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Bioacoustic measurements complement visual biodiversity surveys: preliminary evidence from four shallow marine habitats

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ABSTRACT: New tools, such as passive acoustic monitoring, can be helpful for measuring levels of biodiversity in habitats that are otherwise difficult to sample. Here, we tested the utility of acoustic measurements in shallow coastal waters by conducting short-term simultaneous bioacoustic and biodiversity surveys in 4 habitat types on the Caribbean coast of Panama: mangrove, reef, seagrass, and sand. Acoustic measurements in the 'low band' (<1000 Hz) were positively correlated with cryptic fish richness and abundance, but this band was dominated by the calls of a single species, the Bocon toadfish. Toadfish calls masked other fish sounds and confounded results from recently developed eco-acoustic indices such as acoustic entropy and acoustic complexity. The 'high band' (3000–10 000 Hz), largely indicative of snapping-shrimp sound production, did not differ significantly across habitat types and was not correlated to biodiversity measurements. Our study demonstrates that bioacoustic surveys can help scientists detect certain cryptic, soniferous species, justifying their use in tandem with traditional biodiversity surveys. Additional research is needed in the marine environment to validate the utility of newer eco-acoustic indices.

KEY WORDS: Bioacoustics · Biodiversity · Species richness · Marine habitats · Toadfish

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INTRODUCTION

In an era of accelerating environmental change, research methods to rapidly assess biodiversity and ecosystem function are particularly useful for examining changes across broad spatial and temporal scales (Lefcheck et al. 2016). One promising new technology for this purpose is passive acoustic monitoring (PAM). In any given habitat, the acoustic environment or 'soundscape' comprises sounds made by animals (biophony), sounds made by abiotic sources such as wind or rain (geophony), and sounds made by humans (anthrophony; Pijanowski et al. 2011). Collectively, these biological and abiotic phenomena produce unique sound signatures that can be measured through PAM and can reflect the status of the ecosystem.

PAM is particularly useful in dark, remote, and deep areas of the ocean, which are difficult to sample using other methods. Traditional methods to assess biodiversity in clear, shallow waters (e.g. visual fish counts by divers) are vulnerable to human error (the 'observer effect'), inclement weather conditions, and habitat-specific observer biases. Furthermore, visual surveys inherently overlook cryptic and/or nocturnal species and thus may underestimate biodiversity in certain areas (Willis 2001, Plaisance et al. 2011).

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Several recent studies examining relationships between biodiversity and bioacoustic conditions in the ocean have found mixed results. Kennedy et al. (2010) compared 2 min acoustic recordings from 40 reefs in Panama to corresponding biodiversity surveys. Fish density and diversity were correlated with sound levels in the lowest frequencies, whereas coral and benthic diversity were correlated with higher acoustic frequencies. The authors hypothesized that higher coral diversity increases structural complexity, thus providing more habitat for snapping shrimp (well-known soniferious species in the family Alpheidae) and explaining the higher levels of shrimp-produced sounds. In contrast, most other studies demonstrate links with the lowest frequencies (typically associated with fish sounds; Lobel et al. 2010, Tricas & Boyle 2014). For example, Kaplan et al. (2015) combined short- and long-term recordings from 3 reefs in Hawaii and found positive correlations between low-frequency sounds and coral cover and fish density. Bertucci et al. (2016) examined 8 coral reefs in French Polynesia, and found that the number of fish species, as well as the Shannon-Wiener biodiversity index, were positively correlated with acoustic complexity — a measure of variability in the soundscape — for the lowest acoustic frequencies, but relationships with the higher frequencies were weaker or non-significant. Finally, Freeman & Freeman (2016) found that at 23 reefs in Hawaii, intensity levels in the lowest frequencies were positively correlated with invertebrate density, abundance of certain fish species, habitat complexity, and quantity of crustose coralline algae. Taken together, these findings indicate that the lowest acoustic frequencies generally track better with species diversity and habitat quality than higher acoustic frequencies. However, the mixed results of these previous studies, and the fact that they were conducted within a single habitat type, means that the broader applicability of these new acoustic indices in marine systems remains unclear.

Here, we sought to broaden our understanding of the performance of bioacoustics surveys by quantifying both established and recently developed ecoacoustic indices across 4 distinct habitat types in the tropics to determine which acoustic measurements best reflect patterns in species diversity. Furthermore, we asked whether bioacoustic surveys provide a potential alternative to traditional, visual biodiversity surveys by conducting simultaneous short-term bioacoustic and visual biodiversity surveys in mangrove, seagrass, coral reef, and sand habitats.

