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# Predicting the reef acoustic cuescape from the perspective of larval fishes across a habitat quality gradient

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ABSTRACT: The combined acoustic activity of soniferous organisms living in benthic habitats produces habitat-specific soundscapes, which are predicted to influence fish and invertebrate larval behavior during the settlement process. Not every sound will have the amplitude and frequency characteristics relative to hearing sensitivity to be used as an acoustic cue, thus the cuescape is a subset of the soundscape. These sounds vary through space and time, and little is known about how this variability could influence their role in settlement. We recorded the soundscapes of 4 coral reefs in Caribbean Panama for 6 wk and conservatively identified the sounds most likely to compose the cuescapes used by larval fishes. While these sites represented the variation in reef condition across the study area, we observed the same 4 dominant taxa groups emerge as the most likely producers of acoustic cues. These results were consistent across both time and space when compared to short-term recordings taken at these 4 reefs and at an additional 11 sites 2 yr prior. Next, we used an individual-based model to test the relationship between settlement success and the natural spatiotemporal variability we observed in these potential cues. Temporal variation in the sounds resulted in variation in settlement success; however, even short-range, intermittent cues improved the likelihood of settlement. Overall, we observed similar acoustic cuescapes across reefs that varied in condition, suggesting that cuescapes can be resilient to some forms of reef degradation by retaining sounds potentially useful to larval fishes for both navigation and habitat selection.

KEY WORDS: Coral reef · Soundscape · Larval fish · Larval settlement · Acoustics · Modeling · Cues · Fish behavior

## INTRODUCTION

The life history feature of a pelagic larval stage followed by settlement onto benthic habitat is found in nearly all reef fish species (Brothers & Thresher 1985). The use of cues to improve the likelihood of a successful pelagic–benthic transition has been observed for fish and invertebrate species across systems (Tolimieri et al. 2000, Simpson et al. 2005, Radford et al. 2007, Stanley et al. 2010, Vermeij et al. 2010, Lillis et al. 2013, Atema et al. 2015). The relationship between an environmental cue and its ability to advertise habitat characteristics like location, type, and suitability will depend on the type of cue considered. Reef-based cues can be considered as those generated by components of the reef habitat itself, allowing them to also potentially provide information about the suitability of the habitat. For example, olfactory cues may not only indicate that a reef is nearby (Paris et al. 2013) but can also indicate the

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presence of the natal reef (Gerlach et al. 2007), habitat type through vegetation (Dixson et al. 2011, Huijbers et al. 2012), and reef suitability through conspecifics (Lecchini et al. 2005). An acoustic cue like the sound of waves breaking can indicate the presence of shoreline (Montgomery et al. 2006), but the sounds produced by the reef-dwelling community may also indicate the quality of reef habitat and the type of biological assemblage present (Kennedy et al. 2010, Piercy et al. 2014, Kaplan et al. 2015). This is in contrast to non-reef based cues, like a sun compass (Mouritsen et al. 2013) or magnetic compass (Bottesch et al. 2016, O'Connor & Muheim 2017), which may be a long-distance indicator of the natal reef position but will not provide direct information about the type or quality of habitat. The ability of cues to indicate both location and habitat condition is particularly important when considering how reef degradation and changes in reef community structure may affect the cues that advertise that reef (Gordon et al. 2018). It follows that the cues of particular interest when considering how fish populations respond to habitat change are the cue types that are reef-based and influenced by habitat alterations.

Of the reef-based environmental cues considered, auditory cues are hypothesized to operate over distances that would be relevant to navigation (Montgomery et al. 2006) and they also may provide information as to the type and condition of the underlying reef habitat (Piercy et al. 2014, Kaplan et al. 2015, Gordon et al. 2018). This role of acoustic cues to larval fishes is predicted because of the biologically produced sounds at coral reefs, the physics of sound itself (relatively current-independent and long-distance propagation), and evidence of larvae responding to reef sounds (Leis et al. 2002, Tolimieri et al. 2004, Simpson et al. 2005, Huijbers et al. 2012, Parmentier et al. 2015). Soundscapes are composed of sounds from a variety of biological, geological, and anthropogenic sources (Pijanowski et al. 2011). Here we will primarily focus on the contributions of the reef biota to the soundscape, which includes fish vocalizations (McCauley & Cato 2000, Amorim 2006, Tricas & Boyle 2014) and the acoustic by-products of activities like feeding and defending (Versluis et al. 2000, Radford et al. 2008, Tricas & Boyle 2014). Of these biologically produced sounds, only a subset will have the frequency and amplitude characteristics to serve as cues for larval fishes. Thus, the soundscape is not equal to the acoustic cuescape. The term 'cuescape' has been previously introduced (e.g. Simpson et al. 2008a,b), and here we use the term to refer to the 3-dimensional spatial distribution of sounds that are produced at the reef and are audible to a larval fish at any given instance in time. A sound will be audible to a larval fish swimming in the open water if the sound's amplitude, determined by its source level minus transmission loss, is greater than both the ambient background sound level and the fish's hearing threshold at the frequency of the sound. In general, reef fish larvae have shown auditory responses to frequencies between 100 and 2000 Hz, with typically highest sensitivity to the lower frequencies in this range (<500 Hz; Wright et al. 2005, 2010, 2011). A sound at any frequency within this audible range will be most likely to serve as an acoustic cue if it is produced at a high enough amplitude to be detected by a larval fish at some distance from the sound's source. This is particularly true for sounds used for orienting to the reef, whereas lower-amplitude sounds could be used at smaller spatial scales for habitat selection after a fish locates benthic habitat. When we consider as potential acoustic cues the highest-amplitude content within the frequency range to which fishes are sensitive, we reduce the soundscape to a cuescape that is composed of intermittent cues. This changes the view of the acoustic cuescape from one in which the cue is continuously available, as has been typically considered (Armsworth 2000, Codling et al. 2004), to a view of the cuescape as a 'blinking beacon.' This framework introduces a new characteristic of acoustic cues that must be considered, i.e. the cue rate, and also introduces new questions: What is the relationship between the rate of acoustic cues and settlement success, and how does cue rate vary with reef condition?

