

1 **Acoustic and biological trends on coral reefs off Maui, Hawaii**

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12 **Key words:** Coral reefs, Soundscapes, Biodiversity, Soniferous

13 **Abstract**

14 Coral reefs are characterized by high biodiversity and evidence suggests that reef soundscapes
15 reflect local species assemblages. To investigate how sounds produced on a given reef relate to
16 abiotic and biotic parameters and how that relationship may change over time, an observational
17 study was conducted between September 2014 and January 2016 at seven Hawaiian reefs that
18 varied in coral cover, rugosity, and fish assemblages. The reefs were equipped with temperature
19 loggers and acoustic recording devices that recorded on a 10% duty cycle. Benthic and fish
20 visual survey data were collected four times over the course of the study. On average, reefs
21 ranged from 0 to 80% live coral cover, although changes between surveys were noted, in
22 particular during the major El Niño-related bleaching event of October 2015. Acoustic analyses
23 focused on two frequency bands (50–1200 Hz and 1.8–20.5 kHz) that corresponded to the
24 dominant spectral features of the major sound-producing taxa on these reefs, fish and snapping
25 shrimp, respectively. In the low-frequency band, the presence of humpback whales (December–
26 May) was a major contributor to sound level, whereas in the high-frequency band sound level
27 closely tracked water temperature. On shorter timescales, the magnitude of the diel trend in
28 sound production was greater than that of the lunar trend, but both varied in strength among
29 reefs, which may reflect differences in the species assemblages present. Results indicated that the
30 magnitude of the diel trend was related to fish densities at low frequencies and coral cover at
31 high frequencies; however, the strength of these relationships varied by season. Thus, long-term
32 acoustic recordings capture the substantial acoustic variability present in coral-reef ecosystems
33 and provide insight into the presence and relative abundance of sound-producing organisms.

34

35 **Introduction**

36 Coral reefs vary in their species assemblages in space and time (Parravicini et al. 2013;
37 Williams et al. 2015) and identifying the drivers of this variability has long been a focus of the
38 ecological literature. Much effort has gone into characterizing links between biophysical
39 attributes of coral reefs and fish species assemblages. Parameters such as depth, substrate
40 complexity (rugosity), live coral cover, and coral species richness appear to be important
41 correlates with fish species richness and abundance (McCormick 1994; Friedlander et al. 2003;
42 Messmer et al. 2011; Komyakova et al. 2013).

43 Just as the biological composition of coral reefs changes over time, so too do the
44 associated ambient soundscapes (Staaterman et al. 2014; Kaplan et al. 2015; Nedelec et al.
45 2015). For example, in an approximately year-long study of two Caribbean reefs, sound levels
46 were found to vary on diel and lunar scales (Staaterman et al. 2014). However, the relationship to
47 species present was not well characterized, which limited understanding of the influence of
48 species assemblages on local soundscapes. Contemporaneous work sought to link visual survey
49 data to soundscape measurements and found a relationship between the strength of diel trends in
50 sound production to fish density and coral cover on Caribbean reefs (Kaplan et al. 2015).
51 However, that study was relatively short (four months) and was conducted using only three reefs
52 (Kaplan et al. 2015). While others have compared acoustic parameters to biophysical variables
53 such as coral cover, fish density, and sea state across several reefs (Nedelec et al. 2014; Bertucci
54 et al. 2016), this has often come with the trade-off of using relatively brief recordings that likely
55 overlook the appreciable variation in sound cues over longer timescales (Radford et al. 2008;
56 Staaterman et al. 2014; Kaplan et al. 2015).

57 Collectively, these studies present initial characterizations of some of the putative drivers
58 of this acoustic variability, such as water temperature and the biota present, suggesting a link

59 between reef species assemblages and the local soundscape. Individually, however, these studies
60 often do not adequately characterize the temporal or spatial variability that is likely present. For
61 example, the relevant factors influencing biological sound production may vary in importance
62 over multiple timescales and among communities of sound-producing organisms (Radford et al.
63 2008; Radford et al. 2014). Thus, data collected from several sites over relatively long timescales
64 are most likely to yield insight into the relationships between biodiversity and ambient
65 soundscapes.

66 Despite the limitations of the aforementioned studies, this growing body of work suggests
67 that monitoring the sounds produced by the diverse array of soniferous coral-reef organisms may
68 be a cost-effective and efficient means of assessing reef community assemblages and their
69 changes over time (Lammers et al. 2008; Radford et al. 2014). Acoustic observations could
70 supplement or reduce the need for frequent, traditional, diver-based visual surveys. However, to
71 develop the capability to infer species assemblages and ecological dynamics from acoustic data
72 (i.e., inverse prediction), it is first necessary to examine the relationship between biological
73 sounds on reefs and fundamental ecological parameters, such as fish species richness and
74 abundance and benthic cover.

75 In recent years, there has been interest in applying acoustic biodiversity metrics
76 developed for terrestrial ecosystems to marine soundscapes (e.g., Parks et al. 2014; Bertucci et
77 al. 2016; Staaterman et al. 2017); however, there has been little compelling evidence to suggest
78 that such metrics provide valuable information not available from more traditional measurements
79 like sound pressure level (Staaterman et al. 2017). For example, a recent effort attempted to
80 apply the acoustic complexity index (ACI) to recordings of coral reefs (Bertucci et al. 2016), but
81 its utility was not obvious. Higher ACI values were found in recordings of marine protected

82 areas (MPAs) compared to non-MPAs. However, there were no significant differences between
83 protected and unprotected areas in any visual survey parameter, suggesting that differences in
84 ACI values between protected and non-protected reefs were not reflective of the species
85 assemblages observed in the study (Bertucci et al. 2016). Furthermore, previous work has shown
86 that these indices may be predominately influenced by snapping shrimp activity, which is a
87 major component of coral-reef and temperate soundscapes (Kaplan et al. 2015). At present, more
88 traditional bioacoustic metrics such as sound pressure level (SPL) and the variability in sound
89 level in specific frequency bands over time are likely to be more robust and easier to comprehend
90 than indices such as the ACI.