MATERIALS AND METHODS

Study sites and overview

The study was conducted in the Bocas del Toro archipelago (9.33° N, 82.25° W; Fig. 1), on the Caribbean side of Panama, over a 1 wk period from January 26 to February 3, 2016. The many islands in this region are fringed by mangroves, seagrass, and reefs, and the bay spanning between them reaches depths of 50 m with a tidal range of 50 cm (Guzmán et al. 2005). We surveyed 3 sites (Almirante, San Cristobal, and STRI Point [near the Smithsonian Tropical Research Institute]; see Fig. 1), each of which featured 4 habitat types: mangroves, seagrass, coral reefs, and sand. These are locations of ongoing research conducted by the MarineGEO program (Smithsonian Institution). We sampled the 4 habitat types within a given site on the same day by conducting visual biodiversity surveys and simultaneously initiating the acoustic recordings. Weather conditions were consistent across the 8 d window of data collection, with average wind speeds of 1.75 m s^{-1} and a total of 6 mm of rainfall. All work was conducted under permit #SE/AP-2-16 through the Panamanian Ministerio de Ambiente.

Biodiversity data

SCUBA divers conducted visual fish and invertebrate surveys based on the Reef Life Survey method (RLS; Stuart-Smith 2014) at each site (replicated 2–6 times depending upon accessibility). First, each diver passed over the transect to count all free-swimming and schooling fish >2.5 cm in length; these 'mobile' fish were counted and assigned to binned size-classes along a 50 × 5 m belt transect. Next, cryptic, benthos-associated fish and mobile invertebrates were counted. All organisms were identified to the lowest taxonomic resolution possible. If an individual could not be identified on site, a photograph was taken for later identification.

Species richness was calculated as the total number of species counted in each category, and abundance considered the total number of individual organisms. For diversity measures, we used the Simpson index (Simpson 1949) and the effective number of species (ENS; Jost 2006). In some instances, we identified zero cryptic fish, so for this method we did not calculate additional diversity measures. For mobile fish only, abundance, size, and species were used to estimate biomass in g m^{-2} (Stuart-Smith 2014). Length-