The biological community that inhabits a reef defines one reef trait, and as this community produces the biological soundscape, this soundscape can also be considered to be a reef-defining trait. Characteristics of the soundscape that will define this trait space are the frequency and amplitude of the sounds and the temporal pattern at which they are produced. Reef soundscapes vary over short (e.g. within a day) and long (e.g. seasonal) time scales, with variation driven by factors such as temperature, moon phase, and the diurnal cycle (Staaterman et al. 2013, 2014, Kaplan et al. 2015, Bohnenstiehl et al. 2016, McWilliam et al. 2017). Spatial variation in the identity and abundance of soniferous species and in the temporal patterns of their acoustic behavior can create unique acoustic signatures of reef habitats. These spatial patterns can be driven by species sorting in response to natural variation. For example, different coastal habitats (Radford et al. 2010, Lillis et al. 2014), zones within a reef (Radford et al. 2014, Bertucci et al. 2015), and reefs varying in substrate composition (Kennedy et al. 2010, Piercy et al. 2014) can exhibit unique soundscapes. Spatial variation in soundscapes can also be created by different levels of anthropogenic disturbance between sites, how these sites are managed, and the level to which species are protected from fishing (Piercy et al. 2014). Driven either by natural variation or human-caused disturbance, spatial variation in soniferous communities creates spatial variation in soundscapes. Since the acoustic cuescape is a subset of the soundscape, we would predict that due to these spatial differences in reef soundscapes, the acoustic cues that are available to larval fishes will vary spatially as well. Given the hypothesized role of the acoustic cuescape in larval settlement, the ecosystem function of a reef's ability to attract larvae through this cue type may also vary between reefs. Therefore, it is important to understand how the reef trait of the soundscape varies, and the implications of this variation on one possible function of this trait, larval recruitment.

In this study, our goal was to predict the acoustic cuescape from the soundscape, and test if the rate of cue production that we observed could function to improve larval fish settlement, assuming positive phonotaxis. The study was conducted on reefs that are reflective of those across the Caribbean (Gardner et al. 2003) as they have been subject to overfishing, general degradation of water quality, and recent bleaching (Seemann et al. 2014, Altieri et al. 2017). Despite these widespread impacts, there was variation in reef condition, and we used this range of reef quality to ask if the acoustic cuescape is resilient to habitat degradation. We considered a cuescape to be resilient if there were components of the soundscapes that could potentially serve as acoustic cues despite the perturbations this region has experienced. Further, we investigated if these potential cues vary between reefs that differ in habitat quality. We specifically addressed the following objectives:

(1) Characterize reef soundscapes to identify the sounds that have the potential to serve as acoustic cues based on amplitude and frequency characteristics. All sounds detectable by fishes have the potential to provide information. The function of a sound to a larval fish is in part dependent on the detection distance of the sound, which is in part determined by frequency and amplitude. We selected the high-amplitude content in the frequency range most likely to be detected by fishes to conservatively predict the acoustic cuescapes from the soundscapes recorded at 4 coral reefs in Caribbean Panama.

(2) Investigate the spatial variability of the high-amplitude content as driven by levels of local degradation. We primarily focused on 4 reefs that represented both high- and low-quality sites in the study region to investigate the impact of degradation on the production of predicted cues. We also included recordings taken over a shorter time period at an additional 11 sites to inform the soundscape variation across the region. These recordings were collected in a previous sample year, allowing for comparisons to be made across year-long time scales.

