

Celestial patterns in marine soundscapes

Erica Staaterman^{1,2,3,*}, Claire B. Paris^{1,2}, Harry A. DeFerrari¹, David A. Mann⁴,
Aaron N. Rice⁵, Evan K. D'Alessandro²

¹Applied Marine Physics, Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, FL 33149, USA
²Marine Biology & Fisheries, Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, FL 33149, USA

³Beneath the Waves, Syracuse, NY 13202, USA

⁴Loggerhead Instruments, Sarasota, FL 34238, USA

⁵Bioacoustics Research Program, Cornell Laboratory of Ornithology, Cornell University, Ithaca, NY 14850, USA

ABSTRACT: Soundscape ecology is the study of the acoustic characteristics of habitats, and aims to discern contributions from biological and non-biological sound sources. Acoustic communication and orientation are important for both marine and terrestrial organisms, which underscores the need to identify salient cues within soundscapes. Here, we investigated temporal patterns in coral reef soundscapes, which is necessary to further understand the role of acoustic signals during larval settlement. We used 14 mo simultaneous acoustic recordings from 2 reefs, located 5 km apart in the Florida Keys, USA to describe temporal variability in the acoustic environment on scales of hours to months. We also used weather data from a nearby NOAA buoy to examine the influence of environmental variables on soundscape characteristics. We found that high acoustic frequencies typically varied on daily cycles, while low frequencies were primarily driven by lunar cycles. Some of the daily and lunar cycles in the acoustic data were explained by environmental conditions, but much of the temporal variability was caused by biological sound sources. The complexity of the soundscape had strong lunar periodicity at one reef, while it had a strong diurnal period at the other reef. At both reefs, the highest sound levels (~130 dB re: 1 μ Pa) occurred during new moons of the wet season, when many larval organisms settle on the reefs. This study represents an important example of recently-developed soundscape ecology tools that can be applied to any ecosystem, and the patterns uncovered here provide valuable insights into natural acoustic phenomena that occur in these highly diverse, yet highly threatened ecosystems.

KEY WORDS: Soundscape ecology · Bioacoustics · Time series · Coral reefs · Larval fish · Fish acoustics

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INTRODUCTION

Acoustic habitats, or 'soundscapes,' contain information about environmental conditions, landscape features, and biological composition, and soundscape ecology is an emerging field of research in both terrestrial and marine science (Schafer 1977, Dumyahn & Pijanowski 2011, Pijanowski et al. 2011a,b, Bormpoudakis et al. 2013). The biota living within a given environment can glean critical information from the sounds of their habitat (Bregman et al. 1990). Typical components of a soundscape

include 'geophony,' the sounds caused by weather and seismological activity, 'biophony,' the sounds produced by living organisms, and 'anthrophony,' the sounds generated by human activity (Krause 2008, Pijanowski et al. 2011a). In shallow waters, the largest geophonic contributions are caused by wind and rain, which disturb the water's surface (Wenz 1962, Hildebrand 2009). As in terrestrial environments, in the ocean there are many biophonic contributions to the soundscape, such as sounds made by animals as they call for mates, defend their territories, or escape predators (Myrberg

& Fuiman 2002). Finally, through industrial activity and shipping traffic, anthrophony in the ocean has increased in the last few decades (Andrew et al. 2011) and can interfere with animal communication systems (Clark et al. 2009, Barber et al. 2010, Slabbekoorn et al. 2010). Long-term acoustic recordings are required in order to understand the relative contributions of these sound sources, and to gain insights about the whole ecosystem.

While the geophonic components of underwater soundscapes have been studied for the last half-century (Knudsen et al. 1948, Wenz 1962, Hildebrand 2009), an emphasis on biophony has been more recent (Slabbekoorn & Bouton 2008, Fay 2009, Pijanowski et al. 2011b, Miksis-Olds et al. 2012, McWilliam & Hawkins 2013). Classical bioacoustic research typically focuses on a single species in isolation, without considering the acoustic properties of the entire habitat (Krause 1987). For example, previous studies in marine bioacoustics have documented unique temporal patterns associated with sound production of damselfish (Mann & Lobel 1995), goliath grouper (Mann et al. 2009), red hind (Nelson et al. 2011), and yellowfin grouper (Schärer et al. 2012), but these sounds were not analyzed within the broader context of their acoustic environments. A holistic picture of the soundscape requires the examination of all sources of biophony, since particular sounds follow distinct patterns and occupy specific frequency ranges, according to the 'acoustic niche hypothesis' (Krause 1987). Many of the biological sound sources found in shallow-water, coastal environments remain unidentified (Mann 2012), but because biophony is a major contributor in these habitats (Tavolga et al. 1981, Urick 1983), their soundscapes present complex and exciting research subjects.

Coral reefs, like tropical rainforests, are characterized by high species diversity and thus are expected to have rich acoustic qualities (Rodriguez et al. 2014). Because sound waves experience relatively little attenuation in water compared to air, and sounds travel unidirectionally from their sources (Urick 1983), it has been suggested that reef soundscapes could serve as orientation cues for various types of marine larvae (Montgomery et al. 2006). Understanding the behavioral drivers of larval settlement is necessary for proper management, given the critical role of larval replenishment in marine population connectivity (Armsworth 2002). In the last decade, acoustic playback experiments have demonstrated that larvae from several taxa are capable of detecting acoustic signals and will move towards, or undergo settlement behaviors in response to sounds of their

preferred habitat (Tolimieri et al. 2004, Simpson et al. 2005, Vermeij et al. 2010, Radford et al. 2011, Stanley et al. 2012, Lillis et al. 2013). While it is likely that a suite of cues are utilized by marine larvae as they seek their benthic home (Paris et al. 2008, Arvedlund & Kavanagh 2009, Pineda et al. 2010, Huijbers et al. 2012, Staaterman & Paris 2014), soundscapes are emerging as important signals. It is even possible that larvae could discriminate between unique sound signatures associated with specific habitats (Radford et al. 2010, 2014, McWilliam & Hawkins 2013) and make settlement choices accordingly. Therefore, it is critical to characterize spatial and temporal patterns of these soundscapes in order to better understand the acoustic cues that are available to pelagic larvae.

Several studies have recorded coral reef soundscapes over short time scales (McCauley & Cato 2000, Lammers et al. 2008, Kennedy et al. 2010, Au et al. 2012, Staaterman et al. 2013, Radford et al. 2014), and others have attempted to link acoustic qualities of specific reefs with species composition (Kennedy et al. 2010, Staaterman et al. 2013). However, to our knowledge, there has never been a study examining long-term (across 1 yr) patterns at multiple coral reefs. Here, we analyze 14 mo recordings from 2 nearby coral reefs in the Florida Keys, USA, coupled with environmental data collected at a weather station situated between the 2 sites. The reefs were chosen because they are similar in depth and physical features, so we assume that the geophony of the 2 soundscapes are similar, but there is one important difference: the number of settlement-stage fish larvae that arrive on one reef is nearly an order of magnitude greater than on the other (Grorud-Colvert & Sponaugle 2009). This observed difference was not detected in biophysical modeling of larval dispersal in the Florida Keys, implying that the dissimilarities are not explained by oceanography, but perhaps by animal behavior (Sponaugle et al. 2012a). If the 2 sites possess different soundscape qualities, this may affect the orientation behavior of larval fish in the vicinity of each reef.

This study focused on 3 central questions: (1) How does the reef soundscape change over different timescales? (2) What are the geophonic and biophonic contributions to the soundscape? And (3) do the soundscapes of the 2 reefs differ from one another, and if so, how? We expected to see a strong link between environmental conditions and acoustic measurements, and anticipated that any remaining variability may be attributed to biological sound sources.