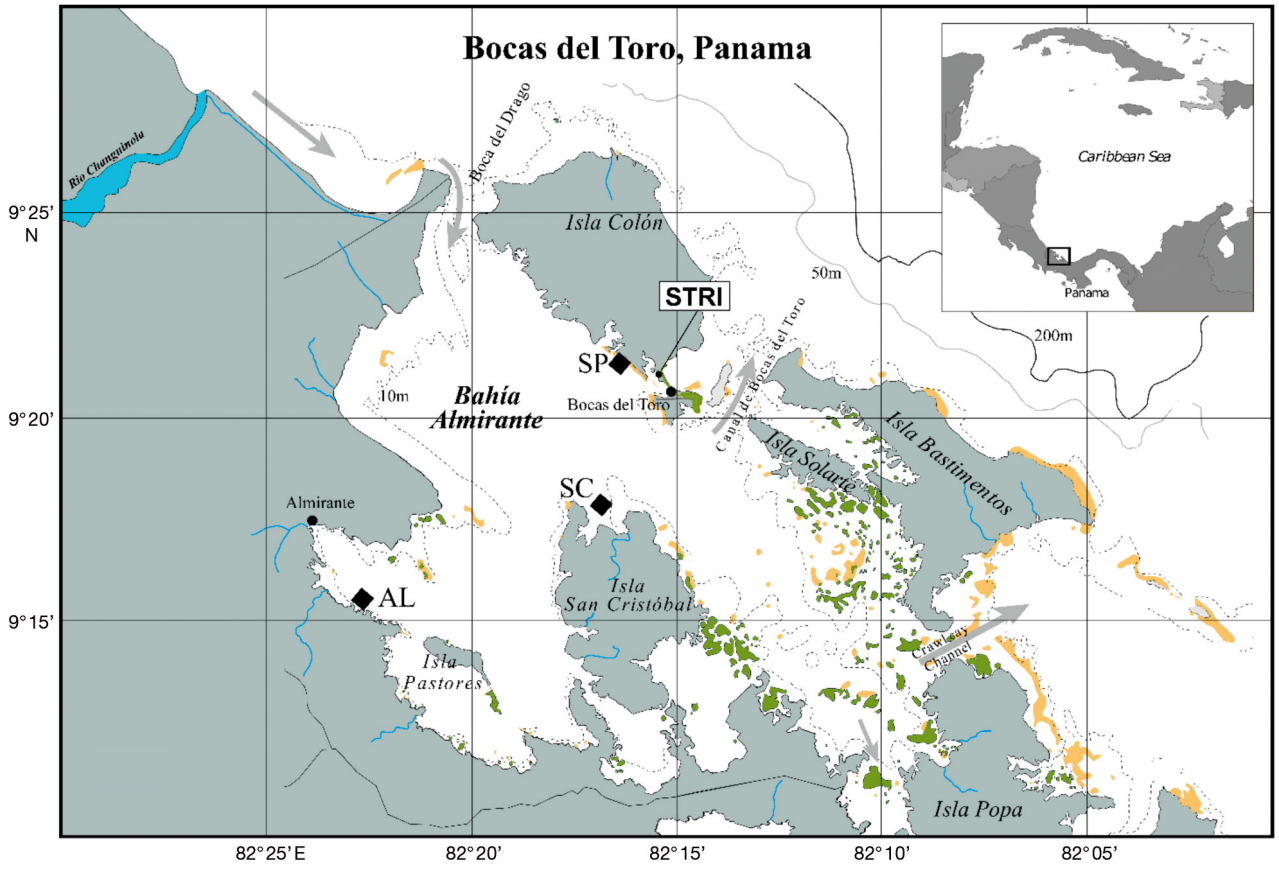

Fig. 1. Study sites (diamonds) in the Bocas del Toro Archipelago: AL – Almirante; SC – San Cristobal; SP – STRI Point (near STRI, the Smithsonian Tropical Research Institute). All 3 sites were just on the edge of the 10 m isobath. Yellow: corals; green: mangroves. Distances between sites — AL to SC: 5.5 km, AL to SP: 11 km, SC to SP: 6.3 km

weight and total length vs. fork length relationships extracted from FishBase (www.fishbase.org) were used to determine biomass values for fishes.

Environmental data

We used a simple habitat assessment score (HAS) to describe habitat complexity at all habitats (Gratwicke & Speight 2005). This score is a single number between 1 and 5 that combines values of rugosity, variety of growth forms, height of habitat architecture, refuge size, percent of live cover, and percent of hard substratum and can be applied to several habitat types. For each sampling location, we assessed HAS scores for 4 randomly chosen replicate plots (2.5 × 2.5 m) which were averaged for further analysis. An EXO2 multi-parameter sonde (YSI Inc.) recorded temperature, dissolved oxygen, salinity, and pH for the duration of the diver surveys.

Acoustic data

After the divers completed their visual surveys, we deployed 1 acoustic recorder in each of the 4 habitat types to record continuously for 24 h (DSG, Loggerhead Instruments; sample rate: 20 kS s^{-1}, hydrophone sensitivities: −150 dB re 1 V μPa^{-1}). Although temporal variation in acoustic conditions is expected (Staaterman et al. 2014), for this study, we focused on short-duration recordings in order to best match the biodiversity surveys, which were only conducted on a single day. The 4 acoustic recordings were simultaneous, with start/end times offset by ±60 min. At STRI Point, the reef recorder malfunctioned and did not begin recording until 3 h after it was deployed.

First, we regularly sub-sampled the continuous data to obtain a 1 min recording for every 10 min. We visually and aurally scanned these 1 min recordings, and when anthropogenic (e.g. boat, diver) noise was present, we chose a different 1 min period within the

10 min window to focus on biological sounds. Thus, for each habitat at each site, we had approximately 144 files of 1 min each.

Once raw acoustic recordings are obtained, several types of measurements can be extracted to describe the soundscape. Power spectral density (PSD) reflects the power of each frequency component of the signal (with 1 Hz resolution) and can be plotted over time to observe temporal patterns. We obtained PSD levels using PAMGuide software (Merchant et al. 2015; Hann window, 50% overlap, Fast Fourier Transform [FFT] length = 10 000 points, resulting in 1 Hz resolution). Acoustic spectra of many biological, abiotic, and anthropogenic sounds have been well described. In the marine environment, low frequencies (<1–2 kHz) comprise sounds of singing fishes and cetaceans, as well as waves and ships, whereas higher frequencies (>3 kHz) are dominated by snapping shrimp in coastal areas (Wenz 1962, Hildebrand 2009). After first reviewing our recordings visually and aurally, we decided that, based on the sound types present, 2 non-overlapping frequency bands would adequately partition the soundscape while not overlooking any sound-producers. Using custom-made Matlab scripts, we obtained the amplitude (in dB re 1 µPa) of 2 bands: the 'low band' (25–1000 Hz) was chosen to focus on the fish sounds (Kasumyan 2008, Lobel et al. 2010), and the 'high band' (3000–10 000 Hz) was chosen to focus on snapping-shrimp 'snaps'.

