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

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1   **TITLE**

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

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21   **RUNNING HEADLINE**

22   Acoustic monitoring of restored coral reefs

ABSTRACT

1. Pantropical degradation of coral reefs is prompting considerable investment in their active

restoration. However, current evaluations of the success of most projects are based solely on

measures of coral cover, which reflect only one aspect of reef health. Passive acoustic monitoring

(PAM), an emerging technique used increasingly in marine and terrestrial environments, has

untested potential to provide complementary and in-depth measures of ecosystem health for reef

restoration monitoring.

2. Here, we use acoustic recordings taken at one of the world's largest coral reef restoration projects

to test the potential of PAM as a useful tool for evaluating restoration success. We analyse

recordings taken simultaneously on reefs that were naturally healthy, degraded by blast fishing, and

actively restored (restoration carried out for >2 years on previously-degraded reefs). We compare

soundscapes using both manual counts of individual biotic sounds (phonic richness) and automated

ecoacoustic indices (acoustic complexity index [ACI] and sound-pressure level [SPL], both measured

in low-frequency (0.05–0.8 kHz; predominantly fish vocalisations) and high-frequency (2–7 kHz;

predominately invertebrate sounds) bandwidths).

3. Healthy and restored reef soundscapes both had significantly higher phonic richness than

degraded reef soundscapes, with no significant difference between the healthy and restored

soundscapes. This pattern was replicated in the low-frequency ACI but not the high-frequency ACI,

whilst there was no significant difference between SPL values from different habitat types in either

frequency bandwidth. Despite showing qualitatively equivalent results with respect to habitat type,

the low-frequency ACI and phonic richness scores were only weakly correlated; these different

ecoacoustic metrics are likely to be driven by different aspects of the reef soundscape.

4. *Synthesis and applications:* These data demonstrate that PAM can provide objective measures of

reef-restoration success that go beyond coral-cover metrics. Low-cost recording hardware and

automated analysis techniques facilitate widespread adoption of this technique, which would allow

48   the reproducibility of these findings to be tested across different biogeographic regions and seasons.

49   PAM represents a potentially valuable new tool for measuring the success of coral reef restoration

50   worldwide.

51   **KEYWORDS:** bioacoustics, coral reef, ecoacoustics, ecosystem monitoring, passive acoustic

52   monitoring, restoration, soundscape

INTRODUCTION

54   A suite of global and local anthropogenic stressors are causing unprecedented damage to tropical

55   coral reefs around the planet (Harborne *et al.* 2017). This imperils biodiversity and jeopardises the

56   livelihoods of hundreds of millions of people who rely on reefs for food, income and storm

57   protection (Cinner 2014). In response, hundreds of conservation programmes worldwide are

58   implementing a range of active physical interventions aimed at restoring heavily-degraded reef

59   systems (Bostrom-Einarsson *et al.* 2020; Duarte *et al.* 2020). These interventions are primarily

60   focussed on increasing coral cover, by using different methods to enhance asexual reproduction (e.g.

61   collecting and replanting coral fragments: Williams *et al.* (2019)), sexual reproduction (e.g. releasing

62   fertilised coral larvae into the water: de la Cruz & Harrison (2017)) and larval settlement (e.g.

63   stabilising loose substrate: Ceccarelli *et al.* (2020)). However, whilst many such restoration

64   programmes are effective at increasing coral cover, very few attempt to measure the wider

65   ecosystem health of restored reefs (Hein *et al.* 2017). For example, healthy fish and invertebrate

66   populations are essential components of ecosystem functioning and service provision on reefs

67   (Graham *et al.* 2015; Sato *et al.* 2020), but their recovery remains inadequately tested by the

68   majority of reef restoration programmes (Bostrom-Einarsson *et al.* 2020).

69   Passive acoustic monitoring (PAM) is a technology in the emerging field of ecoacoustics

70   whereby the health of ecosystems can be estimated from recordings of the sounds made by their

71   inhabiting organisms (Sueur & Farina 2015). Recent technological developments in sound-recording

72   hardware (microphones, hydrophones and digital recorders) and software (computational facilities

73   to store and process large acoustic datasets) have led to increasing use of PAM to produce rapid,

74   objective, cost-effective assessments of ecosystem health (Merchant *et al.* 2015; Gibb *et al.* 2019).

75   On coral reefs, a range of fishes and invertebrates produce sound through both deliberate

76   soniferous behaviour and as by-products of movement and feeding (Versluis *et al.* 2000; Tricas &

77   Boyle 2014). This variety of sound-producing animals create reef soundscapes that vary in space as

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78   well as with time of day, phase of the moon and ecosystem health (Bertucci *et al.* 2016; Mooney *et*

79   *al.* 2020). Soundscapes also play an important role in the functioning of reef ecosystems; they guide

80   the recruitment of many reef organisms (Montgomery *et al.* 2006; Simpson *et al.* 2008), with

81   soundscape degradation altering settlement behaviour in young fishes and invertebrates (Lillis *et al.*

82   2016; Gordon *et al.* 2018). As such, reef soundscapes contain information about the abundance and

83   behaviour of a wide range of organisms, and underpin important functional processes central to

84   population replenishment.

85   Several approaches to PAM have been used to measure coral reef ecosystem health. Some

86   studies have analysed the frequency and time of occurrence of individual biotic sounds; for example,

87   McWilliam *et al.* (2017) described spatial and temporal variation in fish choruses on the Great

88   Barrier Reef. Other studies have applied automated ecoacoustic indices that produce single values

89   describing particular aspects of the whole soundscape. The two most commonly used of these

90   automated indices are sound-pressure level (SPL) and the acoustic complexity index (ACI) (Pieretti &

91   Danovaro 2020). SPL is a root-mean-square average of the amplitude of a soundscape within a given

92   time and frequency range, and the ACI is an algorithm designed to quantify variation in biotic sound

93   by summing the differences between intensities in adjacent frequency bandwidths and time steps

94   (Pieretti *et al.* 2011). SPL and the ACI have been found to differ across a spectrum of reef health:

95   degraded reefs in the Philippines had a lower SPL than nearby protected reefs (Piercy *et al.* 2014);

96   Mo'orean reefs with high fish diversity had higher ACI values than low-diversity reefs (Bertucci *et al.*

97   2016); and severe cyclones and bleaching caused changes across both SPL and ACI on the Great

98   Barrier Reef (Gordon *et al.* 2018). Although doubts remain about the generality of these ecoacoustic

99   indices across different biogeographical contexts (Staaterman *et al.* 2017; Bohnenstiehl *et al.* 2018),

100   there is hope that PAM could offer quantitative, objective, easy-to-collect measures of reef health in

101   both natural and actively-restored reef systems (Obura *et al.* 2019).

102   In this study, we use PAM to assess reef health in naturally healthy, degraded and actively

103   restored patches of habitat within one of the world's largest coral reef restoration programmes.

104   Using recordings taken at multiple times of day in both full and new moon lunar phases, we compare

105   soundscapes using both manual identification of biotic sounds and automated ecoacoustic indices.

106   These approaches allow us to evaluate the success of coral reef restoration in a novel manner that is

107   complementary to existing metrics of success. By measuring the soundscape as an emergent

108   property of the whole reef ecosystem, we can evaluate the impact of reef restoration on a

109   taxonomically broad and functionally important aspect of reef health.