(3) Investigate the temporal variability of the high-amplitude content over a time scale commensurate with a typical pelagic larval duration. Larval fishes are continuously navigating their pelagic environment and being exposed to environmental cues of all types. Therefore, it is challenging to predict the cuescapes these fishes experience by extrapolating from snap-shot recordings. Here we recorded soundscapes at the 4 primary reef sites over a period of 6 wk, 3 times per hour, to predict the temporal variation in the predicted acoustic cues encountered by larval fishes.

(4) Test how temporal characteristics of the acoustic cues influence larval settlement compared to a null model of no cue use. Considering the cuescape as composed of a subset of the available sounds creates in essence a blinking cue that can be defined by a cue rate. We used an individual-based simulation model to investigate how spatiotemporal variability in the rate of the high-amplitude sounds influences their ability to serve as navigational cues for larval fishes seeking settlement, assuming positive phonotaxis.

## MATERIALS AND METHODS

### Site description

This study was conducted in Almirante Bay, Bocas del Toro, in northwestern Panama. The largest islands of this archipelago shelter the bay and create a semi-lagoonal system that minimizes the influence of winds, tides, and surf (Guzmán et al. 2005). The bay supports fringing coral reef, mangrove forest, and seagrass habitats, but the ecosystem has been altered both historically (Aronson et al. 2004, Cramer et al. 2012) and recently (Seemann et al. 2014) by several anthropogenic factors. Fish and invertebrate diversity has been impacted by a decline in structural complexity (Aronson et al. 2004, Dominici-Arosemena & Wolff 2005, Nelson et al. 2016) and severe overfishing (Seemann et al. 2014). Coral health and biodiversity has been impacted by eutrophication and sedimentation (Seemann et al. 2014), hypoxia (Altieri et al. 2017), and a bleaching event in 2010 to which reefs experienced differential recovery (Seemann et al. 2014, A. Altieri unpubl. data). Reefs exposed to less current and located closer to dredged areas, river discharge, and towns recovered poorly as they were more heavily influenced by eutrophication and sedimentation. These factors have created a continuum of habitat quality across the region, as we define by percent live coral cover. We employed this gradient to investigate how it may drive variation in soundscapes. We primarily focused on 4 sites that represent the range of percent live coral cover in the region (Fig. 1), and used an additional 11 sites across the region to test patterns across a broader range of conditions (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m605p173_supp.pdf). To put these values in context, the percent live coral cover across the Caribbean has declined in recent years to about 10% (Gardner et al. 2003), whereas healthier reefs can have cover upwards of 70% live coral cover (Hughes 1994, Hawkins et al. 1999).

To sample the reef soundscapes on a time scale commensurate with a typical pelagic larval duration (Brothers & Thresher 1985) — how we define 'long-term' sampling for this study — we conducted simultaneous recordings at the 4 primary sites in 2015 for 6 wk. To generalize these results across both time and space, we compared them to short-term recordings taken during 2013. We used these recordings to predict the cuescape, which we then used as input into an individual-based simulation model to test if settlement success is (1) improved by the presence of these acoustic cues, and (2) influenced by the temporal pattern of these cues.

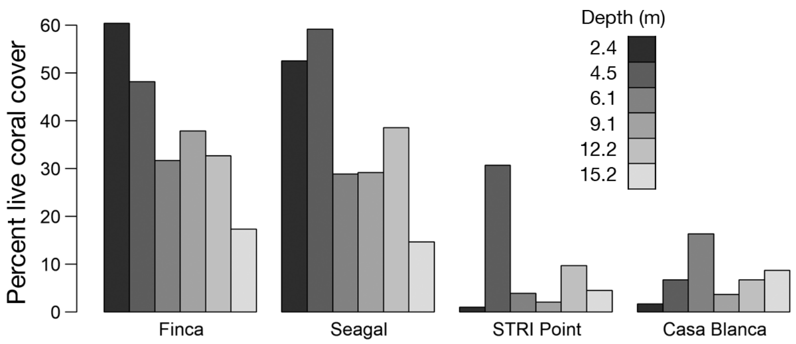

Fig. 1. Percent live coral cover at the 4 primary reef sites. Unpublished data (A. Altieri)

### Long-term sampling

We sampled the soundscape at the 4 primary reef sites for a period of 45 d starting on 15 June 2015, which is during a season of larval recruitment (Robertson 1990). At each reef, we deployed a single hydrophone (SoundTrap, OceanInstruments, frequency range: 20–24 000 Hz, gain: 169–169.5 dB re 1 µPa at full digital scale, resolution: 16-bit) at the base of the reef slope where the reef transitions to sediment. Our use of a single recorder at each reef is supported by Kaplan et al. (2015), who found that the qualitative interpretation when comparing reef soundscapes was not affected by using a single hydrophone at each site. Each hydrophone was attached to a metal rod anchored in a concrete bucket, and was placed by divers at the bottom of the reef. The depth of the units varied by site and ranged from 14.3 to 17.6 m, and the sensor of the hydrophone was approximately 0.3 m above the substrate. The hydrophones were programmed to record for 4 continuous minutes every 20 min at a sampling frequency of 48 kHz. Every 2 wk, we verified operation of all units and gently brushed the sensors free of light sediment.