91 In addition to biological sounds, anthropogenic noise can modify reef soundscapes in
92 significant ways (e.g., Kaplan and Mooney 2015). The extent of human activity can and does
93 vary among reefs because of differing degrees of remoteness, protection (e.g., areas closed to
94 vessels), and heterogeneous utilization rates. Recent work suggests that noise from small vessels
95 may increase the predation risk for some reef fish (Simpson et al. 2016). Accordingly, these
96 human-mediated elements could also influence biological sound production and species
97 assemblages on coral reefs.

98 To parameterize the factors that might influence sound production on reefs across space,
99 time and ecological gradients such as live coral cover and fish density, long-term assessment of a
100 range of geographically and ecologically disparate reefs is needed. This study measured
101 soundscapes and examined visually observable species assemblages at seven Hawaiian reefs that
102 varied in benthic cover and fish species assemblages over an approximately 16-month period.
103 Here, we present results from visual and acoustic surveys of these reefs and describe a new
104 method to quantitatively assess the magnitude of sound production on coral reefs.

105

106 **Methods**

107 **Site selection**

108 Reefs were selected for study on the west side of Maui, Hawaii, in September 2014. The sites
109 were chosen to be similar in depth but different in terms of benthic cover, fish species richness
110 and abundance, structural complexity, geographic location, and degree of protection. These
111 parameters were assessed in an ad hoc manner during the site selection period and confirmed ex
112 post using visual surveys described below. Because of an instrument malfunction, one reef was
113 ultimately excluded from the study, leaving six reefs and one sandy control site (MM17) for data
114 analysis (Fig. 1a; Table 1). Of these, one (Ahihi) was completely closed to vessel traffic, two
115 were Marine Life Conservation Districts closed to some forms of fishing (Honolua and
116 Molokini), and one was a Fishery Management Area closed to the fishing of herbivores
117 (Kahekili).

118 **Visual surveys**

119 Visual surveys were carried out at each study reef in September 2014, February/March 2015,
120 October 2015, and January 2016. Data were collected by the same two divers for the duration of
121 the study to ensure consistency among surveys, with each specializing in either fish or benthic
122 surveys. Fish sizing estimates were calibrated underwater using artificial fish models and inter-
123 observer comparisons prior to data collection. Survey methods were modified from Kaplan et al.
124 (2015). Four benthic transects per reef were conducted using a 10-m sinking lead line that
125 followed the contours of the reef. Each transect started adjacent to the acoustic recorder moored
126 at that reef and fanned out in a radial pattern. At each 10-cm increment, benthic cover was
127 recorded as one of the following categories: live coral (identified to genus), macroalgae, turf

128 algae, sand, bare rock, dead coral, bleached coral, and other invertebrates. All benthic transects
129 were compiled for each survey using the following categories: live coral, bleached coral,
130 macroalgae, crustose coralline algae, turf algae, and “other” (e.g., bare rock, sand, dead coral,
131 other invertebrates).

132 To quantify structural complexity the straight-line distance of the lead line was measured
133 with a fiberglass tape, and rugosity was then calculated as the ratio of the length of the lead line
134 to the length of the straight-line distance.

135 Belt transect surveys for fish were carried out concurrently. These consisted of four
136 transects (30 m long by 2.5 m on either side of the transect). Start points adjacent to the acoustic
137 recorder were selected randomly. Each fish transect took approximately 10 min to complete. The
138 surveyor first swam rapidly along the transect line, recording larger mobile fishes transiting the
139 line, mid-water species, and any conspicuous, rare, or uncommon species. They then turned
140 around and returned along the transect line, slowly and carefully recording all other fishes with a
141 focus on cryptic species. Each observed fish was identified to species and categorized by size
142 (total length) in the following bins: A (0–10 cm), B (11–15 cm), C (16–20 cm), D (21–30 cm), E
143 (31–40 cm), and F (>40 cm). Fish survey data were combined across transects and summarized
144 by species and size classes. Species that have previously been identified as soniferous (Tricas
145 and Boyle 2014) were noted as such in the data set.

146 **Acoustic data**

147 Acoustic data were collected at each reef using ecological acoustic recorders (EARs; Lammers et
148 al. 2008) equipped with an SQ26-01 hydrophone (Sensor Technology Ltd., Collingwood, ON,
149 Canada) with a sensitivity of approximately -193.5 dBV re 1 μ Pa and configured with 47.5 dB of
150 gain. Recordings were collected at a sample rate of 50 kHz (25 kHz at Molokini) on a 10% duty

151 cycle (30 s/300 s). For all deployments, EARs were affixed to concrete blocks using hose clamps
152 and cable ties and placed in sand patches adjacent to or within a reef (Fig. 1b). Hydrophones
153 were approximately 6 inches above the bottom. All EARs, except at Molokini, were deployed in
154 September 2014, refurbished in February/March 2015 and July 2015, and recovered in January
155 2016. The Molokini EAR was involved in a separate study and was deployed and refurbished on
156 a different schedule (November 2013, June 2014, October 2014, February 2015, October 2015,
157 October 2016).