Traditionally, investigators have measured the amplitude of certain frequency bands, as described in the previous paragraph. More recently, motivated by the desire to link biodiversity with bioacoustics, several new eco-acoustic indices were introduced (Sueur et al. 2014). We focused on 2 of these indices: first, total acoustic entropy (H), which reflects the evenness of a signal's frequency and amplitude components over time (Sueur et al. 2008). Sounds with little amplitude or frequency modulation will have entropy values closer to 0, while variable sounds like random noise have values closer to 1. Second, the acoustic complexity index (ACI) calculates the variation in amplitude between adjacent time periods in distinct frequency bands, and then sums this variation across all bands (Pieretti et al. 2011). ACI generally reflects how temporally variable the soundscape is; larger values indicate that there are many individuals at different distances from the recorder, or could reflect many species with different call types and/or call rates. These indices were recently introduced and tested in forest ecosystems (Sueur et al. 2014), but their utility in marine soundscapes is not well understood. To obtain H and ACI for each band, we filtered the raw acoustic data into the low and high bands using a 5th-order Butterworth filter, then processed them using the SoundEcology package in R (ACI time window = 10, FFT size = 400; H window length = 1024; Villanueva-Rivera & Pijanowski 2016).

Since acoustic conditions change over time (Staaterman et al. 2014), we averaged each acoustic measurement for dawn (05:30–07:30 h), day (07:30–18:30 h), dusk (18:30–21:30 h), and night (21:30–05:30 h). Therefore, for the low and high band, we had 3 measurements for each time of day: band level (given as LBL or HBL for low and high band level, respectively), ACI, and H.

Data analysis

First, we explored how the biodiversity data, environmental data, and acoustic data differed across habitat types. Data were pooled for the 3 sites and tested for assumptions of normality (Shapiro-Wilk test) and equal variances (Levene's test). For variables that met assumptions, we conducted 1-way ANOVAs with habitat type as the independent variable; for variables that did not meet assumptions, we instead conducted Kruskal-Wallis tests. We performed multiple comparisons by contrasting means using Tukey's HSD test with a Bonferroni correction. The same procedure was followed using site as an independent variable, to determine whether there were any inherent site biases in the data.

Next, we aimed to quantify the correlations between acoustic data, biodiversity data, and environmental data. We conducted Spearman's rank tests for all of the variables in the acoustic low band against each of the biodiversity variables and the 2 environmental variables that differed significantly across habitats (water depth, HAS score), as these 2 factors can also influence acoustic conditions (Wenz 1962). For the high band, Spearman's rank tests excluded fish diversity measurements, since fishes generally do not produce sounds in this frequency range (Kasumyan 2008, Lobel et al. 2010).

RESULTS AND DISCUSSION

Biodiversity and environmental data

Species richness for mobile fish, cryptic fish, and invertebrates differed significantly across habitat types and was highest on reefs (Table S1, Fig. S1 in