MATERIALS AND METHODS

Study sites

The 2 sites of the recordings were Sand Island Reef (hereafter 'Sand Island', 25.0106° N, 80.2205° W) and Pickles Reef (hereafter 'Pickles', 24.5919° N, 80.2488° W) in the upper Florida Keys. The reef framework is composed of *Acropora* spp. rubble, as well as *Montastraea*, *Porites*, *Siderastrea*, *Millepora*, *Gorgonia*, and *Palythoa* spp. (Ruzicka et al. 2009). Dominant fish families include Scaridae, Haemulidae, Acanthuridae, Labridae, Pomacentridae, Lutjanidae, and Pomacanthidae (Kellison et al. 2012). The reefs are situated on the western edge of the strong Florida Current, which frequently sheds mesoscale and sub-mesoscale eddies (Lee 1975). At Pickles, a recent study by Grorud-Colvert & Sponaugle (2009) found that the most common settlement-stage larvae collected were blennies (Chaenopsidae, Labrisomidae, Tripterygiidae) and gobies (Gobiidae), whereas at Sand Island it was mojarra (Gerreidae), grunts (Haemulidae), jawfish (Opisthognathidae), and blennies (Labrisomidae). Sand Island received significantly greater numbers of fish larvae than Pickles (i.e. the total number of fish collected in the 3 light-traps deployed at each site), and also had higher diversity of young recruits (i.e. fish that had settled within the lunar month). The highest density of recruits occurred in July during both years sampled (Grorud-Colvert & Sponaugle 2009). Recent surveys of benthic species composition and adult fish abundance found significant differences in the presence of bare substrate, crustose coralline algae, dictyota, fleshy macroalgae, and turf algae, and significantly different numbers of redband parrotfish *Sparisoma aurofrenatum* and sergeant major *Abudefduf saxtalis* at the 2 sites (S. Sponaugle & E. D'Alessandro unpubl. data; Table 1).

Acoustic data collection

One passive acoustic recorder, the DSG-Ocean (Loggerhead Instruments), was deployed at each site in December 2010. The DSG-Ocean is a calibrated autonomous recording unit containing an HTI-96 hydrophone (sensitivity: -169.68 and -169.74 dBV/ μ Pa, frequency range: 2 Hz to 30 kHz; High-tech) and a 16-bit computer board. Each DSG-Ocean was set to sample 12 s every 5 min at a rate of 20 kHz (which provides a range of analysis from 1 Hz to the Nyquist frequency, in this case 10 kHz). The instruments were set on mooring systems in a sand patch within

Table 1. Mean differences of fish abundance and substrate presence at Sand Island and Pickles Reefs, based on surveys conducted by SCUBA divers using ten 25 × 2 m transects between December 2010 and January 2011 (S. Sponaugle & E. D'Alessandro unpubl. data). The abundance of 92 species of fish and the presence of 22 substrate types at each 50 cm mark were recorded; *t*-tests were used to compare mean differences between the 2 sites. The table reports only the fish and substrate types that were significantly different (at $p < 0.05$) between the 2 reefs

Variable	Mean difference (Sand Island – Pickles)	Lower CI	Upper CI	p
Bare substrate	-5.10	-7.85	-2.34	<0.01
Crustose coralline algae	-5.50	-9.20	-1.89	<0.01
Dictyota	-10.20	-13.50	-6.94	<0.01
Other fleshy macroalgae	0.90	0.10	1.70	<0.05
Rubble	5.00	3.21	6.78	<0.01
Turf algae	6.90	0.51	13.30	<0.05
Redband parrotfish	-1.10	-1.95	-0.24	<0.05
Sergeant major	7.00	0.11	13.89	<0.05

the reef framework, in 7 m of water and 3.5 m from the nearest edge of reef (Fig. 1). Data were retrieved and batteries were changed every 3.5 mo, which caused a ~2 h interruption of the recordings. The total timespan of the recording lasted 412 d, from December 2010 to January 2012.

Acoustic data processing

Each 12 s acoustic recording was immediately subjected to 2 post-processing steps to obtain (1) the amplitude of the entire sampling bandwidth (1 Hz to 10 kHz) for each sample, as a root mean square (RMS) value, and (2) the distribution of the signal across frequencies, using a fast Fourier transform (FFT; Pierce 1988). A series of FFTs (size: 800 samples, resulting in 25 Hz frequency resolution) were performed and averaged for each 12 s clip. To avoid spectral distortion due to windowing effects, a weighted moving average (weights of $\frac{1}{4}$, $\frac{1}{2}$, $\frac{1}{4}$) was applied to all data after transformation into the frequency domain.

In order to identify patterns within an inherently complex system, it is common practice to partition the acoustic spectrum into different frequency bands which are dominated by anthrophony, biophony, and geophony. Wenz (1962) described 3 components of the underwater acoustic spectrum: the 'low-frequency' spectrum (<10 Hz) caused by turbulence and pressure fluctuations from surface waves, the 'non-wind-

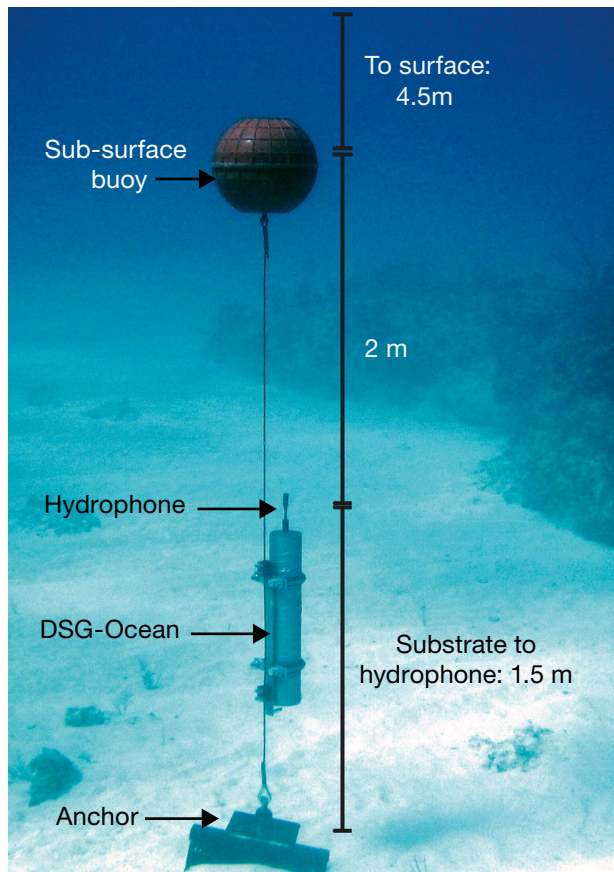


Fig. 1. Passive acoustic recorder used to monitor underwater sounds at Sand Island and Pickles Reefs from December 2010 to January 2012. Each DSG-Ocean recorder was set to record 12 s every 5 min at a rate of 20 kHz

dependent' spectrum (10 to 1000 Hz, with peaks between 20 and 100 Hz), caused by biological sounds and shipping noise, and the 'wind-dependent' spectrum (50 to 10000 Hz, with peaks between 100 and 1000 Hz), which is driven by the wind. While the Wenz-defined spectral components overlap, here we split the data into 2 non-overlapping frequency bands to focus on the dominant sound sources in each. Our 'low-frequency band' (25 to 2000 Hz) included the range in which most fish vocalizations occur (Lobel et al. 2010) and covers the known hearing range of most fishes (Tavolga et al. 1981). This band also included contributions from wind, but discarded the very low frequency sounds from surface pressure waves and turbulence (Wenz 1962). Our 'high-frequency band'

(2000 to 10000 Hz) spanned the range that is typically dominated by snapping shrimp *Alpheus* spp. and odontocete activity (Hildebrand 2009). Using the sensitivity of the hydrophone and known calibration of the recording system, we report the sound pressure level for the whole bandwidth (hereafter 'RMS level') and band level for the 2 bands (in dB re: 1 μ Pa).

To further examine the acoustic composition of the soundscape, we calculated the 'acoustic complexity index' (hereafter 'ACI') as described in (Pieretti et al. 2011). This index calculates the difference in amplitude of adjacent time samples in each frequency bin, then sums across all bins, to provide a measure of the changing composition of a soundscape. Higher ACI values are generated by greater variability in intensity (e.g. from multiple sound sources), whereas sounds generated by anthrophony or geophony, which tend to be more constant in intensity, produce low ACI values (Pieretti et al. 2011). We applied this index to the low-frequency band at each site (cluster size = 1 s, FFT bins = 160, to match the 25 Hz resolution from the original FFT as described above).

Environmental data collection

A nearby NOAA buoy (Molasses MLRF1, 25.012° N, 80.376° W) collected data for wind speed and direction, atmospheric pressure, air temperature, and water temperature (www.ndbc.noaa.gov/station_history.php?station=mlrf1); verified tidal data for Vaca Key, FL (24.427° N, 81.63° W, www.tidesandcurrents.noaa.gov) were also retrieved (Table 2). The wind was separated into 'offshore' and 'alongshore' component vectors by shifting the cardinal axis by +40° (as in

Table 2. Data sources, units, sampling rates, and number of samples (9899 samples for all data types after resampling, see 'Materials and methods'). Raw acoustic data and acoustic complexity applied to both Pickles and Sand Island. Wind data included total magnitude, direction, on- and offshore vector. ACI: acoustic complexity index

Data type	Unit	Sampling frequency	Original no. of samples
Raw acoustic data	μ Pa	12 s every 5 min (12 times h^{-1})	118788
Acoustic complexity	ACI	1 sample for every acoustic recording	118788
Wind	$m\ s^{-1}$	6 times h^{-1}	59394
Water and air temperature	$^{\circ}C$	Once h^{-1}	9899
Atmospheric pressure	hPa	Once h^{-1}	9899
Mean lowest water level	m	Once h^{-1}	9899

Sponaugle et al. 2005). Thus, the ‘alongshore’ vector was parallel to the Florida Keys Reef Tract, and the ‘offshore’ vector was perpendicular to the reefs, aligning with the prevailing wind direction (NOAA 1998).