158 Analyses were carried out in MATLAB 9.1 (MathWorks, Natick, MA). Sound files were
159 corrected for hydrophone sensitivity and resampled to 44 kHz for improved computational
160 efficiency and to retain frequencies of interest (except for recordings from Molokini, which were
161 not resampled because of the lower sample rate). An initial review of the recordings indicated
162 that in some cases clipping was present as a result of high-amplitude shrimp snaps. Accordingly,
163 every 30 s sound file was split into 100 ms windows and every window that contained
164 normalized voltage readings of ± 0.99 , indicative of the presence of clipping, was automatically
165 excluded (Table 2). The entire file was discarded in cases where fewer than 150 windows (i.e.,
166 15 s) were retained. All remaining windows of each retained sound file were individually
167 analyzed as follows. Root-mean-square SPL (dB re 1 μ Pa) was calculated in two frequency
168 bands—low (50–1200 Hz) and high (1800–20500 Hz; 2000–12000 Hz for Molokini)—using
169 four-pole Butterworth bandpass filters. These frequency bands were chosen to correspond with
170 the published frequency ranges of fish calls and snapping shrimp pulses, respectively (Au and
171 Banks 1998; Tricas and Boyle 2014). The intermediate frequencies (1200–1800 Hz) were not
172 assessed given the paucity of biological signals of interest in this range and to provide a spectral
173 buffer between the frequency bands analyzed. To obtain an average SPL value for each sound

174 file, the mean SPL of the first 150 windows was then computed (on the linear scale in Pascals).
175 While a narrower bandwidth at high frequencies was used for Molokini, this choice did not affect
176 results because no explicit comparisons of sound levels were made among reefs.

177 To ensure that these analyses focused on sounds of biological origin, vessel and other
178 extrinsic anthropogenic noise was identified and excised. This was done individually for each
179 reef by visually identifying and aurally confirming such sounds in long-term spectral average
180 plots produced in Triton version 1.91 (Scripps Whale Acoustics Lab, San Diego, CA).

181 Humpback whales (*Megaptera novaengliae*), present during the winter months
182 (approximately December–May), represented an undesired biological sound source, in particular
183 when making among-reef comparisons of low-frequency sound, where humpback whale song
184 overlaps with and can mask lower amplitude fish calls. Thus, low-frequency sound data were not
185 considered between 1 December and 30 April except in visualizations of daily average levels.

186 Comparisons between diel and lunar periodicity were made by constructing periodograms
187 of the SPL time series in both frequency bands. Linear interpolation to fill in missing data was
188 necessary to ensure a constant sampling rate of one recording per 5 min or 288 samples d^{-1} . This
189 was done for all reefs; results from Kahekili, generally representative of all reefs, are presented
190 here.

191 Crepuscular periodicity was a distinct feature of these acoustic data. To quantify the
192 magnitude of those diel changes in sound level, the median sound level at each sampling time
193 (i.e., 288 times d^{-1}) was computed by month for the low- and high-frequency bands. This yielded
194 monthly median curves of sound level by time of day in each frequency band. These curves were
195 normalized to a zero minimum sound level to facilitate comparisons among reefs irrespective of
196 background noise levels. Subsequently, the total area under the curve at dawn and dusk was

197 computed in MATLAB using the *trapz* function to quantify the strength of the diel trend. Dawn
198 was defined as 1 h before to 15 min after sunrise and dusk was defined as 15 min before to 1 h
199 after sunset. All other times were not considered. The timing of sunrise and sunset at each reef
200 was identified for each day of the deployment in MATLAB using the reef coordinates and the
201 *suncycle* tool.

202 **Environmental parameters**

203 Temperature data loggers (HOBO pendant models UA-001-64 and UA-002-64, Onset Computer
204 Corporation, Bourne, MA), sampling every 10 min, were deployed alongside EARs at all reefs
205 for the duration of the study, except for Molokini, where temperature data were only collected
206 from July 2015 until January 2016. Wind speeds were gathered from a nearby NOAA National
207 Ocean Service weather buoy (20.895°N, 156.469°W). Lunar illumination data were obtained
208 from the US Naval Observatory website (<http://aa.usno.navy.mil/data/docs/MoonFraction.php>).

209 **Statistical analysis**

210 To investigate whether there were differences in fish assemblage characteristics within and
211 among reefs, Bray–Curtis dissimilarity values were computed and visualized using non-metric
212 multidimensional scaling (MDS) routines implemented in MATLAB. Correlations between wind
213 speed and SPL were assessed using hourly averages for each variable. Correlations between
214 temperature and SPL were assessed using daily averages for each variable.

215 Only acoustic data collected within 30 d of the visual survey dates were used in
216 comparisons with visual surveys to limit potential impact of temporal changes in the biological
217 community of the reef over longer timescales. Accordingly, high-frequency correlations were
218 made at each of the four visual survey periods whereas low-frequency correlations were only
219 made for visual surveys conducted in September 2014 and October 2015, to avoid including any

220 acoustic data that contained humpback whale song (Au et al. 2000). All correlations were tested
221 for significance using linear regression models.

222

223 **Results**

224 Benthic cover varied among and within the study reefs (Fig. 2a). Live coral cover was
225 generally highest at Molokini and Olowalu and lowest (i.e., zero) at MM17, a sandy non-reef
226 control site. Honolulu had the highest proportion of turf algae and Ahihi had the highest crustose
227 coralline algal cover. Within-reef cover was relatively consistent over time except during the
228 October 2015 survey, when an appreciable proportion of live coral was bleached at every reef,
229 except sand-dominated MM17. Reefs with highest live coral cover, such as Molokini and
230 Olowalu, also had the greatest proportion of bleaching. By January 2016, most of the bleaching
231 had diminished and recovery was observable at every bleached reef, although some, such as Red
232 Hill, suffered mortality.

233 Corals of the genus *Porites* dominated live coral cover at Ahihi, Kahekili, Olowalu, and
234 Red Hill, whereas corals of the genus *Montipora* were dominant at Molokini. At Honolulu, live
235 cover was more evenly split between *Porites* and *Montipora* corals. Other observed genera
236 included *Pocillopora*, *Pavona*, and *Fungia*.

237 Fish survey results were less consistent, with both abundance and observed number of
238 species following different trends at each reef (Fig. 2b–c). For example, both individual
239 abundance and species richness appeared to decrease over time at Ahihi while staying relatively
240 constant at Kahekili and increasing and then decreasing at Red Hill. Nevertheless, there were
241 some consistent patterns. MM17 always had the lowest species richness and individual

242 abundance and Kahekili and Red Hill consistently demonstrated the highest abundance, whereas
243 the observed number of species appeared to be fairly stable at Kahekili, Molokini, and Red Hill.