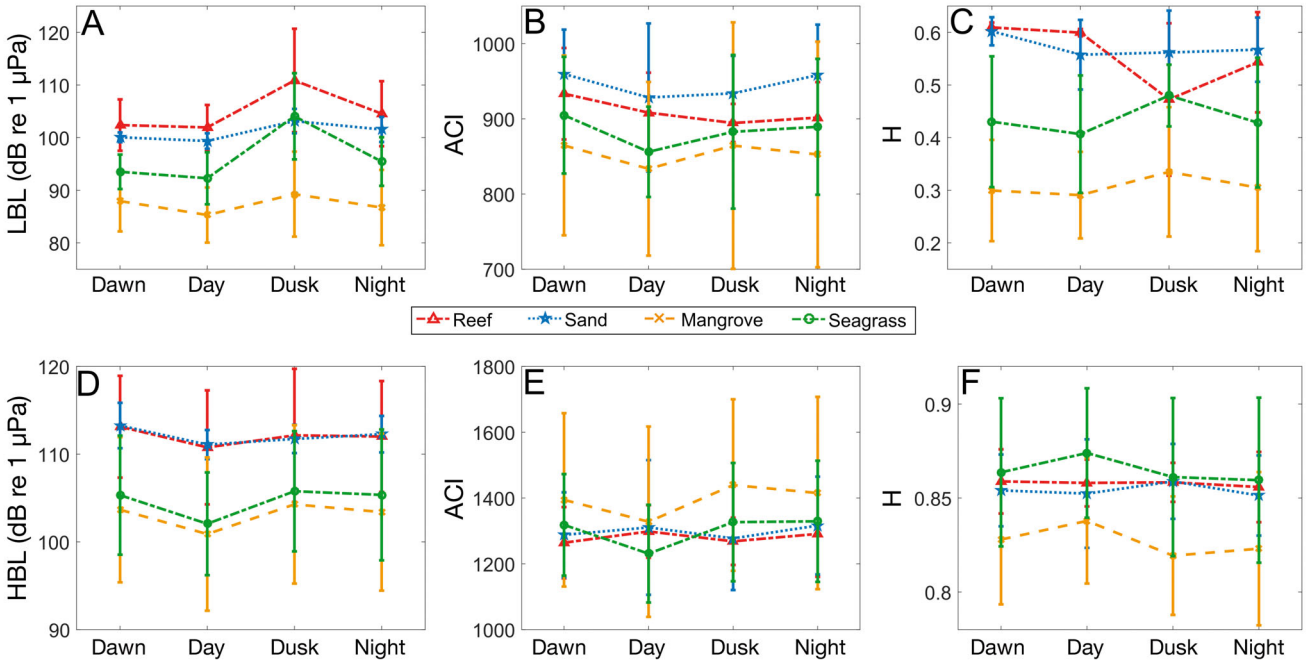

Fig. 2. Average values (with 95% CI) for each acoustic parameter in (A–C) the low band (25–1000 Hz, top row), (D–F) the high band (3–10 kHz, bottom row); note different vertical axes. A,D: low and high band level (LBL and HBL, respectively); B,E: acoustic complexity index (ACI; dimensionless); C,F: acoustic entropy (H; dimensionless). In the low band, LBL and H — but not ACI — were significantly different between habitat types (Table S2 in the Supplement). In the high band, while HBL tended to be highest on reefs and lowest in mangroves, none of these differences were statistically significant (Table S3 in the Supplement)

the Supplement at www.int-res.com/articles/suppl/m575p207_supp.pdf). The Simpson index and ENS showed no significant habitat differences for mobile and cryptic fish. For invertebrates, they were lowest on reefs (Fig. S1). Although not significant, invertebrate abundance was highest on reefs ($p = 0.06$, Table S4), due to a single urchin species, *Echinometra viridis*. This low evenness resulted in lower invertebrate diversity measurements on reefs compared to other habitats.

Only 2 environmental conditions differed significantly by habitat type (Table S1, Fig. S1). First, HAS scores were higher on reefs and mangroves compared to seagrass and sand, and seagrass had a higher score than sand. Second, mangroves were significantly shallower than reefs in terms of water depth.

Acoustic data

Low band

In the low band, acoustic conditions differed significantly between habitat types. At dawn and during the day, LBL on reefs and sand were significantly higher than in mangroves (Fig. 2A). At dusk and at night, LBL on reefs was significantly higher than in mangroves, but none of the other habitats were significantly different from one another (Fig. 2A). H — but not ACI — differed based on habitat type for dawn, day, and night; H was significantly higher on reefs and sand than in mangroves (Fig. 2B,C).

PSD plots of the low band (Fig. 3A) revealed that reefs had the highest amplitudes, with a clear peak occurring at dusk. While other fish sounds were audible at times (Fig. 3B,C), one particular call — produced by the Bocon toadfish *Amphichthys cryptocentrus* (our Fig. 3D; Hoffman & Robertson 1983) — dominated this band and was audible in reef, sand, and seagrass habitats. Considering how loud and frequent these calls were, we suspected that they masked our ability to detect other fish calls. Therefore, we further examined the low band by obtaining a ratio of the amplitude for frequencies <500 Hz (containing most of the energy from toadfish calls) to the amplitude for frequencies >500 Hz (containing other fish calls, with some bleed-over from nearby toadfish calls; Fig. 3E). We found that on reefs, the amplitude of toadfish calls exceeded the amplitude of other fish calls ~80% of the time, often masking other fish and potentially distorting some of our results (see below, this subsection). Furthermore, the overlapping nature of the