110

111   **MATERIALS AND METHODS**

112   **Study area and sites**

113   This study uses acoustic recordings taken in August–September 2018 and June–July 2019 as part of

114   the monitoring programme for the Mars Coral Reef Restoration Project at Badi and Bontosua

115   Islands, in the Spermonde Archipelago (South Sulawesi, Central Indonesia; 4°56.9'S, 119°18.1'E; Fig.

116   1). Reefs in South-East Asia are heavily threatened by local anthropogenic stressors including

117   overfishing, destructive fishing practices, coastal development, and sediment and nutrient runoff

118   associated with deforestation, agriculture and construction (Burke *et al.* 2012). Reefs in the

119   Spermonde Archipelago are particularly threatened by widely practised blast fishing, which causes

120   extensive ecosystem damage with slow natural recovery rates (Fox *et al.* 2003; Ceccarelli *et al.*

121   2020).
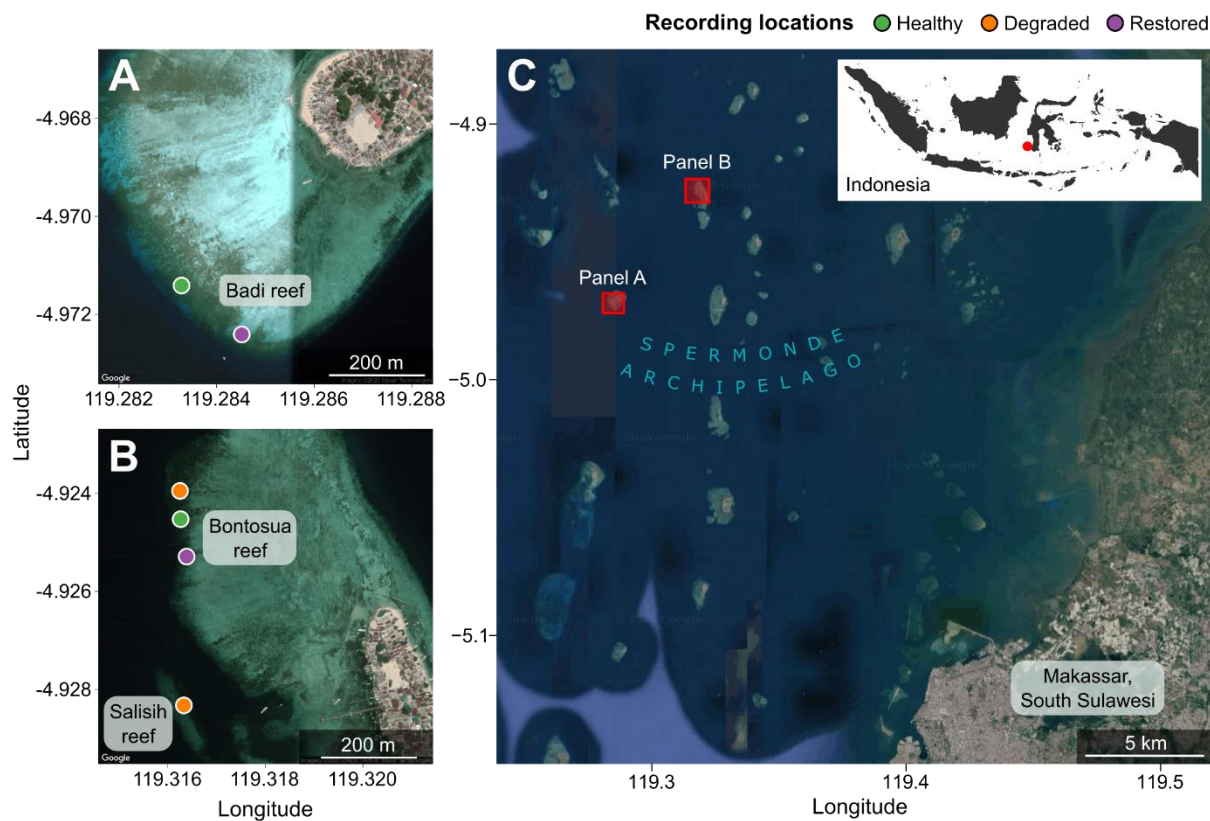
123   *Fig. 1: Map of the study sites and their location in Indonesia. Shown are the locations of recording*

124   *sites (healthy, degraded and restored) at A) Badi reef and B) Bontosua and Salisih reefs; and C) the*

125   *location of the study site within Indonesia. Satellite images obtained from Google Maps, available at*

126   *https://goo.gl/maps/sQrMPoAJQp2d4QHL6 (last accessed on 15/7/2020; map data from Google,*

127   *CNES/Airbus, Landsat/Copernicus and Maxar Technologies).*

128

129   For several years preceding this study, rubble stabilisation and coral gardening was carried

130   out on several hectares of reef historically damaged by blast fishing. Fragments of live coral were

131   attached to networks of modular metal frames ('Reef Stars'; called 'spiders' in previous studies) and

132   deployed in degraded rubble fields; this stabilised rubble and accelerated coral regrowth, leading to

133   substantial increases in live coral cover (see Williams *et al.* (2019) for full details of the restoration

134   technique and its impacts on coral cover). After deployment, all restored reefs were regularly

135   maintained by manual cleaning, repairs of physical damage and active management of disease

136   outbreaks and algal-farming damselfish. The reefs recorded in this study therefore consisted of a

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137   patchy matrix of naturally healthy habitat (no evidence of damage from blast fishing, with 90–95%

138   live coral cover), degraded rubble fields (highly damaged by blast fishing, with 0–20% live coral

139   cover), and restored habitat (Reef Stars of 1–3 years age, with 65–80% live coral cover). Illustrative

140   photos of each of these habitat types are shown in Fig. 2; full details of coral-cover measurements

141   are provided in Supplementary Information. Two examples each of healthy, degraded and restored

142   habitat were selected as recording sites, from across three reefs in the area (Fig. 1). All six recording

143   sites were between 2.0 and 3.3 m depth at low tide; total tidal range during both recording periods

144   was 0.7 m.

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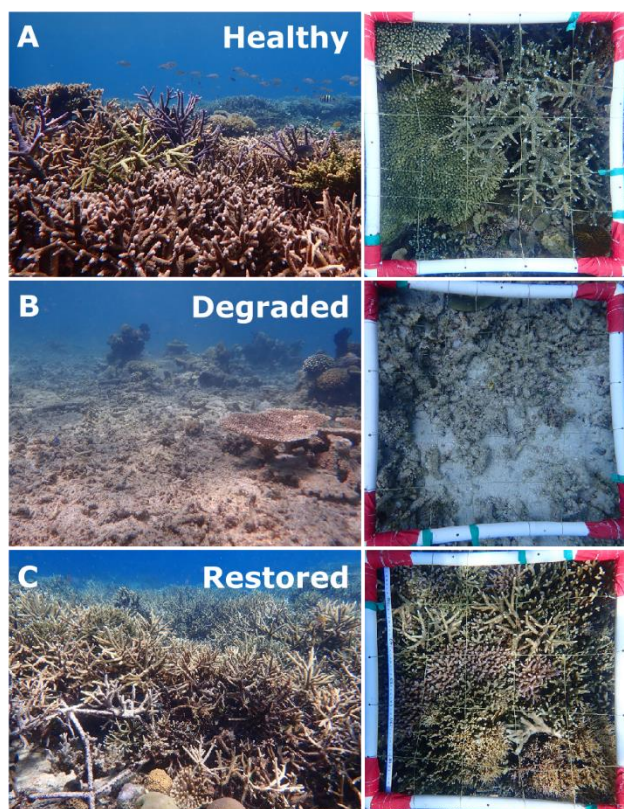
146

147   *Fig. 2: Illustrative photographs and photo quadrats of each habitat type. Shown are examples of A)*

148   *healthy, B) degraded and C) restored habitat measured in this study. Note the visible Reef Star in C;*

149   *other Reef Stars in the photograph are obscured by coral growth. Photo quadrats are 1 x 1 m; full*

150   *coral-cover data are given in Supplementary Information.*

151

152   **Acoustic recordings**

153   Soundscape recordings were taken at each site using hydrophones with inbuilt recorders (SoundTrap

154   300 STD; Ocean Instruments, NZ; sampling rate 48 kHz; manufacturer-calibrated), suspended 0.5 m

155   above the seabed on vertical ropes held between weights and sub-surface floats. Hydrophones were

156   placed at the centre of the 10 x 10 m grid used for coral-cover measurements; a small piece of

157   flagging tape was fixed to this location at each site to ensure that repeat deployments were always

158   in the same place. At least 10 minutes before the scheduled start time of a recording, the

159   hydrophone was placed in position by a snorkeler, who then retreated at least 500 m away.