244 The proportion of soniferous fish individuals and species varied among surveys and reefs
245 but in general was approximately half of the total. For fish up to 15 cm total length (i.e., small
246 fish), the most commonly observed soniferous species was the goldring bristletooth
247 (*Ctenochaetus strigosus*, Acanthuridae). At MM17, the most common small soniferous species
248 was the Hawaiian dascyllus (*Dascyllus albisella*, Pomacentridae) and at Molokini it was the
249 blacklip butterflyfish (*Chaetodon kleinii*, Chaetodontidae). There was more variation among
250 reefs, and within reefs among surveys, in terms of the most abundant large (>15 cm) soniferous
251 fishes. Representative families included Acanthuridae, Balistidae, Chaetodontidae,
252 Holocentridae, Labridae, Monacanthidae, Mullidae, Pomacentridae, Serranidae, and Zanclidae.

253 Small soniferous fish abundance and soniferous fish species richness appeared to
254 correlate positively but with high variability with live (unbleached) coral cover but no such
255 relationship was obvious for large soniferous fish abundance (Fig. 3). There was some variability
256 among reefs in the composition of soniferous fish assemblages (Fig. 3c); MM17 was a clear
257 outlier whereas other reefs were more similar to each other. When all fishes were considered
258 there was very little variation in fish assemblages among reefs or sampling periods (Fig. 3d).

259 Low-frequency SPL followed a strongly seasonal pattern at all sites except Ahihi, with
260 daily average SPL elevated by over 20 dB in winter because of singing humpback whales (Fig.
261 4). High-frequency SPL did not demonstrate such strong seasonality, and levels were more stable
262 over the course of the year. High-frequency levels appeared elevated at Ahihi by 2–3 dB after
263 instrument redeployment in July 2015 compared to other deployment periods. No such elevation

264 was apparent in low-frequency levels, which suggests that this shift could be a result of a change
265 in instrument orientation during the redeployment process.

266 There were weak positive relationships between wind speed and low-frequency SPL (Fig.
267 S1); however, there did not appear to be any relationship between wind speed and high-
268 frequency SPL (Fig. S2) or between temperature and low-frequency SPL (Fig. 5a, Fig. S3) at any
269 reef. Correlations between temperature and high-frequency SPL (Fig. 5b, Fig. S4) were
270 significant at every reef except Olowalu, and positive at every reef except MM17, the sandy
271 control site, where the correlation was negative.

272 SPLs at Kahekili were generally representative of trends at other reefs and were
273 consequently used to compare diel and lunar periodicity. Median low-frequency SPL was
274 generally highest during new moon periods at all times of day, with levels decreasing from
275 quarter to full moon. Overall, levels were highest at dawn during the new moon and lowest at
276 dawn during the full moon, (Fig. 6a). Median levels did not vary substantially by time of day
277 during the quarter moon, with day and nighttime sound levels relatively consistent.

278 Conversely, levels were typically highest during the full moon at high frequencies (Fig.
279 6b). However, there appeared to be more variability overall, with new moon levels nearly as high
280 as full moon levels at dawn and with quarter moon levels highest at night.

281 Characteristic peaks in SPL at dawn and dusk were evident in both frequency bands (Fig.
282 7). After excluding times when humpback whales were present, the maximum SPL on a given
283 day at low frequencies was often located around the crepuscular periods and levels were
284 generally lower at night than during the day. At high frequencies, the greatest rate of change in
285 sound level was almost always found before dawn or after dusk, reflecting the strong link

286 between snapping shrimp activity and crepuscularity. Night levels were higher than daytime
287 levels at every reef.

288 The magnitude of the diel trend appeared to be much greater than that of the lunar trend.
289 Indeed, at Kahekili, the reef with the strongest lunar trend, diel periodicity was approximately
290 four times stronger than lunar periodicity at both low and high frequencies (Fig. 8). The excess
291 strength of the diel trend was even greater for other reefs.

292 The strength of the diel trend in sound production on a given reef—defined here as the
293 area under the curve at dusk and dawn in each frequency band by month—was related to the
294 biological attributes of that reef (Fig. 9). At low frequencies, soniferous fish abundance was
295 positively correlated with the strength of the diel trend in October 2015 (Fig. 9c), but
296 relationships to coral cover and rugosity were not significant (Fig. 9a-b). At high frequencies,
297 positive correlations between coral cover and the strength of the diel trend were evident for all
298 survey periods except January 2016 (Fig. 9e). However, there appeared to be no relationships
299 between the strength of the diel trend at high frequencies and rugosity (Fig. 9d) or soniferous fish
300 abundance (Fig. 9f).

301

302 **Discussion**

303 The goal of this study was to better understand the drivers of biological sound production
304 on coral reefs and the extent to which acoustic records reflect fundamental ecological parameters
305 such as coral cover and reef fish biodiversity. Results from integrating the magnitude of the
306 crepuscular increase in biological sound production indicated that low-frequency sound levels,
307 driven by fish calling activity, were related to fish abundance. High-frequency levels, indicative
308 of snapping shrimp sounds, were related to coral cover. These data underscore the significance of

309 diel periodicity and further support the need to consider time of day when making recordings of
310 coral-reef soundscapes.

311 This study presents a new method of characterizing coral-reef soundscapes, using both
312 the patterns of biological activity (diel trends) and acoustic parameters directly related to the
313 frequencies of interest (sound pressure in the fish and snapping shrimp bands). In previous work,
314 the magnitude of the diel trend was computed by taking the difference between the dawn or dusk
315 peak in sound level and a low point at midnight (Kaplan et al. 2015). While that crude measure
316 also suggested links between biota and the soundscape, the approach was limited because of a
317 relatively low sample rate. Furthermore, by sampling only a maximum and a minimum for each
318 measurement, these results may have been more susceptible to influence by outliers. In the
319 present study, observations were made for 16 months on a 10% duty cycle that provided
320 recordings every 5 min. This long-term and fine-scale assessment of the magnitude of diel
321 periodicity allowed for the area under the curve to be integrated, offering a more robust measure
322 of crepuscular ecological trends.