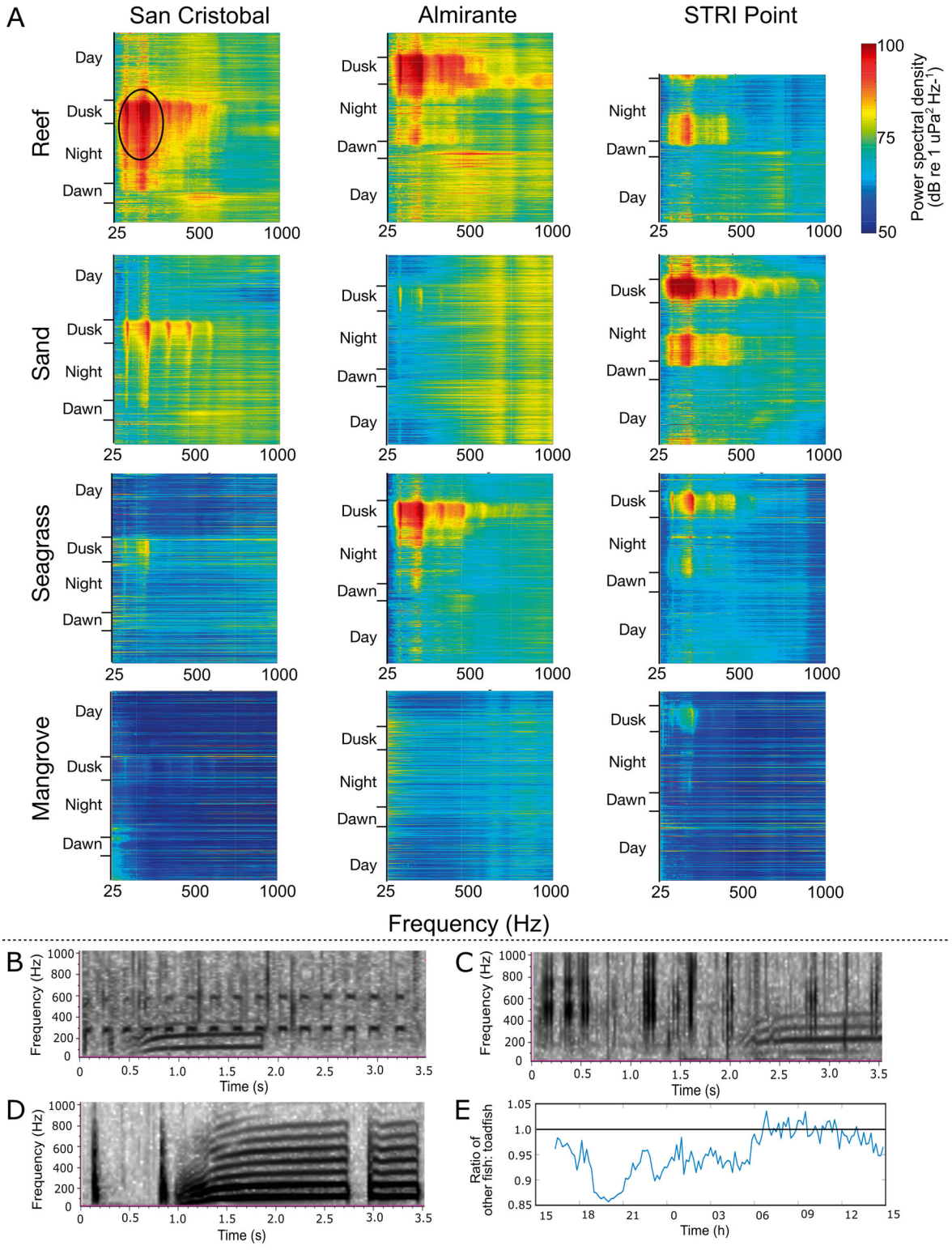

Fig. 3. (A) Power spectral density plots for the low band (25–1000 Hz) at each site. Color axes represent amplitude in each 1 Hz frequency band (vertical axes are slightly offset due to different start times of recordings). Reefs had the highest amplitudes and most temporal variability, and mangroves had the least. A clear toadfish chorus (circled in upper left plot) started at dusk on reefs as well as STRI Point sand and Almirante seagrass sites. (B) Example of another fish sound overlapping with a distant toadfish call (0.5–1.6 s). (C) Example of other fish sounds (likely a damselfish), and a distant toadfish call starting at 2.1 s. (D) Spectrogram from a nearby, very loud toadfish call. (E) Ratio of 'other fish calls' (>500 Hz) vs. toadfish calls (with dominant energy <500 Hz) from Almirante reef. For most of the day, toadfish calls dominated the low band (ratio <1). Only for a short period — at dawn — did the other fish calls become louder than the toadfish (ratio >1)

