrate that active restoration of coral cover can have beneficial impacts on the wider reef ecosystem. The greater phonic richness on restored reefs relative to degraded habitat likely reflects a greater number of soniferous fish species present, and the greater ACI values likely reflect higher diversity, abundance or altered behaviour of invertebrates. Healthy populations of a range of reef organisms underpin ecological functioning and ecosystem service provision on reefs (Graham et al., 2015; Sato et al., 2020). Given the current paucity of evaluations of restoration success that go beyond coral cover (Hein

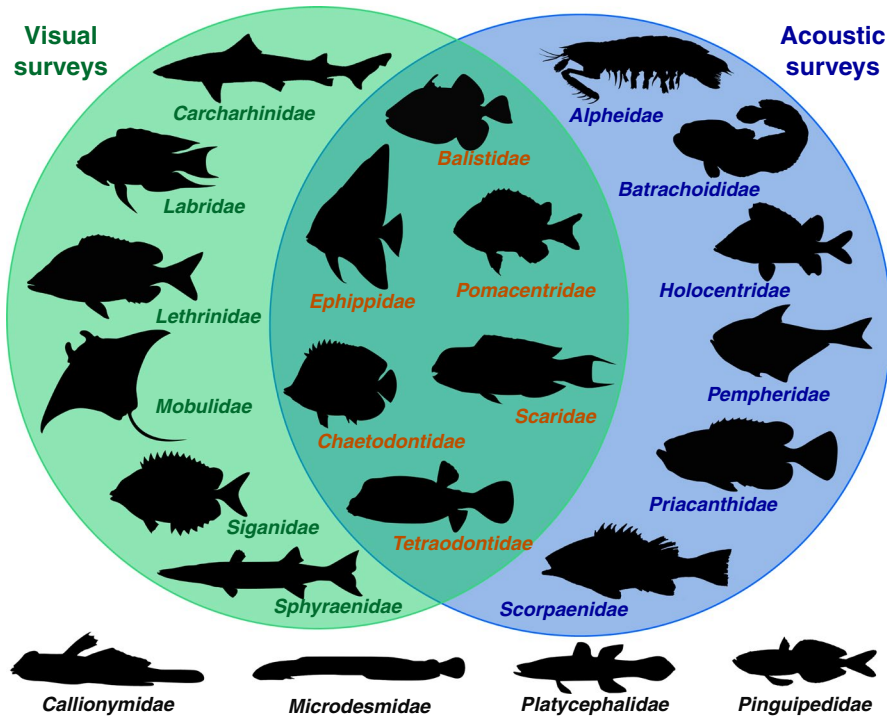


FIGURE 8 Schematic diagram illustrating the potential complementarity of visual and acoustic surveys of coral reefs. The green circle displays examples of families of non-cryptic, diurnally active reef organisms that can be surveyed visually. The blue circle displays examples of soniferous families that can be surveyed using soundscape recordings. Families in the overlapping turquoise segment might be detected by both visual and acoustic surveys. Families outside all coloured segments are cryptic and have not been documented producing sound; they are therefore difficult to survey using either visual or acoustic methods

et al., 2017), these results are important in demonstrating that coral restoration can have holistic effects on the wider ecosystem.

Third, these results are important in highlighting the complementary value that PAM might bring to coral reef monitoring programmes. PAM has the capacity to detect cryptic and nocturnal species; to monitor over extended periods of time; and to provide objective measures that are not susceptible to observer bias (Mooney et al., 2020; Obura et al., 2019). These benefits might allow PAM to work effectively alongside traditional visual methods for surveying reefs; different communities of animals are detected by visual and acoustic surveys, meaning that these methods are likely to be complementary, rather than either approach being better than the other (Figure 8). Reef surveys that use multiple methods are likely to generate a more holistic understanding of ecosystem health than those using any single method in isolation.

Despite the promising results shown in phonic richness, these results also demonstrate that great care must be taken in applying different acoustic metrics to ecosystem monitoring. For example, there was no difference in SPL between any of the habitat types. This may have been because SPL measures the total acoustic energy in a soundscape, unlike phonic richness and the ACI which both measure different aspects of the diversity in a soundscape. Total acoustic energy is likely to be heavily affected by background noise, either from environmental sources (wind, rain, water movement) or from a dominant biotic source (snapping shrimp or repeated chorusing of a single sound type). It is also likely that SPL is particularly susceptible to within-site variation in a complex habitat, as differences in depth, bottom type and habitat complexity influence the reflections of sound waves, altering received sound intensity in different locations. Indeed, previous studies have found that acoustic metrics focussing on diversity (ACI), rather than intensity (SPL), more

reliably differentiate between habitat types (Bertucci et al., 2016). Furthermore, metrics that measure presence/absence of particular sounds, rather than quantified sound intensity, are much easier to measure with low-cost devices because they do not require calibration (Chapuis et al., 2021). Future work might valuably explore additional computational metrics (Harris et al., 2016), or apply recent machine-learning-based approaches to terrestrial PAM (Sethi et al., 2020) in underwater contexts, in order to find the most appropriate computational analysis tools for successful integration of PAM into marine ecosystem monitoring programmes.

A key next step in evaluating the potential of PAM is to expand the biogeographical and seasonal replication of findings such as these. The recordings in this study come from just two reefs of each habitat type, in a single biogeographical region at one time of year. While this does not invalidate these results, it will now be important to test their generality across geographical regions and seasons, especially on systems where seasons can have strong impacts on soundscape dynamics (Staaterman et al., 2014). This lack of certainty that soundscapes consistently reflect ecological conditions, independent of biogeography and seasonality, continues to preclude a comprehensive understanding of the potential value of PAM. Increased spatial and temporal replication might be readily achieved by citizen science; recording devices for PAM are becoming increasingly affordable and user-friendly (Chapuis et al., 2021; Hill et al., 2018), and the rapid development of machine-learning techniques for the analysis of a range of marine and terrestrial soundscapes may soon potentiate automatic calculations of phonic richness (Stowell et al., 2019). Standardised deployment of affordable sound-recording devices with automated analysis of recordings is becoming a realistic prospect in several terrestrial ecosystems (Sethi et al., 2020); similar streamlining of efforts in the marine realm

would represent a unique opportunity to test the generality of PAM as a novel tool for the monitoring of reef restoration worldwide.

5 | CONCLUSIONS

This study demonstrates that detectable acoustic differences exist between the soundscapes of healthy, degraded and actively restored coral reefs. Quantifiable differences between habitat types exist for both manual and computational ecoacoustic metrics, although not all metrics reveal qualitatively equivalent patterns. Focussing on coral reef restoration, this study provides exciting proof-of-concept data on which future monitoring efforts might valuably build; if biologically meaningful and robust metrics can be standardised, PAM has the potential to contribute to the assessment of restoration success across ecosystems worldwide.

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CONFLICT OF INTEREST

The authors have declared no conflicts of interest.








AUTHORS' CONTRIBUTIONS

T.A.C.L., A.N.R. and S.D.S. conceived the research idea and designed the study; T.A.C.L., B.W., L.C., M.E.P., M.J.S., H.R.H. and E.B.M. contributed to fieldwork and data collection; T.A.C.L., B.W., L.C., A.N.R. and S.D.S. analysed the data; T.A.C.L. wrote the first draft of the manuscript and all authors contributed to subsequent revisions. Our study brings together authors from a number of different countries, including scientists based in the country where the study was carried out. All authors were engaged early on with the research and study design to ensure that the diverse sets of perspectives they represent was considered from the onset.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.Ogb5mkm2c> (Lamont et al., 2021).

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