323 **Comparisons to physical parameters**

324 Rugosity did not appear to relate to acoustic data in either frequency band. This is perhaps a
325 surprising result, given that other work has identified links between rugosity and fish density
326 (e.g., McCormick 1994), and it may have been anticipated that greater rugosity values would be
327 suggestive of more habitat for snapping shrimp and even fishes. While there was no linear
328 correlation, the strength of the low-frequency diel trend did peak at several reefs of mid-level
329 rugosity. These reefs also tended to have higher fish abundance. While speculative, this may
330 indicate that reefs whose rugosity is driven largely by coral cover and not rock formations (i.e.,

331 reefs with intermediate rugosity) may be associated with higher fish abundance and greater diel
332 trend strengths.

333 Wind speed also did not appear to relate to acoustic data; however, such relationships
334 have been identified in other studies (e.g., Staaterman et al. 2014). This divergence could be
335 because wind speed data were obtained from a buoy in Kahului Harbor, near but not directly
336 adjacent to any of the recording sites. Alternatively, these reefs, many of which were close to
337 shore, may have been somewhat protected from the wind, which would suggest that soundscape
338 parameters were influenced by other factors.

339 Temperature did correlate significantly and positively with the high-frequency sound
340 levels of the snapping shrimp band, suggesting a relationship between snapping activity and local
341 temperature. The magnitude of this relationship varied among reefs, indicating that reef-specific
342 habitats may influence this relationship. This correlation between shrimp behavior and
343 temperature is consistent with other coral and oyster reef studies (e.g., Kaplan et al. 2015;
344 Bohnenstiehl et al. 2016); however, the causal link between temperature and snapping shrimp
345 activity has yet to be fully elucidated. Further work should investigate the mechanistic or
346 physiological drivers of this relationship. As seas warm, sound production rates may increase in
347 this high-frequency band. The negative correlation noted at MM17 could be a result of early
348 arrival of humpback whale song in the fall months (i.e., before the December cutoff after which
349 low-frequency recordings were not considered).

350 **Comparisons of visual and acoustic data**

351 Reefs were selected to cover the broadest possible gradient in benthic cover and fish density.
352 While reefs did vary appreciably in benthic cover, fish species assemblages proved to be more
353 similar among reefs than was originally desired (Fig. 3c–d) Furthermore, visually observed reef

354 fish species assemblages varied within reefs among survey periods, despite relatively frequent
355 observations (every 4–5 months). These changes may reflect community dynamics but might
356 also be a limitation of this method. Visual surveys are only snapshots of the fish community at a
357 particular point in time. These communities may vary by time of day, season, settlement, or in
358 stochastic ways not captured by the surveys (e.g., Sale et al. 1984; Galzin 1987; Syms and Jones
359 2000). More frequent observations would provide a more comprehensive estimation of the
360 community variability. Nevertheless, if timed correctly, visual surveys can reveal rare and
361 potentially important events such as coral bleaching or pulses of abnormally high fish
362 abundance, such as that at MM17 in September 2014, when abundance of pennant butterflyfish
363 (*Heniochus diphreutes*) was uncharacteristically high. However, it is not yet clear whether
364 acoustic records reveal such short-term changes. While acoustic data clearly identify temporal
365 cycles on diel, lunar, and seasonal scales, additional replications would be needed to determine
366 whether soundscape data have the resolution needed to identify transient ecological phenomena
367 such as bleaching events.

368 The changes over time reflected in these visual and acoustic data underscore how short-
369 term observations (in both visual and acoustic data sets) may not generally be representative of
370 reef dynamics. Because there was no clear indication of how fast community changes took place,
371 care was taken to relate visual survey data to acoustic data only in months where the two datasets
372 overlapped.

373 Diel and lunar periodicity in SPL, which has been extensively described elsewhere
374 (Staaterman et al. 2014; Kaplan et al. 2015), was also evident here in both frequency bands at all
375 reefs. The exception was MM17, the sandy control site, where only limited and low-amplitude
376 variability was evident. Diel periodicity was notable, appeared to be much greater in magnitude

377 than lunar periodicity (Fig. 8), and may reflect the diversity of fish acoustic behaviors on these
378 reefs.

379 Sound levels in the low-frequency band were highest during the new moon periods and
380 lowest during the full moon. Larval fish settlement generally occurs during the new moon
381 (D'Alessandro et al. 2007) and is often lowest during the full moon, supporting the hypothesis
382 that sound may play a role as a settlement cue (e.g., Simpson et al. 2005). Less is known about
383 snapping shrimp behavior, which remains an area ripe for further investigation.

384 Notably, the strength of the diel trend provides a new means to assess coral-reef
385 soundscapes and the activity of the local biological community. The low-frequency fish-band
386 diel trend values tended to increase with soniferous fish abundance (Fig. 9), although these
387 correlations were variable and not always significant. This may be because an asymptote of
388 soniferous fish abundance was reached on these reefs. However, this variability is reflective of
389 reef environments which, as noted earlier, are not rigidly stable communities but areas in flux
390 (Sale et al. 1984; Meyer and Schultz 1985; Shulman 1985; Galzin 1987; Syms and Jones 2000).
391 High-frequency diel trend values increased with percentage coral cover, suggesting that snapping
392 shrimp activity may correlate with benthic cover.

393 In conclusion, the results presented here broadly characterize the soundscapes of these
394 study reefs. Overall, this study demonstrates that, despite the considerable variability in
395 biological sound production within and among reefs, the magnitude of the diel trend in sound
396 production was related at low frequencies to fish density and at high frequencies to coral cover.
397 Thus, while inverse prediction of species assemblages using the analysis techniques employed
398 here was not possible, acoustic recordings do provide a good indicator of community-level sound
399 production and how it changes over time.