Data analysis

Each time-series was analyzed in both the time domain and frequency domain. Because many biological sounds are known to vary on seasonal and lunar cycles (e.g. McCauley & Cato 2000, Radford et al. 2008), we divided the data into temporal categories using astronomical data from the US Naval Observatory (<http://www.usno.navy.mil/>). We defined these categories as ‘wet season’ (20 May to 17 Oct), ‘dry season’ (18 Oct to 19 May), ‘new moon’ (<14 % illuminated, spanning ~6 d), and ‘full moon’ (>86 % illuminated, spanning ~6 d). We calculated the mean and standard deviation of each series for these time periods (Table 3). For the acoustic data, we also calculated the hourly amplitude for each day in order to observe the time of day when peak sound levels and maximum acoustic complexity occurred.

When periodic phenomena are sought among noise, Fourier analysis and autocorrelation functions can be used to determine which periods best explain the variance in the series (Wenz 1961, Legendre & Legendre 1998). To do this, we first conducted a resampling routine on the acoustic and wind data to

match the sampling frequency of the environmental data (once per hour; Table 2), then we either detrended or centered the data, applied a filter, and calculated the autocorrelation and power spectral density. When 2 series’ power spectra possess peaks at similar frequencies (e.g. 1 cycle d⁻¹), this means that both series have a regular cycle at that frequency, but it doesn’t necessarily mean that the peak occurs at the same time of day or that there is any causal relationship. Therefore, we isolated the peaks from each series’ power spectra to compare the phase angles from shared peaks (Pierce 1988).

To disentangle the effect of wind on ocean sounds, we conducted an ANCOVA using offshore wind as a covariate to test for differences between the sites during particular seasons and moon phases. Because the wind was autocorrelated up to 9 d, but the new and full moon periods were separated by 14 d, we were able to maintain the assumption that the acoustic samples were independent for the ANCOVA. In other words, we assumed that any wind-dependent contribution to the soundscape would have the same autocorrelation lag as the wind itself, which allowed us to test for differences between moon phases and seasons while controlling for wind as a covariate. Continuous variables were checked for equal variances using a Levine’s test, and for normal distribution using Q-Q plots. After fitting the model, adjusted means for each site were generated and plotted.

Table 3. Mean and standard deviation of each time series for the defined time periods: wet season (20 May to 17 Oct), dry season (18 Oct to 19 May), and the new and full moons of each of these seasons. RMS: root mean square sound pressure level; ACI: acoustic complexity index

Data source	Wet season			Dry season		
	Overall	New moon	Full moon	Overall	New moon	Full moon
Pickles						
RMS	124.1 ± 4.6	126.1 ± 4.4	121.1 ± 3.8	124.4 ± 4.7	126.1 ± 4.1	123.9 ± 4.7
Low-frequency band (dB re 1 µPa)	112.5 ± 5.4	114.4 ± 4.9	109.3 ± 4.9	113.2 ± 5.6	115.1 ± 5.1	112.2 ± 5.2
High-frequency band (dB re 1 µPa)	116.4 ± 4.6	116.7 ± 1.1	115.9 ± 1.3	115.4 ± 1.4	115.8 ± 1.4	115.2 ± 1.5
ACI	726.0 ± 16.6	726.1 ± 17.3	727.7 ± 17.5	738.9 ± 18.8	739.5 ± 18.7	738.3 ± 18.4
Sand Island						
RMS	126.2 ± 5.9	129.3 ± 5.1	121.3 ± 4.7	123.3 ± 5.6	124.2 ± 5.1	123.1 ± 5.4
Low-frequency band (dB re 1 µPa)	114.8 ± 4.6	117.2 ± 4.1	111.2 ± 3.8	113.4 ± 4.5	114.3 ± 4.4	112.9 ± 4.0
High-frequency band (dB re 1 µPa)	115.8 ± 1.1	115.9 ± 1.1	115.5 ± 1.2	114.3 ± 1.7	114.7 ± 1.5	114.2 ± 1.7
ACI	702.0 ± 13.0	704.1 ± 13.9	696.1 ± 11.6	704.9 ± 14.3	709.9 ± 12.4	703.7 ± 13.3
Environment						
Total wind speed (m s ⁻¹)	4.8 ± 2.6	5.6 ± 2.4	3.2 ± 2.2	6.4 ± 2.8	6.4 ± 2.7	6.3 ± 2.6
Alongshore wind vector (m s ⁻¹)	2.9 ± 2.3	3.3 ± 2.2	2.1 ± 1.9	3.9 ± 2.7	3.4 ± 2.5	4.1 ± 2.8
Offshore wind vector (m s ⁻¹)	3.4 ± 2.2	4.1 ± 2.2	2.0 ± 1.7	4.4 ± 2.6	4.8 ± 2.6	4.0 ± 2.2
Air temperature (°C)	28.2 ± 1.2	28.1 ± 1.3	28.4 ± 1.2	22.6 ± 3.4	23.8 ± 1.9	22.7 ± 2.7
Water temperature (°C)	29.4 ± 1.1	29.3 ± 1.1	29.5 ± 1.1	24.3 ± 1.9	24.5 ± 1.7	24.5 ± 1.7
Atmospheric pressure (hPa)	1014.7 ± 2.22	1014.9 ± 2.3	1014.5 ± 2.3	1018.1 ± 3.7	1018.0 ± 3.0	1018.8 ± 4.1
Mean lowest water level (m)	0.27 ± 0.12	0.27 ± 0.15	0.29 ± 0.11	0.15 ± 0.14	0.14 ± 0.13	0.19 ± 0.15

Finally, we both listened to and visualized the raw acoustic data to better understand differences between the soundscapes at the 2 sites. A spectrogram can be read like a musical score; time is represented on the *x*-axis, acoustic frequencies on the *y*-axis, and the color bar scales with the amplitude of the sounds at particular frequencies. One month and short-term spectrograms from each site are included to exemplify the typical biophony at each site.

RESULTS

General trends in the time series

At both sites, RMS levels increased between March to June, and the highest amplitudes occurred between May and August (Fig. 2A). The dry season was characterized by sharp peaks that lasted several days, whereas large lunar differences were evident in the wet season. While both sites had similar RMS levels during full moons of the wet season (which were the quiet times), during new moons, the amplitude was greater at Sand Island than at Pickles (Fig. 2A, Table 3). There was a seasonal trend in the high frequency band (Fig. 2B), with highest amplitudes occurring during the wet season, and Pickles had greater amplitudes than Sand Island throughout most of the year. In the low frequency band (Fig. 2C, Table 3), both sites exhibited an increase in amplitude at the end of the dry season, and Sand Island had greater amplitudes, especially during new moons of the wet season. The highest acoustic complexity occurred during the end of the dry season, and Pickles had higher complexity than Sand Island throughout the whole year (Fig. 2D, Table 3).