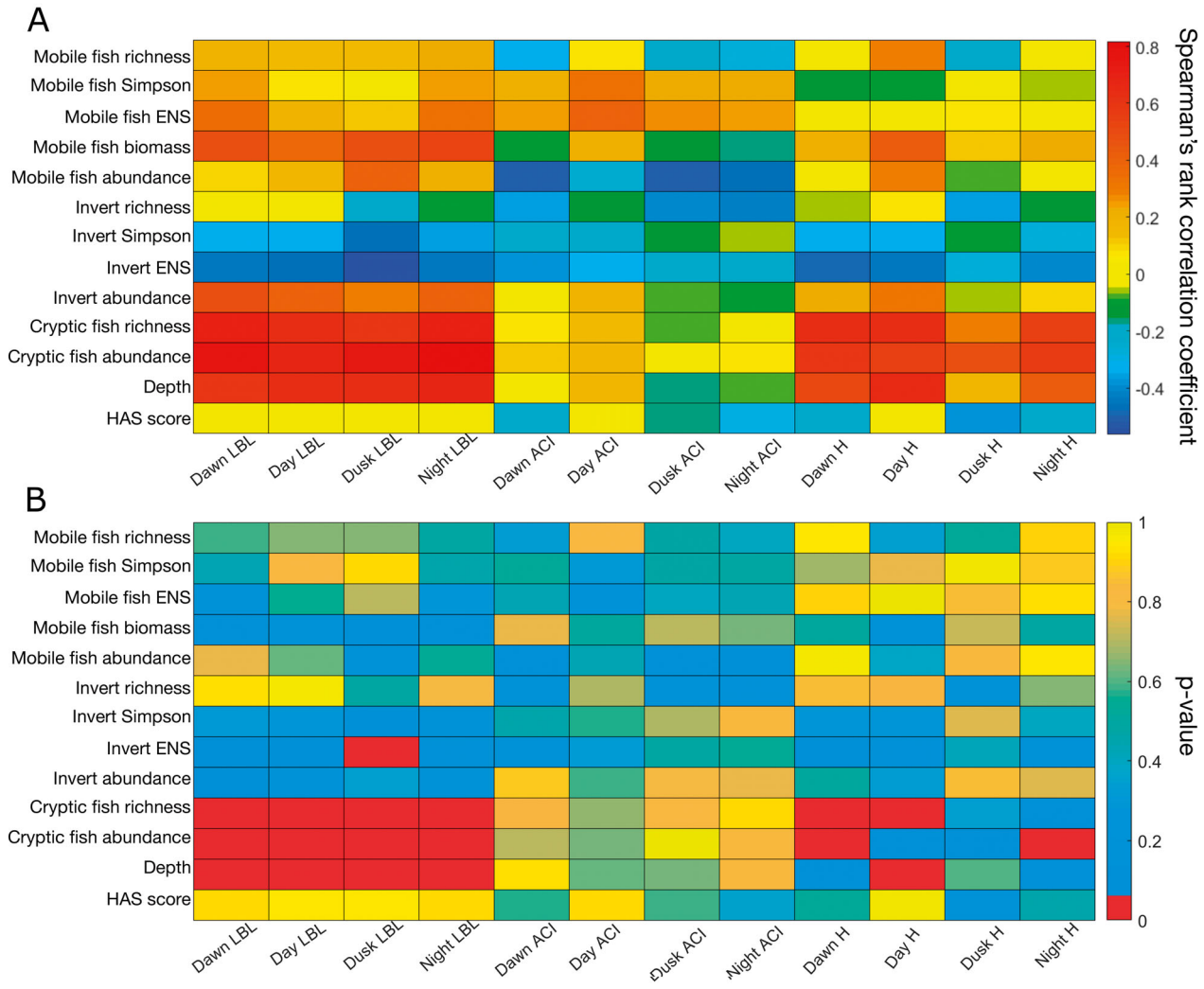

Fig. 4. (A) Spearman's rank coefficients (cool colors: negative correlation, warm colors: positive) and (B) corresponding p-values (red indicates $p < 0.05$) for diversity variables, depth, and habitat assessment score (HAS) against the low acoustic band. We included fish and invertebrate ('Invert') measurements because fishes (Lobel et al. 2010) and some invertebrates (e.g. urchins, lobsters; Radford et al. 2008, Staaterman 2016) produce sounds in the lowest frequencies. The high abundance of a single urchin species drove down the effective number of species (ENS) and Simpson index on reefs, which were also the loudest habitats (Figs. 2 & 3), explaining the negative correlation between these indices and low band level (LBL). On the other hand, there was a positive correlation between cryptic fish richness and abundance with LBL as well as acoustic entropy (H) at certain times of day. Some gobies produce low-frequency sounds (Myrberg & Stadler 2002), and many of the cryptic fishes counted by our diver team were gobies (*Coryphopterus* spp.). We did not count a single toadfish in our diver surveys, but acoustic surveys revealed their presence in several habitat types. If we had counted toadfish, we may have observed stronger relationships between bioacoustics and biodiversity. The positive relationship between water depth and LBL was likely due to the fact that our deepest sites — reefs — had the most habitat for toadfish (and likely the highest toadfish density), and the fact that shallow environments (e.g. mangroves) restrict the transmission of low-frequency sounds. ACI: acoustic complexity index

toadfish calls revealed some of the limitations of the newer eco-acoustic indices. ACI and H are calculated based on the evenness of a signal. When there are many distinct sound-types, or gaps between individual calls, a sound will be uneven, and these indices will be high. However, when many individuals of the same species call at once, their calls blend together, thus increasing the monotony of the signal and decreasing H and ACI (Fig. S2 in the Supplement). We found that during the peak of toadfish chorusing on reefs, H and ACI were lowest while LBL was highest. The nuances of these eco-acoustic indices suggest that, at least for animal choruses in the marine environment, simpler measurements like LBL may be more reliable indicators of abundance and/or diversity, as Kaplan et al. (2015) also suggested, or that these indices simply need further development and testing.