400

401 **Acknowledgements**

402 Funding for this research was provided by the PADI Foundation, the WHOI Access To The Sea
403 initiative and Ocean Life Institute, and the National Science Foundation grant OCE-1536782.

404 We thank Lee James and Meagan Jones for generously providing vessel support. This research
405 benefited from helpful analysis advice from David Mann and Andy Solow and comments from
406 three anonymous reviewers. Alessandro Bocconcelli, Steve Faluotico, Merrra Howe, Jim Partan,
407 Laela Sayigh, Russell Sparks, and Darla White provided engineering and technical assistance in
408 the field. This work was permitted by the Hawaii Department of Land and Natural Resources
409 (SAP 2015-29 and Special Use Permit 95132).

410

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482

483 **Figure captions**

484 **Fig. 1 a** Map depicting the location of the seven study sites in Maui, Hawaii. **b** An ecological
485 acoustic recorder deployed at Olowalu

486 **Fig. 2** Visual survey results by reef (ordered by low to high coral cover as recorded in the first
487 survey) and survey period (September 2014, February/March 2015, October 2015, January
488 2016). **a** Benthic cover, **b** abundance of soniferous and other fish, **c** fish species richness. Data on
489 sound-producing species were obtained from Tricas and Boyle (2014). CCA: crustose coralline
490 algae; TA: turf algae

491 **Fig. 3 a** Relationship between number of soniferous fish individuals (small: open circles; large:
492 filled circles) and live, unbleached coral cover. **b** Relationship between number of soniferous
493 fish species and live, unbleached coral cover. Non-metric multidimensional scaling (MDS) plots
494 of Bray–Curtis dissimilarity values for **c** soniferous and **d** all fishes. Results from all four visual
495 survey periods are included, and, for the MDS plots, are stratified by sampling period (circles:
496 September 2014; diamonds: February 2015; squares: October 2015; pentagons: January 2016)

497 **Fig. 4** Daily average sound pressure level (SPL) in **a** low-frequency and **b** high-frequency bands
498 for the duration of the study at each reef

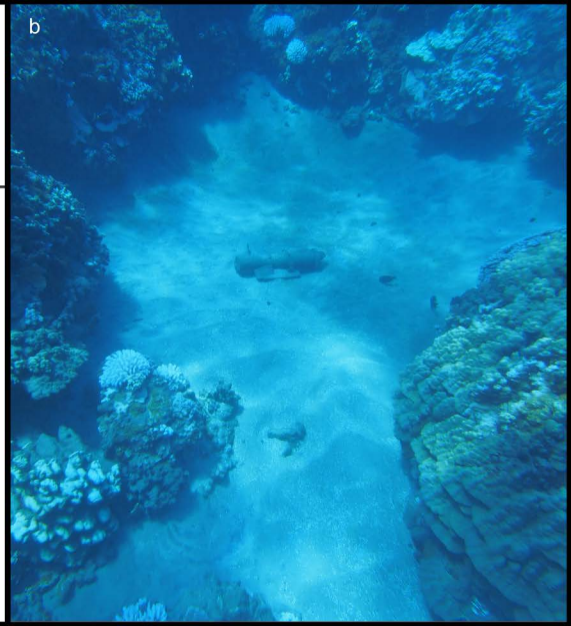
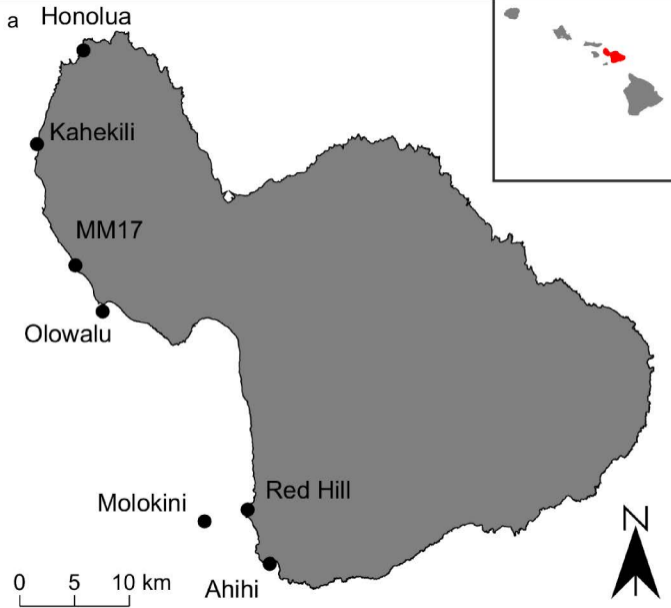
499 **Fig. 5** Linear regression lines of daily average water temperature and sound pressure level (SPL)
500 at **a** low and **b** high frequencies across the study reefs (only significant correlations are shown).
501 Equations of the lines, evaluations of fit, and significance levels are in electronic supplementary
502 material Figs. S3, S4.