Clear dawn and dusk peaks were evident in the high band at both sites (Fig. 3A,B), which coincided with seasonal changes in daylight. In the low band, amplitudes increased during new moons of the wet season (Fig. 3C,D), which can be seen as horizontal yellow lines spanning the whole day. Acoustic complexity for the low band was highest during nights between January and July, and lowest during the early mornings between June and November (Fig. 3E,F). At both sites, the lowest

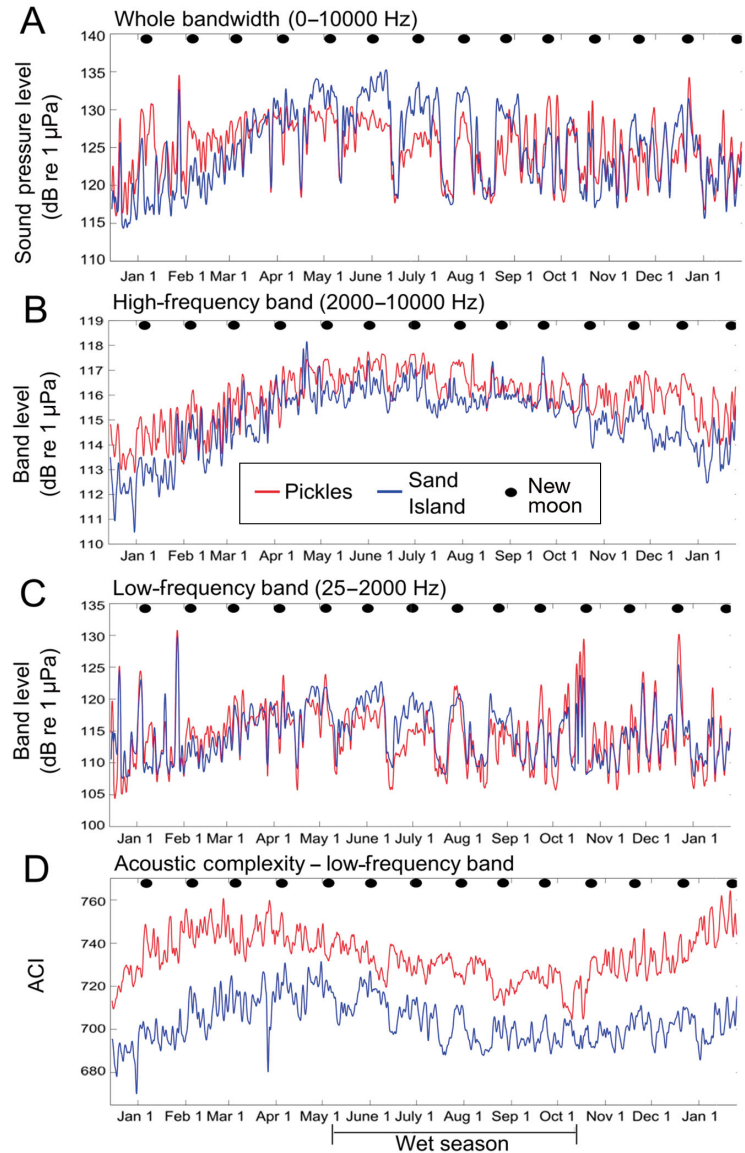


Fig. 2. Acoustic data recorded at Sand Island and Pickles Reef showing (A) Root mean square (RMS) level for the whole bandwidth (1 Hz to 10 kHz); (B) band level for the high frequency band (2000 to 10 000 Hz); (C) band level for the low frequency band (25 to 2000 Hz); and (D) acoustic complexity index (ACI) for the low-frequency band. All data were smoothed with a 50 pt Hanna filter. Acoustic amplitudes were greatest during the wet season, but acoustic complexity was greatest at the end of the dry season. Lunar periodicity can be observed in the RMS level (A), low frequency band (C), and ACI (D), during the wet season; the magnitude of the lunar fluctuation was generally greater at Sand Island than at Pickles

acoustic complexity occurred during morning hours, especially between June and November. Pickles had higher amplitudes than Sand Island for the high band dawn and dusk choruses, as well as greater acoustic complexity. Sand Island had greater lunar-associated increases in amplitude for the low band than Pickles (Fig. 3C,D).

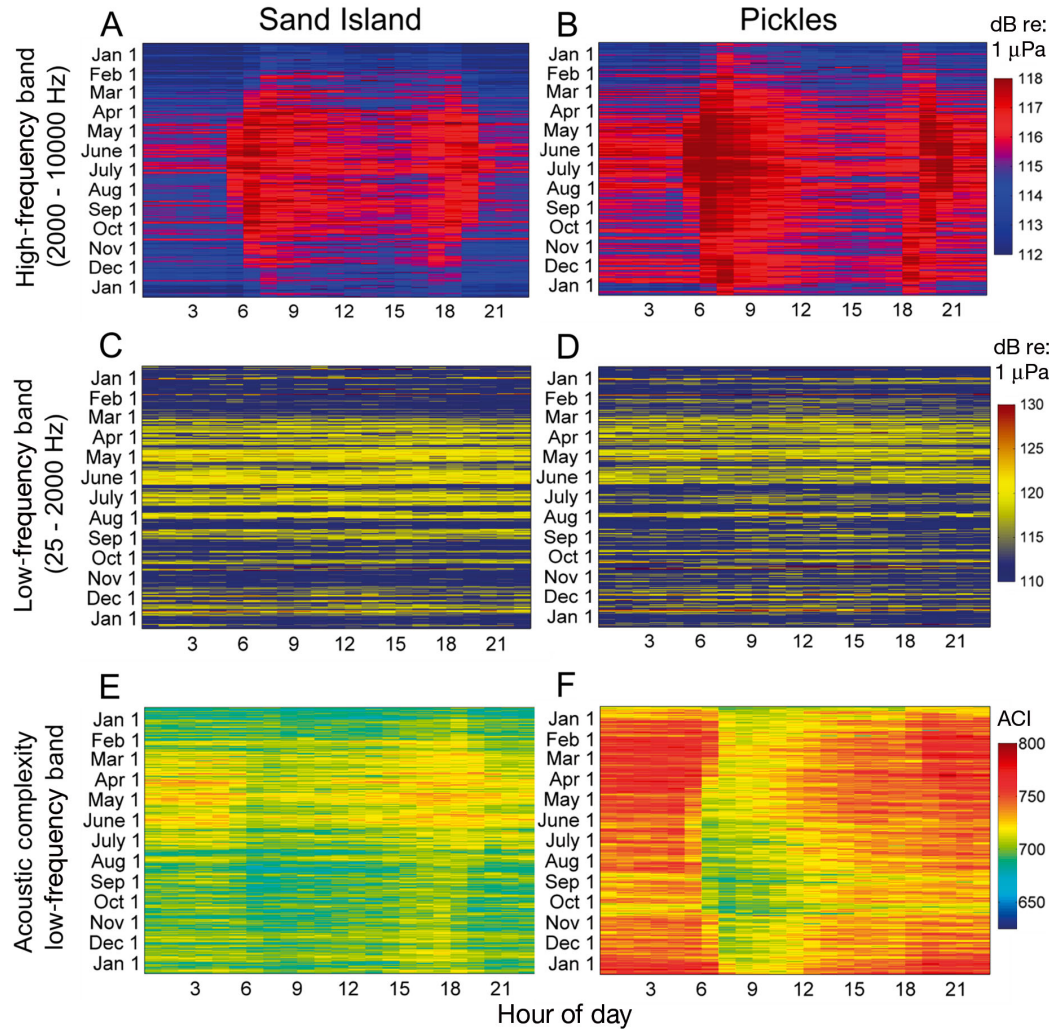


Fig. 3. Amplitude of the (A,B) high and (C,D) low bands (color bar in dB re: 1 μPa) as well as acoustic complexity for the low band (E,F; color bar in ACI) for each hour of the day at Sand Island and Pickles Reefs. In the high band, clear dawn and dusk peaks can be observed, shifting with the changing daylight throughout the year. In the low band, horizontal yellow bands correspond to the increase in amplitude during new moon periods of the wet season. Acoustic complexity was high during nighttime hours throughout the year; it was greatest during the end of the dry season and lowest towards the end of the wet season

We refer readers to Supplement 1 (www.int-res.com/articles/suppl/m508p017_supp/) for plots of all environmental data in the time and frequency domains, and limit our focus here to the wind and tidal data. The greatest wind speeds occurred in the dry season (Table 3), when there were short (5 to 8 d) peaks. In the wet season, there appeared to be some lunar periodicity (Table 3, Fig. S3 in Supplement 1); the offshore wind was greatest during new moons, whereas during full moons the wind dropped to the lowest speeds observed all year (Table 3, Fig. S3). The power spectrum for offshore wind revealed a peak at once per sidereal month and once per solar day (Fig. S3B). The tidal data exhibited a clear seasonal pattern as well as a strong peak at a frequency of once and twice per lunar day (Fig. S7B).