160   Hydrophones were retrieved after the hour-long recording had finished.

161   Multiple one-hour recordings were taken at each site; these spanned full and new moon

162   periods in both 2018 and 2019, at five different time points: sunrise (half an hour either side of

163   sunrise); morning (one hour between 09:00 and 12:00); afternoon (one hour between 12:00 and

164   15:00); sunset (half an hour either side of sunset); and night (half an hour either side of midnight).

165   Recording schedules were organised with counterbalanced blocking designs, such that there was a

166   similar number of recordings taken of each habitat type, comprising an approximately even spread

167   of time points and lunar phases. Three different hydrophones were used to facilitate simultaneous

168   recording of different sites; hydrophone ID was also factored into the blocking design such that each

169   site was recorded a similar number of times by each hydrophone.

170   A single one-minute sample containing no anthropogenic noise was selected at random from

171   each of the 91 hour-long recordings, for acoustic analysis. Samples were not taken from hour-long

172   recordings that were spoiled by hydrophone failure or continuous anthropogenic noise. There were

173   a total of 91 samples taken across all six sites; in total, each habitat type was represented by at least

174   28 samples and each time point was represented by at least 10 samples. Full details of the sampling

175   procedure, including the number of samples representing each habitat type, reef, time point and

176   lunar phase, are provided in Supplementary Information.

177

178   **Calculation of phonic richness**

179   Audio inspection of each of the 91 samples was carried out by an experimentally blind observer

180   (T.A.C.G.), who noted the presence of distinct biophonic sounds. A total of 10 biophonic sounds

181   were identified; some of these have similar spectral characteristics to sounds documented on coral

182   reefs by previous studies (Tricas & Boyle 2014; Parmentier & Frederich 2016; McWilliam *et al.* 2017),

183   while others have not been documented by other literature on coral reef bioacoustics. For full

184   qualitative and quantitative descriptions of each sound type, see Table 1 and Fig. 3; for

185   representative audio recordings of each sound type, see Supplementary Information.

186   The number of distinct sound types present in each sample was defined as its phonic

187   richness. Rates of sound production for each sound type were not quantified, as there were many

188   instances where group calling made the start and end of individual calls difficult to identify. To

189   ensure repeatability of the results, 20 samples were selected at random to be listened to again. The

190   same observer scored the recordings again, whilst blind to both the identity of the recording and its

191   original score. On all 20 occasions, the result was the same on both scorings.

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193   *Table 1: Qualitative and quantitative descriptions of each of the 10 distinct biophonic sound types present in recordings, and their frequency of occurrence*

194   *(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 & 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 & 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

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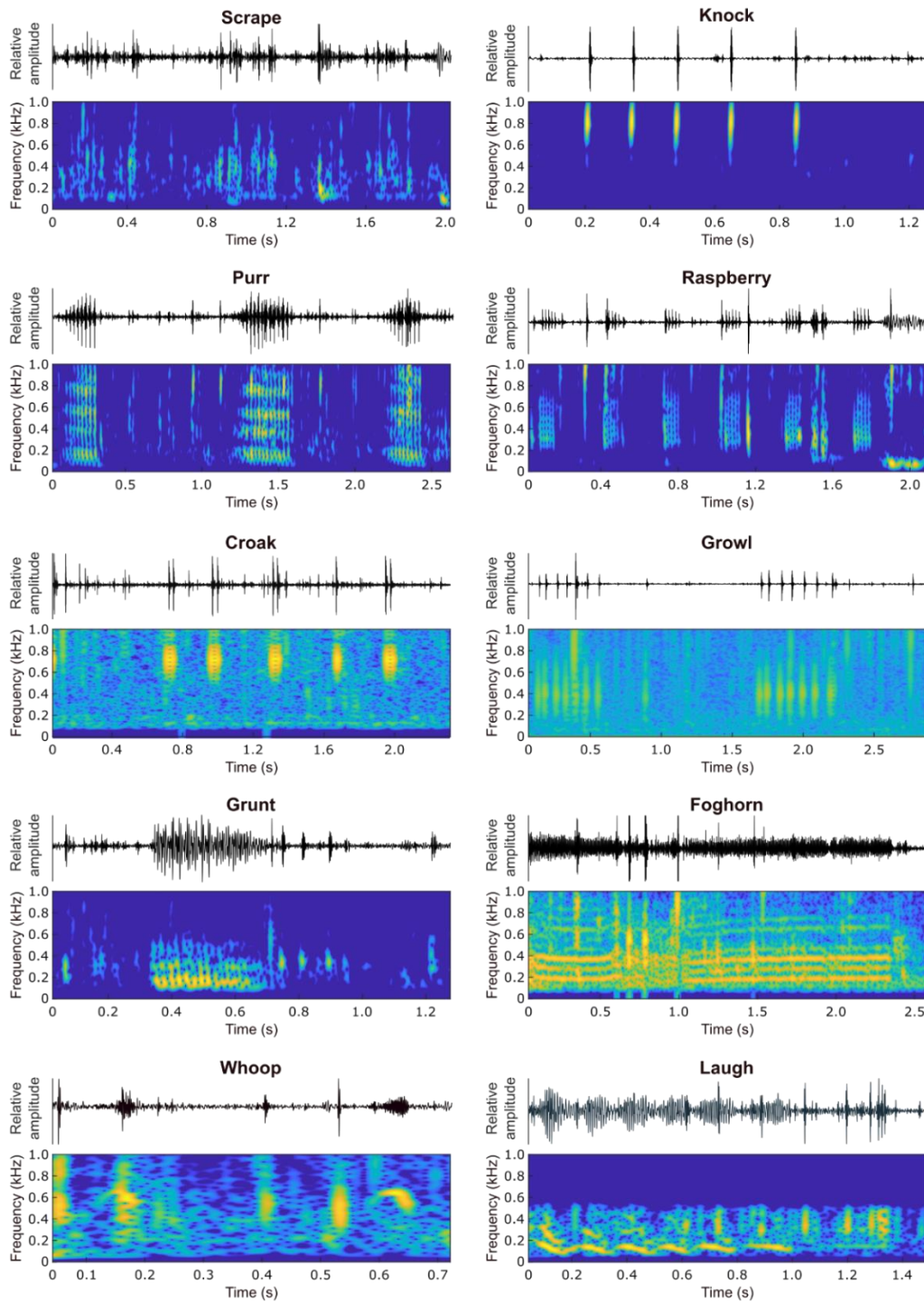
Fig. 3: Illustrative waveforms and spectrograms of each of the 10 distinct biophonic sound types,

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. Recordings are available in

Supplementary Information.

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202   **Calculation of ecoacoustic indices**

203   The acoustic complexity index (ACI) and SPL were calculated for each sample, as the two most

204   commonly used automated ecoacoustic metrics in marine soundscape research (Pieretti & Danovaro

205   2020). Both metrics were calculated across the duration of the whole sample, in both a low-

206   frequency (50–800 Hz) and a high-frequency (2000–7000 Hz) bandwidth. These two bandwidths are

207   likely to contain different ecological information, because fish vocalisations are predominantly

208   pitched lower than 800 Hz (Tricas & Boyle 2014); the higher-frequency band is therefore likely to

209   have been dominated by invertebrate sounds. ACI was calculated using *seewave* (Sueur *et al.* 2008)

210   in *R* v3.6.2 ([https://www.r-project.org/)](https://www.r-project.org/), using an FFT window of 512 samples, resulting in a 93.75 Hz

211   frequency resolution and a 10.6 ms temporal resolution. SPL was calculated using *paPAM* (Nedelec

212   *et al.* 2016), with a Hamming Fast-Fourier Transform (FFT) window of 512 samples and a 50%

213   overlap.