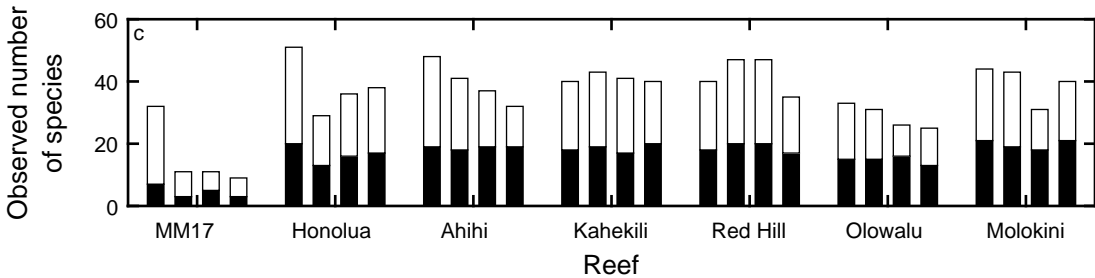
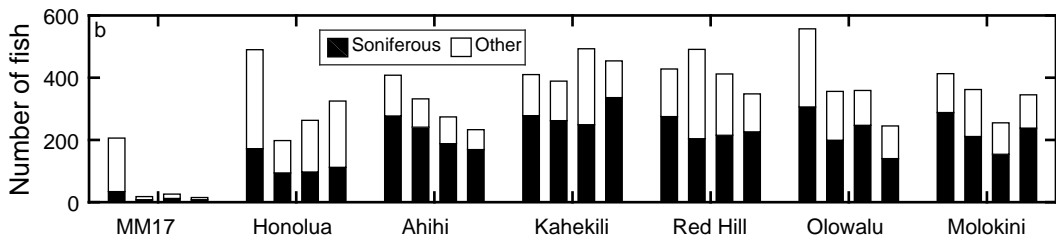
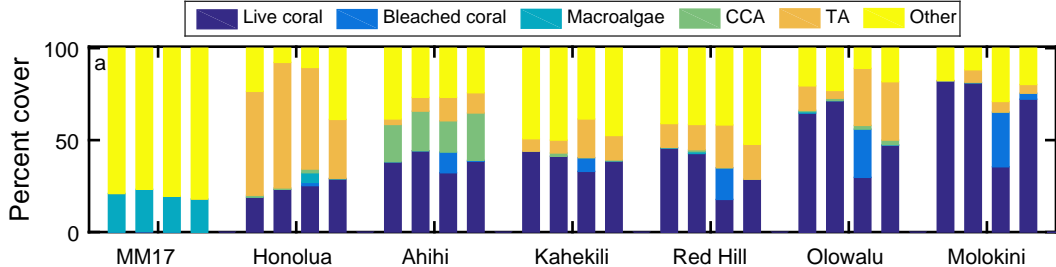
503 **Fig. 6** Boxplots representing **a** low-frequency and **b** high-frequency sound pressure level (SPL)
504 at Kahekili during the new moon (black) first/last quarter (purple), and full moon (green) at four
505 times of day

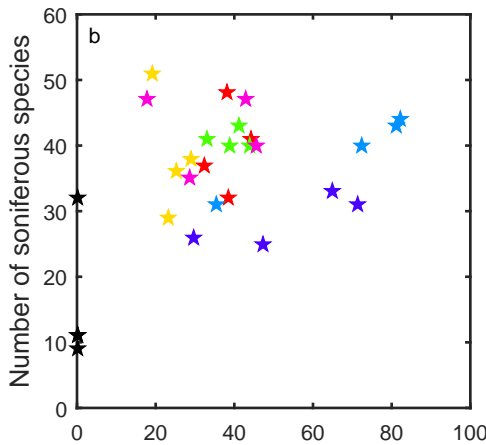
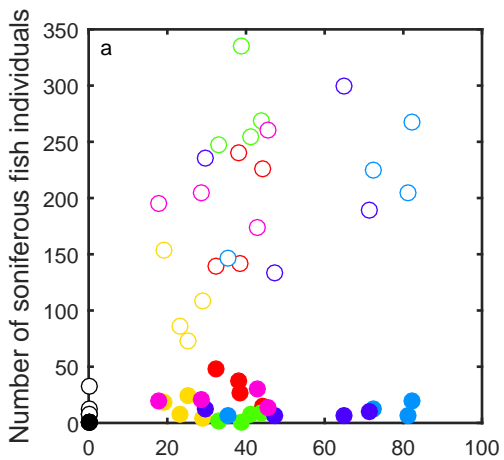
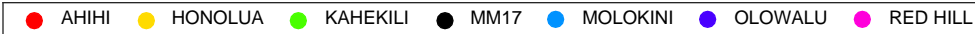
506 **Fig. 7** Median sound pressure level (SPL) (25–75 percentiles) at **a** low frequency and **b** high
507 frequency for each reef by hour of the day. Orange shading indicates dawn and blue shading
508 indicates dusk

509 **Fig. 8** Fourier transforms depicting the magnitude of periodicity in sound pressure level (SPL) at
510 **a** low and **b** high frequencies for Kahekili. Colors represent individual deployment periods

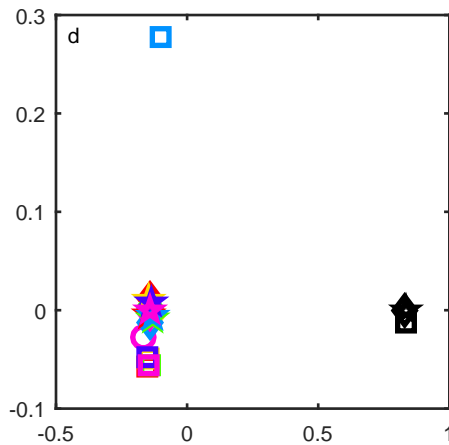
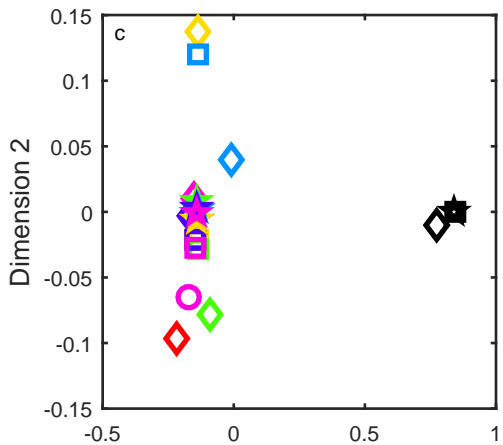
511 **Fig. 9** Strength of diel trend at **a, b, c** low frequency and **d, e, f** high frequency by month and reef
512 with associated rugosity (**a, d**), coral cover (bleached and unbleached) (**b, e**), and fish abundance
513 (**c, f**). Lines of best fit were plotted only when significant relationships were identified (grey
514 lines; see Table 3 for equations of the lines and evaluation of fit). Circles: September 2014;
515 diamonds: February 2015; squares: October 2015; pentagons: January 2016