Periodic components of the data

We found that each variable was autocorrelated at different lag times (Fig. 4). The wind data had fairly low lag times of up to 9 d, while larger-scale environmental descriptors like air temperature and water temperature had seasonal patterns, apparent as very long lag times (>60 d; Fig. 4). Vertical bands are indicative of highly periodic data, which we observed for the tides, ACI, and high-frequency bands at both sites (Fig. 4), and can be better understood by examining the power spectra (Fig. 5). The low-frequency band at both sites had peaks at once per sidereal month (27.32 d), which is the time it takes for the moon to make one complete orbit around the earth. The ACI for Sand Island, but not Pickles, had peaks at

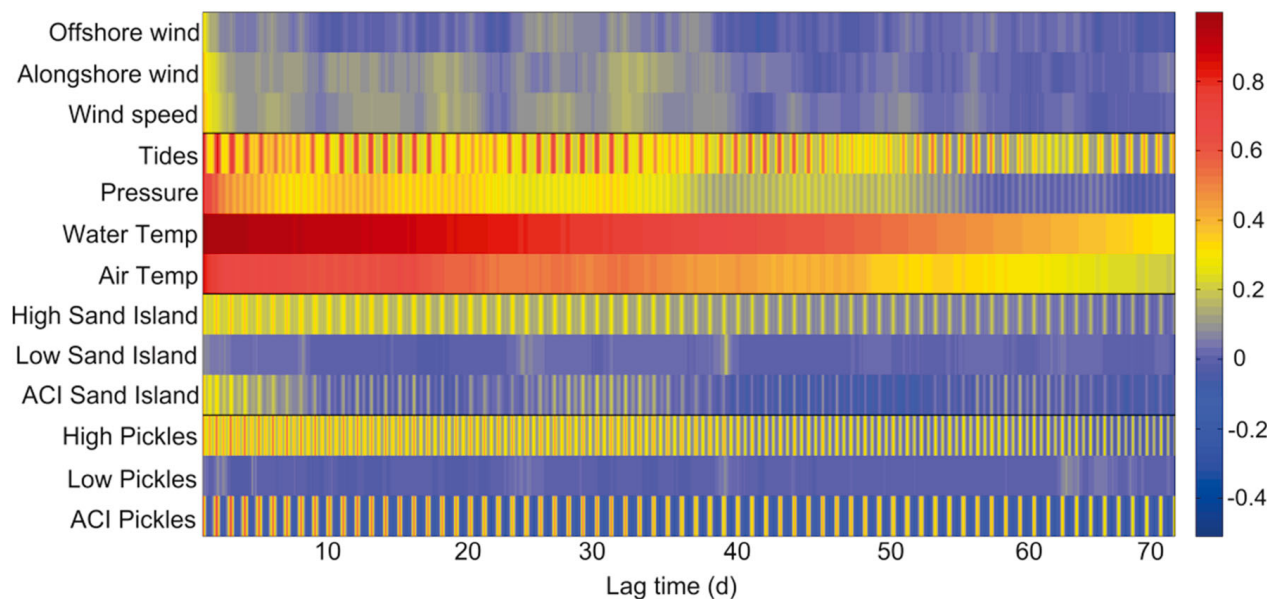


Fig. 4. Autocorrelation plots for each variable, across lag time in days (color bar represents autocorrelation values). Wind had relatively low autocorrelation values, with lag times of only several days. Strongly periodic signals, such as the tides, acoustic complexity index (ACI), and the high frequency band at each site, appear as vertical bands. Both water temperature and air temperature had high autocorrelation values out to 70 d, which was expected due to the seasonal trends in these data

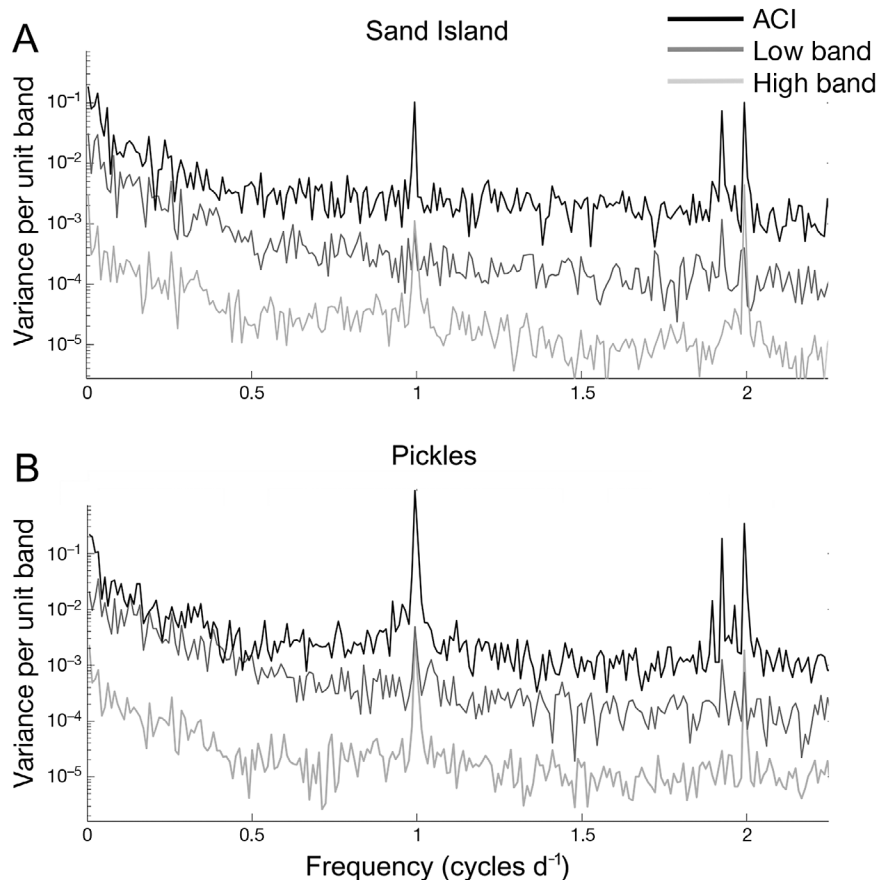


Fig. 5. Power spectra for (A) Sand Island and (B) Pickles showing acoustic complexity (ACI) (black), the low-frequency band (dark grey) and the high-frequency band (light grey). ACI was highly periodic at both sites at frequencies of once per solar day, twice per solar day, and twice per lunar day. At Sand Island (but not Pickles), the ACI also had peaks at once per synodic and once per sidereal month. The low band at both sites was periodic at frequencies of once per sidereal month, once per solar day, and at once and twice per lunar day. Finally, the high band at both sites had a strongly periodic component at once and twice per solar day. In general, Sand Island had more prominent lunar cycles than Pickles, whereas Pickles had stronger diurnal cycles

once per sidereal month as well as once per synodic month (29.5 d) (Fig. 5), the time from one new moon to the next (<http://asa.usno.navy.mil>). In terms of daily cycles, ACI had peaks at once and twice per solar day (24 h 0 min, or 86 400 s), and twice per lunar day (24 h 50 min, or 89 400 s). The low band at both sites had peaks at once per solar day, and once and twice per lunar day. Finally, the high band had peaks at once and twice per solar day. In general, the peaks on a daily scale were greater at Pickles, while Sand Island had greater peaks on the lunar scale (Fig. 5).

Geophony

Since the offshore wind shared peaks with the low band at periods of once per sidereal month and once per solar day, we isolated the peaks from the power spectra and compared their phase. The wind and low band at both sites were in phase at a period of once per sidereal month, but the magnitude of the lunar difference in the acoustic data exceeded that of the wind. The once per day peaks in the wind and acoustic data were not in phase. We performed similar steps for peaks shared between the tides and low band at once and twice per lunar day, and we found that the tides were not in phase with the acoustic data.

For the low band, after controlling for offshore wind, the ANCOVA revealed a significant interaction between season and site ($F_{1,19585} = 13.8$, $p < 0.01$), as well as moon phase and site ($F_{2,19585} = 8.03$, $p < 0.01$), but there was no significant interaction between season, moon phase, and site ($F_{2,19585} = 0.07$, $p = 0.94$; Fig. 6). In addition, there was a significant interaction between offshore wind and site ($F_{1,19585} = 83.8$, $p < 0.01$). For the high band, when controlling for offshore wind, there were no significant interactions between season and site ($F_{1,19763} = 0.67$, $p = 0.41$) or moon phase and site ($F_{2,19763} = 1.6$, $p = 0.20$) or season, moon phase, and site ($F_{2,19763} = 0.92$, $p = 0.40$, Fig. 6).