214

215   **Statistical analysis**

216   Each of the ecoacoustic metrics (ACI and SPL in high- and low-frequency bandwidths respectively,

217   and phonic richness) were compared across the three pairs of healthy, degraded and restored sites

218   using a Linear Mixed Model (LMM) if data were normally distributed, or a Poisson-distributed

219   Generalised Linear Mixed Model (GLMM) if correction for positive skew was required. Visual

220   examination of histograms and normal quantile plots of model residuals was used to confirm model

221   goodness-of-fit. In all models, habitat type (healthy, degraded or restored) was included as a fixed

222   effect, and time of day (sunrise, morning, afternoon, sunset or night), lunar phase (new or full), date,

223   hydrophone ID (one of the three hydrophones) and reef location (Badi, Bontosua or Salisih) were

224   included as categorical random effects. All models were optimised by stepwise deletion of random

225   terms with variance of less than 0.001, starting with the term with lowest variance, in order to

226   minimise risk of over-fitting. The overall effect of habitat type on the dependent variable was tested

227   using ANOVA comparisons to null models that were identical except for the omission of the fixed

228   term. If this comparison was statistically significant ($p<0.05$), post-hoc Tukey's HSD testing followed

229   to provide between-habitat comparisons. Canonical correspondence analysis was also used to

230   visualise the groupings of different sound types present in each habitat type; habitat type, time

231   point, lunar phase and reef location were used as constraining environmental variables.

232   Finally, correlation tests were carried out between ecoacoustic metrics that displayed

233   significant effects of habitat type. A correlogram was used to assess pairwise comparisons between

234   variables for each sample, and Pearson's (linear) and Spearman's rank (monotonic) correlation tests

235   were calculated for each individual comparison. All model residuals met assumptions of normality

236   and homoscedasticity, and a Bonferroni adjustment for multiple testing was applied when

237   considering the statistical significance of the multiple pairwise comparisons.

238   All statistical analyses and figure creation was carried out in *R* v3.6.2 (https://www.r-

239   project.org/); specific package information is available in Supplementary Information.

240

241   **RESULTS**

242   Of the 10 sound types present in recordings (Table 1), two occurred most frequently in diurnal

243   recordings, five occurred most frequently at sunrise or sunset, and three occurred most frequently

244   at night (Fig. 4A). Seven of these 10 sound types occurred at least 50% more often in healthy and

245   restored habitat than in degraded habitat (Fig. 4B). This led to a significant effect of habitat type on

246   phonic richness (GLMM: $\chi^2 = 8.82$, df = 2, $p = 0.012$; Fig. 4C); healthy and restored habitat had a

247   significantly higher phonic richness than degraded habitat, with no significant difference between

248   the healthy and restored habitat (Fig. 4C; full model and post-hoc comparisons in Supplementary

249   Table S2). Canonical correspondence analysis on all recordings with a phonic richness greater than 0

250   (n = 71) revealed that the distributions of sound types present in healthy and restored habitat were

251   similar to each other, and both differed from those present in degraded habitat (Fig. 5).
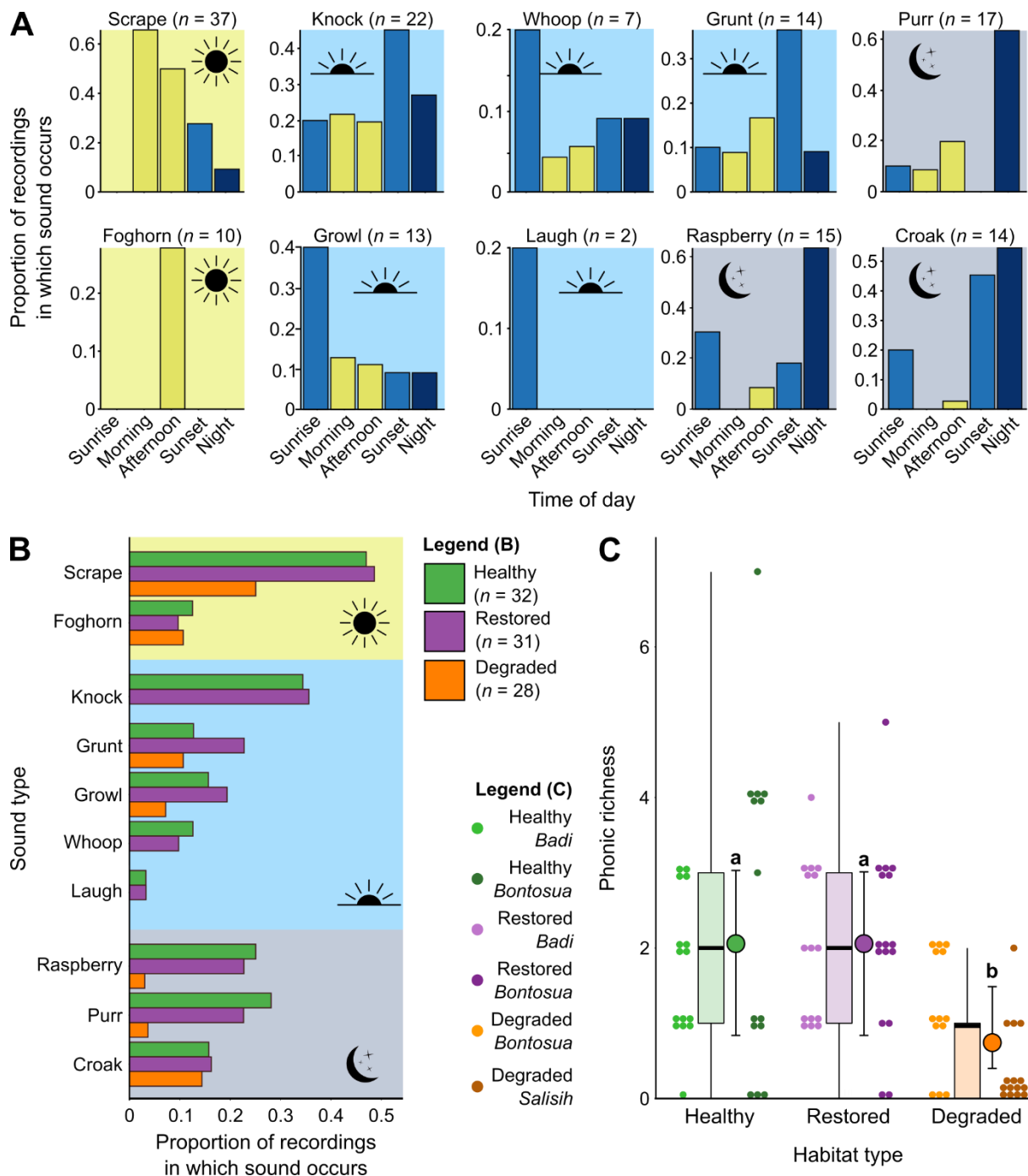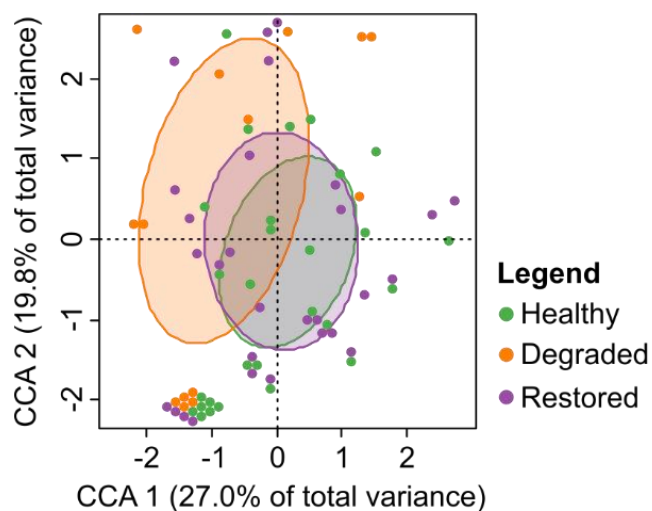

253   *Fig. 4: Phonic richness of healthy, degraded and restored habitat. A & B) The proportion of recordings*