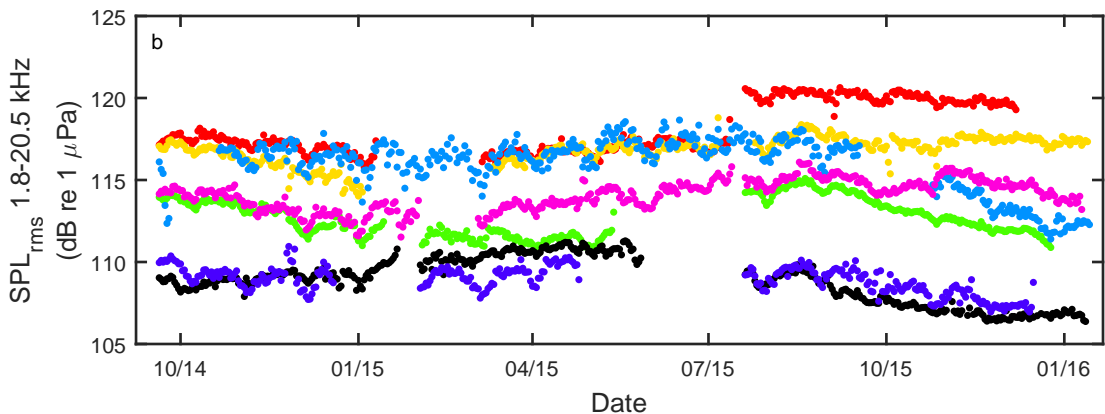
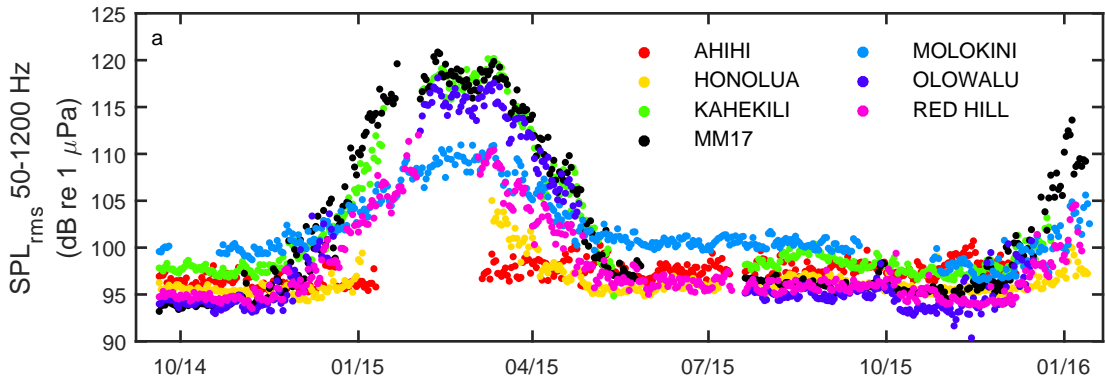


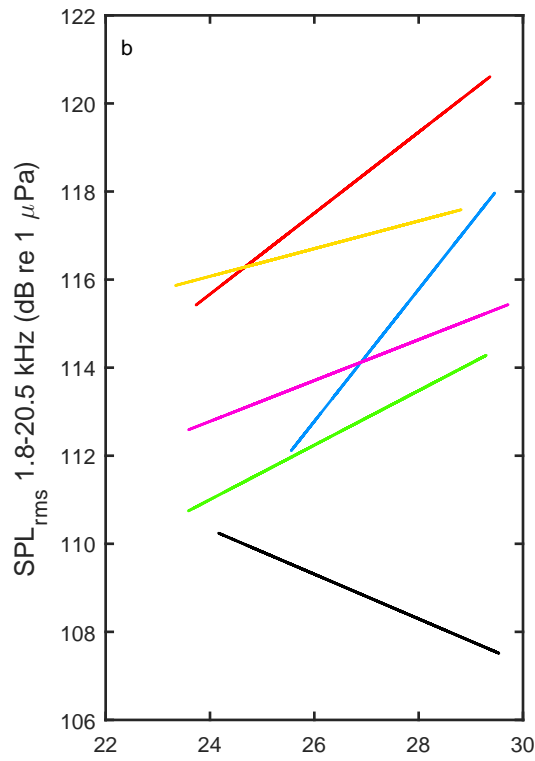
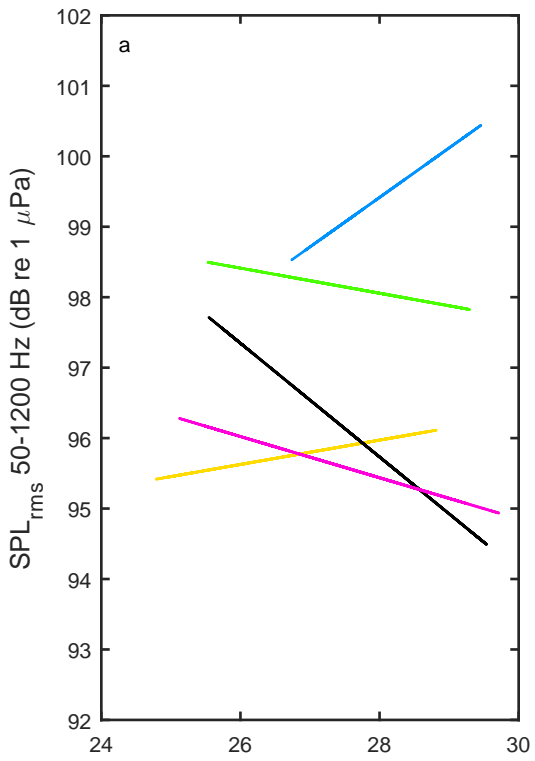
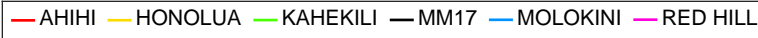


Live coral cover (%)



Dimension 1





Temperature (°C)