Biophony

Lunar patterns were evident in the spectrograms for the low band at both sites (Fig. 7). At Sand Island, acoustic complexity also had a lunar phase (Figs. 5A & 7A), which matched the pattern in the most prevalent sounds at this site: ‘growls’ and ‘thumps’ (Fig. 8A,B) which often occurred together, and were most prevalent during quarter moon and new moon periods. The dominant frequency of the growls was

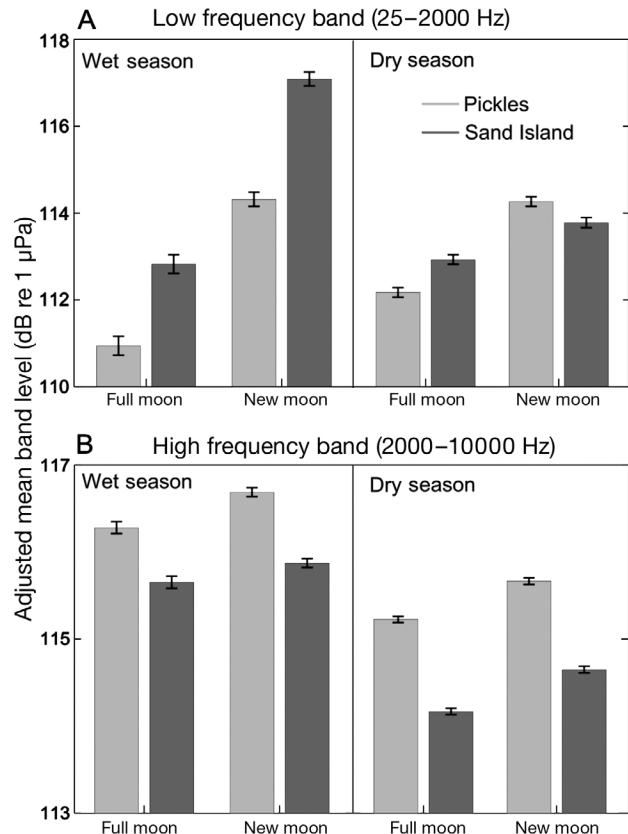


Fig. 6. Adjusted mean band level ($\pm 95\%$ confidence interval) for each site (light grey: Pickles, dark grey: Sand Island) at new and full moons during each season, generated from the results of the ANCOVA. (A) In the low-frequency band, after accounting for variability due to offshore wind, there was only a slight difference between new and full moons in the dry season. However, during the wet season, the differences were pronounced at both sites, and Sand Island had greater amplitudes than Pickles during both lunar phases. (B) In the high-frequency band, Pickles had higher amplitudes across all moon phases and seasons

25 to 50 Hz (duration: 0.4 to 0.8 s, frequency range: 25 to 350 Hz, audio file Supplement 2 at www.int-res.com/articles/suppl/m508p017_supp/), and the dominant frequency of the thumps was 75 to 95 Hz (duration: 0.1 to 0.15 s, frequency range: 25 to 1600 Hz). While many fish calls remain unidentified (Mann 2012), given the known general characteristics of fish vocalizations (Lobel et al. 2010), it is not unreasonable to assume that many of the percussive, thump-like, growl-like, and grunt-like sounds observed at the 2 sites were produced by fishes (Fig. 8). At Pickles, although both growls and thumps were audible and also exhibited a lunar pattern, they were less prevalent and generally lower in amplitude than at Sand Island. Instead, the low-frequency band at Pickles comprised a variety of vocalizations from

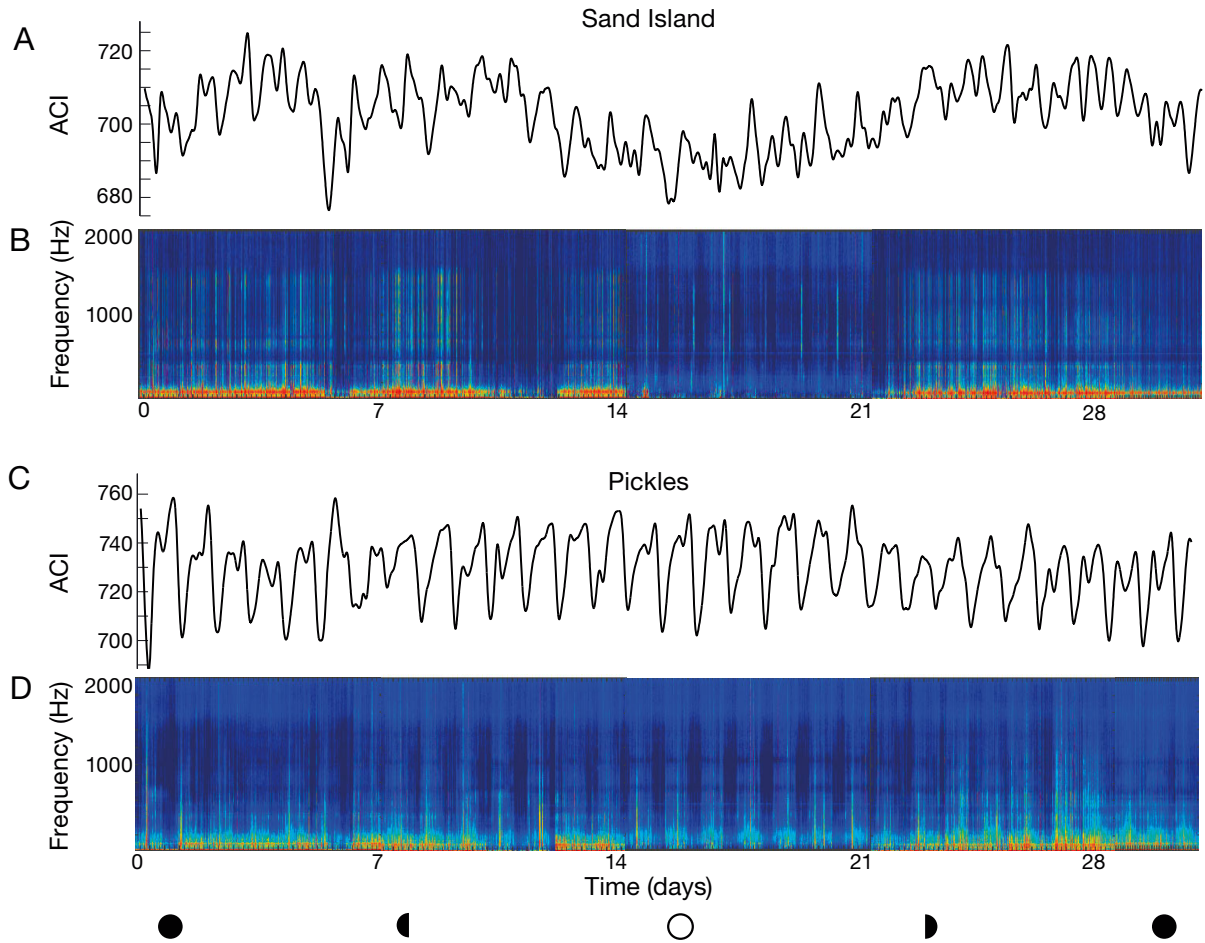


Fig. 7. (A,C) Acoustic complexity index (ACI) for the low-frequency band at Sand Island Reef and Pickles Reef during July 2011, smoothed with a 20 pt filter; (B,D) spectrograms from the low-frequency band at the 2 reefs. A spectrogram can be read like a musical score, with frequency on the *y*-axis and time on the *x*-axis, with warmer colors corresponding to louder sounds. Spectrogram parameters—fast Fourier transform size: 3509, overlap: 50%. The quietest times at both sites occurred during the full moon, and the loudest time occurred during the new moons (B,D). Sand Island had both lunar and diurnal periods in acoustic complexity (A), while Pickles had a highly periodic diurnal signal (C), with more complex times occurring at night. These daily patterns in acoustic complexity at Pickles match the spectrogram (lighter areas depict the presence of more sound sources)

other fish, such as grunts and damselfish, in the range of 200 to 1600 Hz (Lobel et al. 2010) (Figs. 7D & 8C,D, audio file in Supplement 3). The 1 mo spectrogram showed that these fish sounds were most common during the night, when acoustic complexity was also highest (Figs. 3F & 7C,D); this finding is consistent with the once per day peak in the power spectrum for the low band at Pickles (Fig. 5B).

DISCUSSION

The information obtained from the recordings at these 2 reefs reveals just how little we know about the soundscapes of ocean habitats, which are highly variable across space and time. The 14 mo duration allowed us to disentangle the relative contributions

of geophony and biophony to the soundscapes of these reefs over a range of timescales. The tools applied here can be used for long-term acoustic recordings from any type of ecosystem. Although our primary focus was not on spatial differences (1 recorder reef⁻¹), it is still useful to make comparisons between the 2 sites if for no other reason than to demonstrate that it is difficult to make generalizations about soundscapes from single-location or single-moment recordings.