254   *in which each sound type occurred, by time of day (A) and habitat type (B). Sample sizes (n) in A*

255   *indicate the total number of recordings in which the sounds occurred. Bars in A correspond to*

256   *broader time categories, with yellow representing diurnal (morning or afternoon), blue representing*

257   *crepuscular (sunrise or sunset) and grey representing nocturnal (night) recordings. Background*

258   *colours in A and B indicate which of these time categories each sound occurred most frequently in,*

259   *using the same colour code. C) The effect of habitat type on phonic richness. Shown are raw data*

260   *from both sites of each habitat type (small points, jittered such that directly overlaid points appear*

261   *adjacent to one another), and model estimates and 95% confidence intervals (large points and error*

262   *bars) from a Poisson-distributed Generalised Linear Mixed Model (GLMM). Boxplots combine raw*

263   *data from both sites of each habitat type; thick lines indicate the median, boxes indicate 25 and 75%*

264   *quartiles, and whiskers indicate the full range of the data. Different letters represent significant*

265   *differences in Tukey's HSD post-hoc testing (p<0.05), following a significant effect of habitat type in*

266   *the GLMM (for full model and post-hoc comparisons, see Supplementary Table S2).*


267

268   *Fig. 5: Canonical correspondence analysis (CCA) plot of phonic richness in recordings of healthy*

269   *(green), degraded (orange) and restored (purple) reefs. Each point represents a single recording;*

270   *points are jittered such that directly overlaid points appear adjacent to one another. Recordings with*

271   *no individual sounds detected (phonic richness = 0) were removed from the dataset prior to this*

272   *analysis. The clustering of 16 points in the bottom left represent recordings in which only scraping*

273   *sounds occurred (phonic richness = 1), which was the most common result in the dataset. Ellipses*

274   *represent the area encompassing the standard deviation of all points within each group.*

275

276   There was a significant effect of habitat type on the ACI (LMMs, low frequency: χ^2 = 13.08, df

277   = 2, p = 0.002; high frequency: χ^2 = 40.46, df = 2, $p<0.001$), although the between-group results were

278   not consistent across the two frequency bandwidths. Degraded habitat had significantly lower ACI

279   scores than both healthy and restored habitat in both frequency bandwidths. However, although

280   there was no significant difference between the ACI values of healthy and restored habitat in the

281   high-frequency bandwidth, restored habitat had significantly higher ACI values than healthy habitat

282   in the high-frequency bandwidth (Fig. 6A; full model and post-hoc comparisons in Supplementary

283   Table S2). There was no significant effect of habitat type on SPL in either frequency bandwidth (Fig.

284   6B; low frequency: χ^2 = 0.69, df = 2, p = 0.708; high frequency: χ^2 = 2.31, df = 2, p = 0.315; full model

285   and post-hoc comparisons in Supplementary Table S2).

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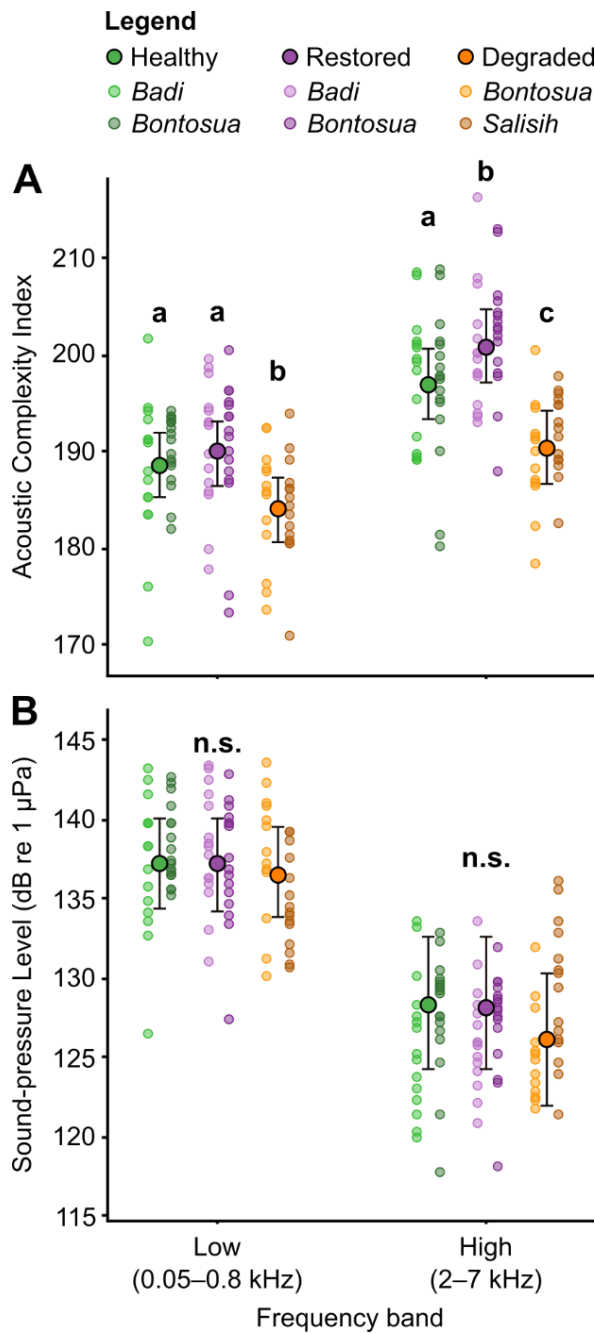
Fig. 6: A) Acoustic complexity index and B) sound-pressure level of recordings of healthy, degraded

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 (p<0.05), following a significant effect of habitat type in the LMMs; 'n.s.' indicates there was

no significant effect of habitat type in the LMMs. For full models and post-hoc comparisons, see

Supplementary Table S2.

295

296   Of the ecoacoustic metrics that were significantly affected by habitat type (phonic richness

297   and low- and high-frequency ACI), only the low- and high-frequency ACI values shared a strong

298   positive correlation at a Bonferroni-adjusted α of 0.012 (Fig. 7; n = 91 for all comparisons). This

299   relationship was significant for both linear Pearson's correlation ($ρ$ = 0.33, $p<0.01$) and monotonic

300   Spearman's rank correlation (r = 0.39, $p<0.01$). By contrast, phonic richness had weak monotonic

301   correlations with both low-frequency ACI (r = 0.26, p = 0.01) and high-frequency ACI (r = 0.21, p =

302   0.04), and no linear correlation with ACI in either frequency bandwidth (low frequency: $ρ$ = 0.19, p =

303   0.07; high frequency: $ρ$ = 0.12, p = 0.25).

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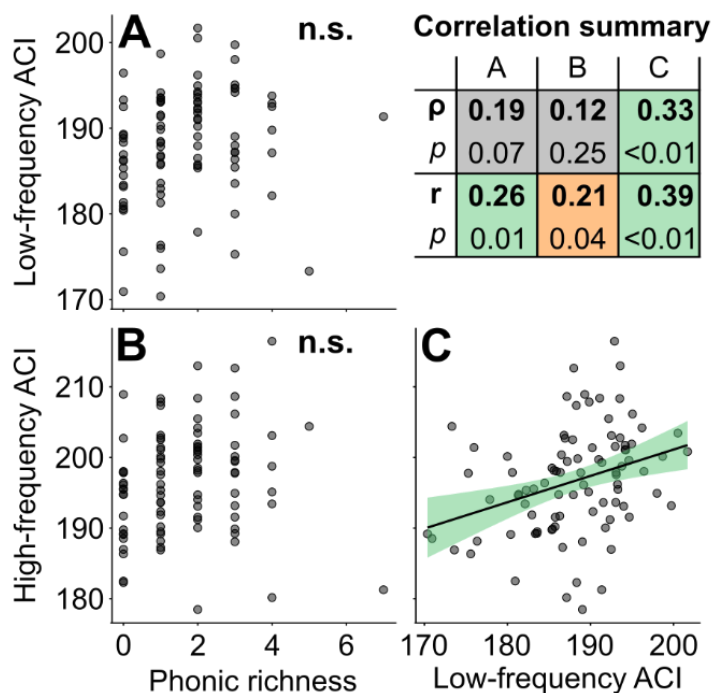
306   *Fig. 7: Correlations between ecoacoustic metrics that demonstrated a significant effect of habitat*