Since many mobile, reef-associated fishes like groupers, grunts, and damselfishes produce sounds (Kasumyan 2008, Lobel et al. 2010), we expected to see positive relationships between mobile fish diversity and the low band. While mobile fish biomass appeared positively correlated with LBL at dawn and at night, this relationship was not significant (Spearman's rank test, $p = 0.10$), and there was no relationship between acoustic measurements and mobile fish diversity. On the other hand, we observed significant positive relationships between cryptic fish richness and abundance with LBL and H (Fig. 4; Spearman's rank test, $p < 0.05$). Many of the cryptic fishes observed by our diver team were gobies (*Coryphopterus* spp.), and some gobies are known to produce low-frequency sounds (Myrberg & Stadler 2002). While we did not specifically identify goby sounds, it is possible that they did contribute to this frequency band. Interestingly, although the Bocon toadfish was the single most important cryptic fish from an acoustic perspective, we did not see a single toadfish on our diver surveys. If we had seen the toadfish, or at least counted potential burrows (i.e. coral outcrops), we may indeed have observed additional positive relationships between fish abundance/biomass and acoustic conditions. The toadfish is one of several soniferous species that are cryptic during the day and acoustically active at night (e.g. Holocentridae, Ophidiidae; Luczkovich et al. 2008, Mann 2012), so future work should consider acoustic methods as a means to detect additional species, perhaps in conjunction with other emerging methods for cryptic species detection (Goatley & Brandl 2017). This dichotomy of acoustic dominance and visual absence emphasizes the sensitivity of different methods for different components of marine biodiversity, and highlights the utility of acoustic surveys for recognizing animals that cannot be detected through visual censuses.

A single urchin species, *E. viridis*, increased abundance values and decreased the Simpson index and ENS values for invertebrates on reefs, which were also the loudest habitats (Figs. 2 & 3). This explains the negative relationship between invertebrate diversity and LBL (Fig. 4; Spearman's rank test, $p < 0.05$). Urchins are known to produce sounds while feeding (Radford et al. 2008), so it is likely that this sound contributed to the low acoustic band.

Finally, depth was positively correlated with LBL at all times, and with H during the day (Fig. 4; Spearman's rank test, $p < 0.05$). Our deepest habitats (reefs) had the most preferred toadfish habitat, which partially explains the positive relationship between water depth and LBL. Very shallow water and soft-bottom sediments also limit transmission of low-frequency sounds (Urick 1983), which may have affected our results from mangrove habitats (<1 m depth). This phenomenon also explains the lack of correlation between habitat complexity — which was high on both reefs and mangroves — and LBL, which was high only on reefs. Future work should consider that relationships between acoustic conditions and biodiversity in extremely shallow areas like mangroves may be confounded by these physical constraints.

High band

None of the acoustic parameters in the high band were significantly different across the 4 habitat types (Fig. 2D–F). Reef and sand habitats had the highest HBL, but this trend was not significant (Table S3 in the Supplement). At least one of our sand sites was littered with coral rubble, and one seagrass site had a few large coral outcrops, which provide habitat for snapping shrimp. This explains the lack of clear difference between habitat types for HBL. Future studies should make an effort to quantify these fine-scale habitat features. Spearman's rank tests showed that acoustic conditions in the high band were not correlated to invertebrate diversity or habitat complexity (Fig. S3 in the Supplement). The RLS survey method focuses on mobile invertebrates such as urchins, brittle stars, and sea cucumbers, but snapping-shrimp 'snaps' are the dominant sound-source at frequencies above 3 kHz (Hildebrand 2009). We did not count a single snapping shrimp (Alpheidae) in our diver surveys, because they hide in crevices inside coral and can only be observed through destructive sampling (i.e. breaking open the coral). Like the toadfish, the fact that these species are not counted in the RLS method, but can be measured acoustically, demonstrates the need for methods such as bioacoustics to complement visual surveys.

CONCLUSIONS

Our comparison of bioacoustic and visual surveys across habitats suggests that complementary methods are needed to comprehensively survey marine biodiversity, even in clear, shallow-water environments. Specifically, we suggest that, although our results are limited to short-duration surveys, bioacoustic recordings can augment traditional visual surveys by detecting cryptic, soniferous species that would otherwise go unnoticed. Indeed, our results

show that PAM can overcome some limitations of other methods (e.g. limited temporal replication, restricted to areas with sufficient visibility and safe diving depths), but also has its own limitations (e.g. physical propagation of sounds in different environments; many animal sounds are still unknown). Furthermore, new eco-acoustic indices require additional ground-truthing in marine environments before they can become reliable indicators of bioacoustic activity. Taken together, our 'snapshot' results suggest that acoustic recordings can complement other rapid survey methods, and should be part of the toolkit that researchers use to assess biodiversity and human impacts on marine systems. This study enhances our understanding of coastal marine soundscapes and urges others to continue exploring links between bioacoustics and biodiversity in marine systems.

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