Patterns and contribution of wind and tides

As the dry season transitioned to the wet season, wind speeds generally decreased while sound levels increased (Table 3, Figs. 2 & S1–S3 in Supplement 1).

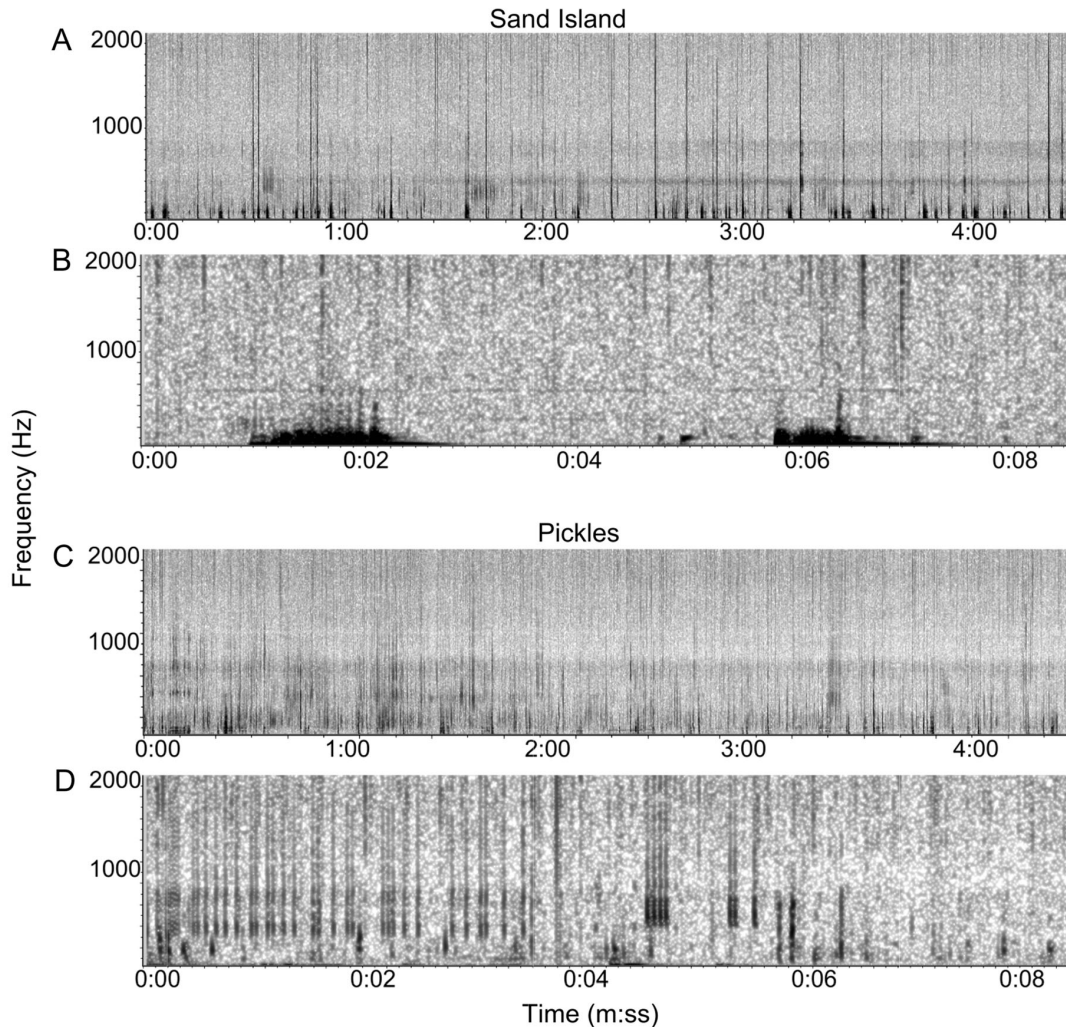


Fig. 8. Representative short-term spectrograms from Sand Island and Pickles for dusk new-moon periods during the wet season (data from 1 July 2011). Spectrogram parameters; (A,C) fast Fourier transform (FFT) size: 3509, overlap: 50%; (B,D) FFT size: 1050, overlap 90%. The shading scale corresponds to sound intensity, with quieter sounds represented by lighter shades, and louder sounds represented by darker shades. Sand Island's soundscape was dominated by 'growl' and 'thump' sounds, whereas Pickles' soundscape was more complex and had more percussive sound sources

The low-frequency band, which contains most of the wind-generated sound (Wenz 1962), had sharp peaks in the winter, but these high-wind events were not periodic phenomena (Fig. 4). Currents due to tidal flow or high winds can affect measurements of underwater soundscapes (Urlick 1983) by generating 'self-noise' on a mooring system. At the frequency of once per solar day, the offshore wind had a peak due to the afternoon sea breeze (Winsberg 2003), but by isolating peaks from the power spectra and comparing their phases, we found that the sea breeze did not coincide with the once per day acoustic peak. We also found that the once and twice per lunar day acoustic peaks were not in phase with the tides (Figs. 4, 5 & S7 in Supplement 1). Thus, the diurnal acoustic patterns must be caused by other sound

sources, which was verified by listening to the recordings and examining the acoustic complexity.

The lunar period in the offshore wind during summer months, which was in phase with the low-frequency band, was surprising. Although the atmosphere can experience tidal cycles similar to the ocean tides (Sandford et al. 2006), these cycles occur with the period of a synodic month, rather than a sidereal month. The reason for the once per sidereal month peak in the offshore wind data is unknown, but seems to be a coincidence that occurred only in 2011, as it was not apparent in 2010 or 2012 (NOAA MLRF1 buoy data). To further explore the relationship between the wind and the acoustic data, we generated a series of predicted sound pressure levels from the measured wind speed, based on relation-

ships in Knudsen et al. (1948). While some of the lunar variability we observed was attributed to the wind, the observed sound levels exceeded those that were predicted by the wind, especially during the new moons at Sand Island (Fig. S8 in Supplement 1). When including the wind as a covariate, we observed differences in the low band both within and between sites, especially during the wet season (Fig. 6). These discrepancies indicate that the wind was not the sole source of sound that varied on a lunar cycle. This was verified with the spectrograms, which clearly showed that certain fish vocalizations (e.g. the 'growl') also followed lunar periods (Fig. 7, see later sections of the discussion). Therefore, we can conclude that although the wind did affect the soundscapes, it was not the sole contributor to the low band and does not explain all of the variance observed. It would be interesting to investigate whether some of the biological patterns we observed were caused by a reaction to elevated noise levels due to wind (i.e. the 'Lombard Effect'; Locascio & Mann 2005, Parks et al. 2011).

Patterns and contribution of other non-biological sound sources

Other sources of ocean noise include thermal agitation, pressure fluctuations on the surface, turbulence, rain, seismic activity, and shipping traffic (Wenz 1962). Thermal agitation is not expected to be a major contributor at frequencies <10 kHz, and pressure fluctuations and turbulence primarily affect frequencies <25 Hz, which was discarded from our frequency analysis (Wenz 1962). Therefore, within the range sampled for this study (25 to 10 000 Hz), we would not expect these sources to be major components of the soundscape. Unfortunately, there was no record for rain near the site of the recorders, so we must assume that the 2 sites experienced similar conditions, and that rain events would not represent a primary contribution to the different periodic patterns observed in the data. For both distant shipping and seismological activity, which can affect underwater soundscapes in the low frequencies, we assume that these sound sources would be far enough from the reefs that they would affect the 2 sites similarly. Local boat traffic may have differentially affected the sound levels at the 2 sites. Because the recordings were 12 s in length but were spread 5 min apart, when a small boat passed overhead, it was detectable on just 1 recording (E. Staaterman pers. obs.). Therefore, we assume that the sporadic pres-

ence of boats would be diluted by our large number of data points. While anthropogenic activity would be interesting to characterize, it was not the primary objective of this study and will instead be investigated in future research. Finally, many of the sources listed above are not periodic phenomena, and while they are interesting to examine, here we maintain our focus on the cyclical elements of coral reef soundscapes.

Patterns and contribution of biological sound sources

A seasonal pattern was observed for the high band and for acoustic complexity, and to a lesser extent, the low band. Acoustic complexity was greatest at both sites during the transition from the dry to the wet season, when many soniferous marine fish begin their spawning activities (Lobel et al. 2010). Snapping shrimp activity is typically highest in the spring and summer, especially during dawn and dusk (Lammers et al. 2008, Radford et al. 2008). With our recordings, the amplitude in the high band mirrored the seasonal change in daylight (Fig. 3), making it clear that snapping shrimp activity has a strong relationship to light levels. Odontocete sounds may have also contributed to the high band (Hildebrand 2009), but these signals would be short in duration and transient in nature, and our study demonstrated a highly periodic component that is linked to the daily activity of snapping shrimp.