307   *type. Shown in A–C is a correlogram of all pairwise relationships between phonic richness and high-*

308   *and low-frequency ACI (acoustic complexity index). The correlation summary gives the Pearson's ρ*

309   *(linear; top row) and Spearman's rank r (monotonic; bottom row) correlation coefficient for each*

310   *pairwise comparison, along with its associated* p-*value; values highlighted in grey are non-significant*

311   *(*p>*0.05), those in orange are significant individually but not when Bonferroni adjustment for multiple*

312   *testing is included (0.012<*p<*0.05), and those in green are significant when Bonferroni adjustment is*

313   *included (*p<*0.012). In panel A and B, 'n.s.' indicates no significant linear correlation. In panel C (the*

314   *only relationship with a significant linear correlation), the solid line and green ribbon represent the*

315   *linear model output and associated standard error.*

316

317   **DISCUSSION**

318   This study tests passive acoustic monitoring (PAM) as a method for evaluating ecosystem recovery at

319   one of the world's largest coral reef restoration projects. Restored habitat (live coral cover >65%)

320   had similar levels of phonic richness to healthy habitat (live coral cover >90%), with degraded habitat

321   (live coral cover <20%) displaying significantly lower phonic richness than both healthy and restored

322   habitat (Fig. 4). A qualitatively similar pattern to this was found in the ACI values (Fig. 6A), despite

323   only weak correlations between the ACI and phonic richness values for each recording (Fig. 7). There

324   was no effect of habitat type on SPL (Fig. 6B). Taken together, these results suggest that both

325   manual and automated approaches to PAM may be useful tools in monitoring the success of coral

326   reef restoration, but automated indices such as the ACI and sound-pressure level SPL are not driven

327   by changes in phonic richness of audible biotic sound types.

328   The observed patterns in phonic richness might be explained by various different

329   mechanisms. Greater phonic richness may reflect a more abundant and/or diverse community of

330   soniferous organisms; or different behaviours exhibited by soniferous organisms; or a combination

331   of both mechanisms. The organisms responsible for making the sounds driving these patterns are

332   unknown. Some of the sound types described in this study (Table 1; Fig. 3) have been previously

333   described; for example, a range of percussive and pulse-train sounds have been associated with

334   triggerfish (family Balistidae), damselfish (Pomacentridae) and butterflyfish (Chaetodontidae); growl

335   and grunt sounds have been associated with soldierfish (Holocentridae); scraping sounds have been

336   associated with the feeding of macroherbivores such as parrotfish (Scaridae) and triggerfish

337   (Balistidae); and whooping sounds have been associated with the Ambon damselfish *Pomacentrus*

338   *amboinensis* (Tricas & Boyle 2014; Parmentier & Frederich 2016). However, other sound types are

339   less familiar; for example, we are not aware of any previous descriptions of the 'laugh' sound (Table

340   2; Fig. 3). Each individual sound type does not necessarily correspond to a single sound-producing

341   species; some fishes are capable of multiple phonation types (Parmentier *et al.* 2010, 2019), and

342   may be making more than one of the sounds described in this study. Conversely, there is a high

343   degree of overlap in the spectral characteristics of sounds produced by different fishes (Tricas &

344   Boyle 2014), and some of these sound types may be produced by more than one species. As such,

345   phonic richness is best considered as an indirect proxy for the abundance and diversity of the

346   soniferous community, rather than a precise count of the number of soniferous species present.

347   Results from the two ecoacoustic indices were not qualitatively equivalent (Fig. 6); the low-

348   frequency bandwidth ACI followed a qualitatively equivalent pattern to that observed in phonic

349   richness, but this pattern was different to that in the high-frequency bandwidth, and there was no

350   effect of habitat type on SPL in either frequency bandwidth. Further, despite the qualitative

351   equivalence of the pattern observed in low-frequency ACI and phonic richness scores, there was only

352   a weak monotonic correlation between these two metrics, and no significant linear correlation (Fig.

353   7). It is clear that the outputs of ecoacoustic metrics are not equivalent across frequency

354   bandwidths, and different metrics do not reflect the same results as each other. It is likely that these

355   observed discrepancies are caused by different indices being driven by different aspects of the

356   soundscape. For instance, the majority of the biotic sounds driving phonic richness have peak

357   frequencies between 150 and 800 Hz, and therefore cannot have been driving the results of

358   ecoacoustic indices in the high-frequency bandwidth; this explains the lack of correlation between

359   phonic richness and the high-frequency ACI values. By contrast, the low-frequency ACI values

360   correlate strongly with the high-frequency ACI values, suggesting a common driver. Indeed, previous

21

361   work has demonstrated that ACI values correlate better with levels of invertebrate snapping sound

362   than with fish vocalisation rates (Bohnenstiehl *et al.* 2018). Taken together, these results suggest

363   that the ACI may be describing the variation in background invertebrate noise, rather than the

364   diversity of individual fish calls within a reef soundscape. Although habitat type had a qualitatively

365   equivalent effect on both phonic richness and the low-frequency ACI, it is likely that this was driven

366   by different aspects of the soundscape in each case.

367   The documented acoustic recovery described here is important for three main reasons. First,

368   it demonstrates the return of an important functional property of actively-restored reef systems. On

369   healthy reefs, a loud and diverse soundscape guides the orientation and settlement behaviours of

370   many juvenile reef organisms that spend their larval stage in the open ocean (Montgomery *et al.*

371   2006; Simpson *et al.* 2008; Leis *et al.* 2011; Lillis *et al.* 2018). When reefs degrade, their denuded

372   soundscapes are less attractive to young fishes and invertebrates, potentially jeopardising this

373   acoustically guided settlement behaviour (Lillis *et al.* 2016, 2018; Gordon *et al.* 2018). The recovery

374   of soundscapes suggests that restored reefs have the potential to regain their attractiveness to

375   settlement-stage organisms; this is encouraging as it means that restored reefs may have the

376   capacity to attract future generations of reef organisms, improving the prospects of long-term

377   ecosystem stability.

378   Second, these results are important because they demonstrate that active restoration of

379   coral cover can have beneficial impacts on the wider ecosystem. The greater phonic richness and ACI

380   on restored reefs relative to degraded habitat likely reflect a greater abundance or altered behaviour

381   of soniferous fishes and invertebrates respectively. Healthy populations of a range of reef organisms

382   underpin ecological functioning and ecosystem service provision on reefs (Graham *et al.* 2015; Sato

383   *et al.* 2020). Given the current paucity of evaluations of restoration success that go beyond coral

384   cover (Hein *et al.* 2017), these results are important in demonstrating that coral restoration can have

385   holistic effects on the wider ecosystem.

386   Third, these results are important in demonstrating the complementary value that PAM

387   might bring to monitoring of coral reef ecosystems. PAM has the capacity to detect cryptic and

388   nocturnal species; to monitor over extended periods of time; and to provide objective measures that

389   are not susceptible to observer bias. (Obura *et al.* 2019; Mooney *et al.* 2020). These benefits might

390   allow PAM to effectively complement traditional visual methods for surveying reefs. Several

391   functionally important reef organisms are cryptic or only active at night, so cannot be surveyed with

392   traditional visual methods. However, in an analogous manner, several functionally important reef

393   species also do not make any sounds, so cannot be surveyed by PAM. This imperfect overlap in the

394   communities detected by visual and acoustic surveys means that these methods are likely be

395   complementary (Fig. 8). Reef surveys that use multiple methods are likely to generate a more

396   holistic understanding of ecosystem health than those using any single method in isolation.

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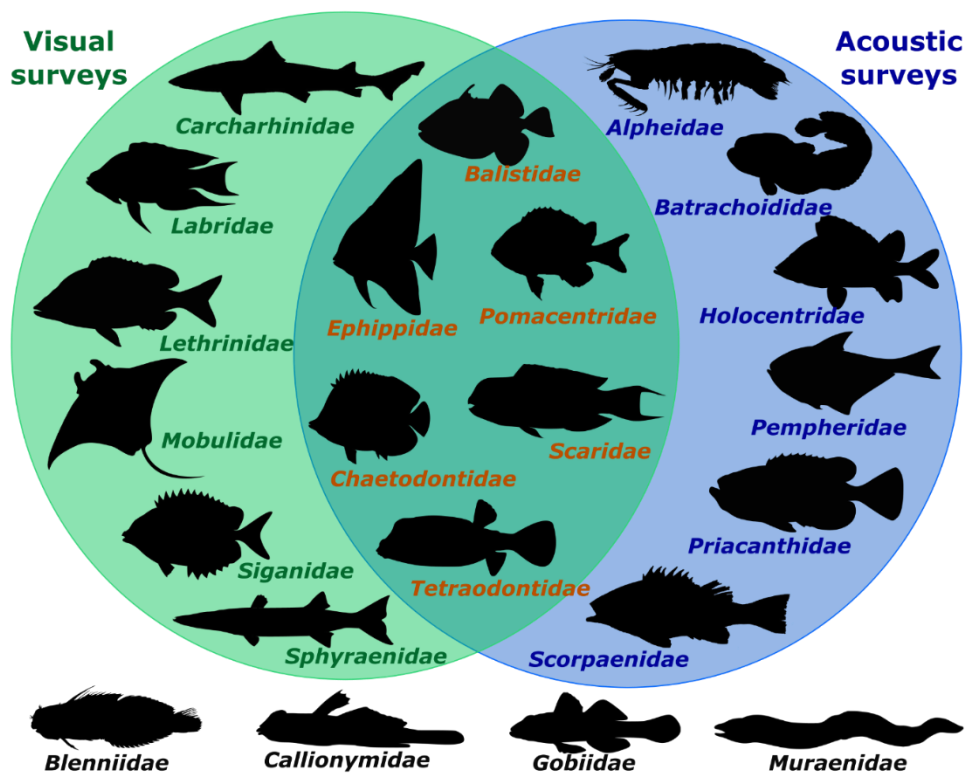
398

399   *Fig. 8. Schematic diagram illustrating the potential complementarity of visual and acoustic surveys of*

400   *coral reefs. The green circle displays examples of families of non-cryptic, diurnally active reef*

401 *organisms whose abundance is reflected in visual surveys. The blue circle displays examples of*

402 *soniferous families whose abundance is reflected in soundscape recordings. Families in the*

403 *overlapping turquoise segment might be detected by both visual and acoustic surveys. Families*

404 *outside all coloured segments are both cryptic and silent, and are therefore difficult to survey using*

405 *either visual or acoustic methods.*

406

407   Given the promising results shown in this study, there are now exciting gains to be made by

408 expanding the biogeographic and seasonal replication of PAM as a method of evaluating the success

409 of reef restoration. The recordings in this study come from just two reefs of each habitat type, in a

410 single biogeographic region at one time of year. Whilst this does not invalidate these findings, it will

411 now be important to test their generality across geographic regions and seasons, especially on

412 systems where seasons can have strong impacts on soundscape dynamics (Staaterman *et al.* 2014).

413 This increased spatial and temporal replication might be readily achieved by citizen science;

414 recording devices for PAM are becoming increasingly affordable and user-friendly (Hill *et al.* 2018),

415 and the rapid development of machine-learning techniques for the analysis of a range of marine and

416 terrestrial soundscapes may soon potentiate automatic calculations of phonic richness (Stowell *et al.*

417 2019; Sethi *et al.* 2020). If standardised deployment of affordable sound-recording devices with

418 automated analysis of recordings became commonplace on a wide range of restoration projects, this

419 would represent a unique opportunity to test the generality of PAM as a novel tool for the

420 monitoring of reef restoration worldwide.

421

422 **CONCLUSIONS**

423 This study demonstrates that detectable acoustic differences exist between the soundscapes of

424 healthy, degraded and actively restored coral reefs. Quantifiable differences between habitat types

425   exist for both manual and automated ecoacoustic metrics, although not all metrics reveal

426   qualitatively equivalent patterns. This study provides exciting proof-of-concept data on which future

427   monitoring efforts might valuably build. PAM has the potential to facilitate more comprehensive

428   understanding of the recovery of reef ecosystems, providing practitioners with a new metric to

429   evaluate the success of reef restoration interventions worldwide.

430

445

446   **AUTHOR CONTRIBUTIONS**

447   T.A.C.G., A.N.R and S.D.S. conceived the research idea and designed the study; T.A.C.G., B.W., L.C.,

448   M.E.P., M.S., H.R.H. and E.M. contributed to fieldwork and data collection; T.A.C.G., B.W., L.C., A.N.R.

449   and S.D.S. analysed the data; T.A.C.G. wrote the first draft of the manuscript and all authors

450   contributed to subsequent revisions.

451

DATA AVAILABILITY STATEMENT

453 Upon publication, raw data will be made available from the University of Exeter's institutional

454 repository at doi.org/xxxxxxxx.

455

REFERENCES

457 Bertucci, F., Parmentier, E., Lecellier, G., Hawkins, A.D. & Lecchini, D. (2016). Acoustic indices provide

458 information on the status of coral reefs: an example from Moorea Island in the South Pacific.

459 *Sci. Rep.*, 6, 33326.

460 Bohnenstiehl, D.R., Lyon, R.P., Caretti, O.N., Ricci, S.W. & Eggleston, D.B. (2018). Investigating the

461 utility of ecoacoustic metrics in marine soundscapes. *J. Ecoacoustics*, 2, R1156L.

462 Bostrom-Einarsson, L., Babcock, R.C., Bayraktarov, E., Ceccarelli, D., Cook, N., Ferse, S., *et al.* (2020).

463 Coral restoration – A systematic review of current methods, successes, failures and future

464 directions. *PLoS One*, 15, e0226631.

465 Burke, L., Reytar, K., Spalding, M. & Perry, A. (2012). *Reefs at Risk Revisited in the Coral Triangle*.

466 World Resources Institute, Washington D.C.

467 Ceccarelli, D.M., McLeod, I.M., Bostrom-Einarsson, L., Bryan, S.E., Chartrand, K.M., Emslie, M.J., *et al.*

468 (2020). Substrate stabilisation and small structures in coral restoration: State of knowledge,

469 and considerations for management and implementation. *PLoS One*, 15, e0240846.

470 Cinner, J. (2014). Coral reef livelihoods. *Curr. Opin. Environ. Sustain.*, 7, 65–71.

471 Duarte, C.M., Agusti, S., Barbier, E., L, B.G., Castilla, J.C., Gattuso, J., *et al.* (2020). Rebuilding marine

472 life. *Nature*, 580, 39–51.

473   Fox, H.E., Pet, J.S., Dahuri, R. & Caldwell, R.L. (2003). Recovery in rubble fields: long-term impacts of

474   blast fishing. *Mar. Pollut. Bull.*, 46, 1024–1031.

475   Gibb, R., Browning, E., Glover-Kapfer, P. & Jones, K.E. (2019). Emerging opportunities and challenges

476   for passive acoustics in ecological assessment and monitoring. *Methods Ecol. Evol.*, 10, 169–

477   185.

478   Gordon, T.A.C., Harding, H.R., Wong, K.E., Merchant, N.D., Meekan, M.G., McCormick, M.I., *et al.*

479   (2018). Habitat degradation negatively affects auditory settlement behavior of coral reef fishes.

480   *Proc. Natl. Acad. Sci.*, 115, 5193–5198.