After accounting for the wind, both sites had greatest amplitudes in the low band during new moons, and the magnitude of the variation was greater in the wet season than the dry season (Fig. 6, Table 3), a finding that is consistent with Radford et al. (2008). In low latitudes, many soniferous marine animals are active during wet season new moons (Breder 1968, Cato 1978, McCauley & Cato 2000, McCauley 2012). However, it was surprising that the lunar cycle in the low band occurred once per sidereal month, rather than once per synodic month, the latter being more typical of biological rhythms (Morgan 2000). While mice show activity cycles on a period of once per sidereal day (Brown 1975), and growth rates of some plants seem to follow period of once per sidereal month (Kollerstrom & Staudenmaier 2001), to our knowledge, a lunar-sidereal period in marine animal behavior has not been previously described. The fact that the ACI at Sand Island did have a peak at both once per sidereal and once per synodic month (Fig. 5), and the spectrograms revealed quiet periods spanning the entire week of the full moon (Fig. 7),

indicates some degree of periodicity on both of these scales. However, the biological reason underpinning this phenomenon, and the behavioral distinction between sidereal and synodic periods, deserves further study.

Remarkably, the loudest time periods on these 2 reefs in the Florida Keys coincided with the time when most larval fish recruit to coral reefs (Limouzy-Paris et al. 1994, D'Alessandro et al. 2007, Sponaugle et al. 2012b). While the results from this study cannot necessarily imply a causal relationship, this association is significant, given the surge of recent work on the attraction of larval fish to reef sounds (e.g. Simpson et al. 2005, Radford et al. 2011). Are larval fish more likely to settle on reefs during new moons because they can detect the reef acoustically, and there is a stronger signal during these periods (Cato 1978)? Or does the arrival of the larvae itself produce an acoustic signal (e.g. through hydrodynamic or feeding sounds; Kasumyan 2008) that we detected in our recordings? The findings from our study open interesting questions that warrant future research.

On a daily time scale, peaks in the low band and acoustic complexity occurred at once per solar day, and once and twice per lunar day (Fig. 5). Sound-producing individuals are vulnerable to detection from predators, but this risk is lessened at night, especially during moonless nights. Acoustic complexity was high at night (Fig. 3E,F), indicating that more animals were acoustically active during this time. Because the once and twice per lunar day peaks in the low band were not in phase with the tide, these sounds must be of biological origin. Perhaps the animals adjusted their calling rates or feeding activity based on ambient light levels, enacted behaviors based on an endogenous clock (Morgan 2000), or sensed when the moon reached the same position in the sky from one night to the next.

Differences between sites

Both sites followed similar patterns, but in general, Sand Island had greater amplitudes in the low-frequency band while Pickles had greater amplitudes in the high band, and Pickles had higher acoustic complexity. Within the low band, the primary biophonic contributions at Sand Island were the very low frequency 'growls' and 'thumps' which took place throughout the entire day but were almost entirely absent during full moon periods (Fig. 7B). These sounds were likely produced by fishes, although the species are unknown. Within the low

band at Pickles, greater acoustic complexity, especially at night, can be seen in the 200 to 1600 Hz range on the spectrograms where several sounds were audible simultaneously (Figs. 7D & 8C,D). In the present study, which was one of the first studies to apply the newly-developed ACI to marine soundscapes, we found strong agreement between ACI and the visual patterns of the soundscapes (Fig. 7), demonstrating that this may indeed be a viable metric in marine systems. To summarize: a high amplitude, very low frequency, lunar signal emanated from the Sand Island site, while a more complex, diel signal emanated from the Pickles site.

We did observe differences in both the types of sounds and temporal patterns of these 2 reefs' soundscapes, but we must acknowledge the caveat that these were single-site recordings within each reef. Therefore, it is difficult to know whether the findings shown here are representative of the entire reef, or just particularly noisy or quiet regions of the reef. In the future, multiple hydrophones should be used over shorter time scales to ground-truth the patterns gleaned from single-point recordings and to understand whether they can be generalized to describe entire acoustic habitats.

Nonetheless, recent surveys of benthic species composition and adult fish did uncover some significant differences in the biological composition of the 2 sites, which may be linked to their acoustic qualities. Sand Island had significantly more rubble, fleshy macroalgae, and turf algae than Pickles, while Pickles had more bare substrate, crustose coralline algae, and dictyota (our Table 1; S. Sponaugle & E. D'Alessandro unpubl. data). Although there were no significant site differences in terms of live coral cover, the relationship between acoustic qualities and other substrates (e.g. rubble, algae) should be explored further, as certain acoustic characteristics could be used as habitat indicators (Kennedy et al. 2010). Some soundscape differences may be explained by differences in the abundance of soniferous fishes. There were significantly more sergeant majors *Abudefduf saxtalis* at Sand Island than Pickles (S. Sponaugle & E. D'Alessandro unpubl. data); because this species is known to vocalize in the lowest frequencies (Maruska et al. 2007), this may have contributed to the greater amplitudes observed at this site. In contrast, Pickles had more redband parrotfish *Sparisoma aurofrenatum*, and the feeding sounds of parrotfish are important sources of mid-frequency noise on coral reefs (Lobel et al. 2010, Munger et al. 2011). Although not statistically significant, the Pickles site had more bluestriped, French, and small-

mouth grunts (*Haemulon* spp.) than Sand Island (S. Sponaugle & E. D'Alessandro unpubl data). Grunts are known to produce sounds in the range of approximately 100 to 1600 Hz, which is the range in which the Pickles site had higher acoustic complexity and a greater apparent number of sound sources (Lobel et al. 2010). While passive acoustic monitoring holds great promise as an ecological assessment tool (Luczkovich et al. 2008, Sueur et al. 2008, 2012, Pieretti et al. 2011, Gasc et al. 2013), more work is required in order to carefully link ecological and acoustic measures.

Larval fish recruit to Florida reefs during the new moon periods of the wet season (D'Alessandro et al. 2007), when Sand Island had higher amplitudes than Pickles. Greater numbers of settlement-stage larval fish have been observed to arrive at Sand Island compared to Pickles (Grorud-Colvert & Sponaugle 2009). The low-frequency, high-amplitude growls and thumps would propagate a great distance and, depending on the hearing abilities of the fish species, could provide a reliable signal to guide the larvae towards the coast (Tavolga et al. 1981, Mann et al. 2007). This signal was present at Pickles as well, but was lower in amplitude than at Sand Island, which may explain the smaller number of larval fish that have been captured there (Grorud-Colvert & Sponaugle 2009). In a study that used high-resolution biophysical modeling to map the trajectories of fish larvae in the Florida Keys, the authors did not find a significant difference in the number of larvae that arrived at these 2 sites (Sponaugle et al. 2012a). This finding suggests that the site differences are not explained by oceanographic features, but may be explained by a behavioral response from the fish. The hypothesis that the unique soundscapes of these 2 sites play a role in fish recruitment warrants further investigation through playback experiments. Specifically, it would be interesting to test whether larval fish have a preference for louder signals (e.g. Sand Island) or more complex signals (e.g. Pickles).

CONCLUSIONS

The long duration of our acoustic recordings, along with the availability of environmental data, allowed us to disentangle the relative contributions of geophony and biophony to these reef soundscapes. The low band, which spans the auditory range of fish, had the greatest amplitudes during new moons of the wet season, coinciding with peak larval fish recruitment periods. Acoustic complexity was greatest at night

and during the transition between the dry and wet season, when many fish are beginning their reproductive activities for the year. One reef had a high amplitude, low-frequency acoustic signal with strong lunar periodicity, whereas the other reef had a lower-amplitude, more complex signal with strong diurnal periodicity. In addition, the high-frequency band at both sites was highly periodic at cycles of once and twice per day, corresponding to dawn and dusk snapping shrimp activity. The patterns uncovered here provide insights into the potential role of coral reef soundscapes in the orientation behavior of pelagic larval fish. Our study highlights the fact that long-term recordings, coupled with the analytical tools applied here, can be used to uncover natural patterns of acoustic signals that are relevant to resident animals in any marine or terrestrial habitat. Finally, this study contributes to the growing field of soundscape ecology by providing critical baseline data in the face of our changing oceans.

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Editorial responsibility: Nicholas Tolimieri, Seattle, Washington, USA

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