481   Graham, N.A.J., Jennings, S., MacNeil, M.A., Mouillot, D. & Wilson, S.K. (2015). Predicting climate-

482   driven regime shifts versus rebound potential in coral reefs. *Nature*, 518, 94–97.

483   Harborne, A.R., Rogers, A., Bozec, Y.-M. & Mumby, P.J. (2017). Multiple Stressors and the

484   Functioning of Coral Reefs. *Ann. Rev. Mar. Sci.*, 9, 5.1-5.24.

485   Hein, M.Y., Willis, B.L., Beeden, R. & Birtles, A. (2017). The need for broader ecological and

486   socioeconomic tools to evaluate the effectiveness of coral restoration programs. *Restor. Ecol.*,

487   25, 873–883.

488   Hill, A.P., Prince, P., Covarrubias, E.P., Doncaster, C.P., Snaddon, J.L. & Rogers, A. (2018).

489   AudioMoth : Evaluation of a smart open acoustic device for monitoring biodiversity and the

490   environment. *METHODS Ecol. Evol.*, 9, 1199–1211.

491   de la Cruz, D.W. & Harrison, P.L. (2017). Enhanced larval supply and recruitment can replenish reef

492   corals on degraded reefs. *Sci. Rep.*, 7, 13985.

493   Leis, J.M., Siebeck, U. & Dixson, D.L. (2011). How nemo finds home: The neuroecology of dispersal

494   and of population connectivity in larvae of marine fishes. *Integr. Comp. Biol.*, 51, 826–843.

495   Lillis, A., Apprill, A., Suca, J.J., Becker, C., Llopiz, J.K. & Mooney, T.A. (2018). Soundscapes influence

496   the settlement of the common Caribbean coral Porites astreoides irrespective of light

497   conditions. *R. Soc. Open Sci.*, 5, 181358.

498   Lillis, A., Bohnenstiehl, D., Peters, J.W. & Eggleston, D. (2016). Variation in habitat soundscape

499   characteristics influences settlement of a reef-building coral. *PeerJ*, 4, e2557.

500   McWilliam, J.N., McCauley, R.D., Erbe, C. & Parsons, M.J.G. (2017). Patterns of biophonic periodicity

501   on coral reefs in the Great Barrier Reef. *Sci. Rep.*, 7, 17459.

502   Merchant, N.D., Fristrup, K.M., Johnson, M.P., Tyack, P.L., Witt, M.J., Blondel, P., *et al.* (2015).

503   Measuring acoustic habitats. *Methods Ecol. Evol.*, 6, 257–265.

504   Montgomery, J.C., Jeffs, A., Simpson, S.D., Meekan, M. & Tindle, C. (2006). Sound as an Orientation

505   Cue for the Pelagic Larvae of Reef Fishes and Decapod Crustaceans. *Adv. Mar. Biol.*, 51, 143–

506   196.

507   Mooney, T.A., Iorio, L. Di, Lammers, M., Lin, T., Nedelec, S.L., Parsons, M., *et al.* (2020). Listening

508   forward: approaching marine biodiversity assessments using acoustic methods. *R. Soc. Open*

509   *Sci.*, 7, 201287.

510   Nedelec, S.L., Campbell, J., Radford, A.N., Simpson, S.D., Merchant, N.D. & Fisher, D. (2016). Particle

511   motion: the missing link in underwater acoustic ecology. *Methods Ecol. Evol.*, 7, 836–842.

512   Obura, D.O., Aeby, G., Amornthammarong, N., Appeltans, W., Bax, N., Bishop, J., *et al.* (2019). Coral

513   Reef Monitoring, Reef Assessment Technologies, and Ecosystem-Based Management. *Front.*

514   *Mar. Sci.*, 6, 580.

515   Parmentier, E. & Frederich, B. (2016). Broadening of acoustic repertoire in Pomacentridae: tonal

516   sounds in the Ambon damselfish Pomacentrus amboinensis. *J. Zool.*, 300, 241–246.

517   Parmentier, E., Kever, L., Casadevall, M. & Lecchini, D. (2010). Diversity and complexity in the

518   acoustic behaviour of Dacyllus flavicaudus (Pomacentridae). *Mar. Biol.*, 157, 2317–2327.

519   Parmentier, E., Solagna, L., Bertucci, F., Fine, M.L., Nakae, M., Compère, P., *et al.* (2019).

520   Simultaneous production of two kinds of sounds in relation with sonic mechanism in the

521   boxfish Ostracion meleagris and O. cubicus. *Sci. Rep.*, 9, 4962.

522   Piercy, J.J.B., Codling, E.A., Hill, A.J., Smith, D.J. & Simpson, S.D. (2014). Habitat quality affects sound

523   production and likely distance of detection on coral reefs. *Mar. Ecol. Prog. Ser.*, 516, 35–47.

524   Pieretti, N. & Danovaro, R. (2020). Acoustic indexes for marine biodiversity trends and ecosystem

525   health. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.*, 375, 20190447.

526   Pieretti, N., Farina, A. & Morri, D. (2011). A new methodology to infer the singing activity of an avian

527   community: The Acoustic Complexity Index (ACI). *Ecol. Indic.*, 11, 868–873.

528   Sato, M., Nanami, A., Bayne, C.J., Makino, M. & Hori, M. (2020). Changes in the potential stocks of

529   coral reef ecosystem services following coral bleaching in Sekisei Lagoon , southern Japan :

530   implications for the future under global warming. *Sustain. Sci.*, 15, 863–883.

531   Sethi, S.S., Jones, N.S., Fulcher, B.D., Picinali, L., Clink, D.J., Klinck, H., *et al.* (2020). Characterizing

532   soundscapes across diverse ecosystems using a universal acoustic feature set. *Proc. Natl. Acad.*

533   *Sci. U. S. A.*, 117, 17049–17055.

534   Simpson, S.D., Meekan, M.G., Jeffs, A., Montgomery, J.C. & McCauley, R.D. (2008). Settlement-stage

535   coral reef fish prefer the higher-frequency invertebrate-generated audible component of reef

536   noise. *Anim. Behav.*, 75, 1861–1868.

537   Staaterman, E., Ogburn, M.B., Altieri, A.H., Brandl, S.J., Whippo, R., Seemann, J., *et al.* (2017).

538   Bioacoustic measurements complement visual biodiversity surveys: preliminary evidence from

539   four shallow marine habitats. *Mar. Ecol. Prog. Ser.*, 575, 207–215.

540   Staaterman, E., Paris, C.B., DeFerrari, H.A., Mann, D.A., Rice, A.N. & D'Alessandro, E.K. (2014).

541   Celestial patterns in marine soundscapes. *Mar. Ecol. Prog. Ser.*, 508, 17–32.

542 Stowell, D., Wood, M.D., Pamuła, H., Stylianou, Y. & Glotin, H. (2019). Automatic acoustic detection

543 of birds through deep learning: The first Bird Audio Detection challenge. *Methods Ecol. Evol.*,

544 10, 368–380.

545 Sueur, J., Aubin, T. & Simonis, C. (2008). Equipment Review Seewave , a free modular tool for sound

546 analysis and synthesis. *Bioacoustics*, 18, 213–226.

547 Sueur, J. & Farina, A. (2015). Ecoacoustics: the Ecological Investigation and Interpretation of

548 Environmental Sound. *Biosemiotics*, 8, 493–502.

549 Tricas, T.C. & Boyle, K.S. (2014). Acoustic behaviors in Hawaiian coral reef fish communities. *Mar.*

550 *Ecol. Prog. Ser.*, 511, 1–16.

551 Versluis, M., Schmitz, B., von der Heydt, a & Lohse, D. (2000). How snapping shrimp snap: through

552 cavitating bubbles. *Science*, 289, 2114–2117.

553 Williams, S.L., Sur, C., Janetski, N., Hollarsmith, J.A., Rapi, S., Barron, L., *et al.* (2019). Large-scale

554 Coral Reef Rehabilitation After Blast Fishing in Indonesia. *Restor. Ecol.*, 27, 447–456.

555