Each 4 min wav file was detrended and the voltage was converted to pressure using the manufacturer-provided calibration information for each hydrophone. We wrote a MATLAB script (v. R2012a; MathWorks) to automate the process of producing spectrograms of each sound file (window type: Hamming, window size: 16 384 samples, overlap: 8192 samples). The frequencies below 50 Hz were removed due to self-noise of the recording units. Spectrogram images were imported into ImageJ (v. 1.48), and in each image, we identified the presence of small engine boat traffic and rain. Points were placed at the beginning and end of time periods with no boat or rain interference, and the coordinates of these points for each image were imported into a custom MATLAB program. A system that matched these coordinates to time points in the recordings allowed for the extraction of 'clean' segments of each file. Considering the range across the 4 sites, the minimum number of recordings for which we had useable data ranged from 19 to 23 out of the 45 total possible for the 36 night-time periods. Some time periods had all 45 recordings with useable data across all sites. The minimum number of recordings for which we had useable data of the 44 total possible for the 36 daytime periods ranged from 9 to 14. The maximum ranged from 39 to 43 recordings with useable data. Given our concentration on the biological soundscape, we could not always use all 240 s of each sample. If boat noise only interfered with a portion of any of the remaining samples, only that portion was removed. Again considering the range across the 4 sites, the average length of a useable recording taken during the night ranged from 215 to 222 s (standard deviations of 28.7 and 25.1 s, respectively). The average length of a useable recording taken during the day ranged from 127 to 141 s (standard deviations of 21.1 to 20.9 s, respectively). The frequency of boat activity was highest during the day, accounting for more samples removed and shorter useable time portions during the daytime.

We produced spectrograms for the extracted segments, using the same aforementioned spectrogram parameters, and averaged across the time axis to create a power spectrum for each sound file. These power spectra allowed us to qualitatively compare the distribution of acoustic energy across frequencies of biological interest. To compare day and night soundscapes, we calculated the average day and night power spectrum for each site by averaging all power spectra for the time periods between 07:00 and 18:00 h (day) and between 18:20 and 06:40 h (night).

To identify the high-amplitude events in these reef soundscapes, we divided the time series (using the subsetted data with the removal of the boat and rain noise) into a series of 10 s subsamples. For this analysis, we only used the frequencies in the range audible to fishes (0.1–2 kHz). A spectrogram was created for each subsample, as described above. We created a time-averaged power spectrum for each 10 s subsample, and in each spectrum, we found the maximum amplitude and the frequency at which it occurred. To investigate the temporal pattern of this content, we binned the results by the time period (72 $d^{-1}$) at which each subsample was recorded. We also plotted amplitude versus frequency for each event. While these amplitudes do not represent the maximum recorded amplitude of these events (since they are averaged over the 10 s time period), they allow us to compare the relative amplitudes of these sources to predict how they might contribute to the cuescape. We emphasize our focus on relative amplitude; we cannot predict the source sound levels since we have no knowledge of the distance between the organisms producing these sounds and the hydrophones. The sound levels we report are specific to the hydrophones' positions (30 cm above the sediment and at the reef edge) and are not the sound levels fishes may be experiencing higher in the water column (Leis 2004, Huebert & Sponaugle 2009) and at distance from the reef. These predictions would require source levels and a propagation model to predict transmission loss that takes into account the complexities of the physical environment. Since that is beyond the scope of this paper, we consider the likelihood of sounds to be used as cues using relative amplitude and frequency. We do this using the pressure component of sound. While particle motion is an important consideration in fish hearing (Nedelec et al. 2016), we assume that the frequencies with the highest amplitude as measured in pressure are also those with the highest amplitude as measured in particle motion (Mann et al. 2007). This assumption is appropriate for plane waves propagating in a free field and for any progressive wave far from the source. The assumption breaks down near a source, and in a standing wave field near the boundaries, where pressure and particle velocity are no longer proportional.

Of the 4 taxa groups that emerged as being the core contributors to the high-amplitude content, we were able to identify 2 as snapping shrimp (likely *Synalpheus* species) and the Bocon toadfish *Amphichthys cryptocentrus*. The other 2 remain unidentified: a single-species fish chorus producing calls between 0.5 and 6 kHz (hereafter referred to as the 'unnamed fish chorus') and a species assemblage that may be a mix of fishes and invertebrates that produced sounds between 400 and 800 Hz, with a peak amplitude around 600 Hz (hereafter referred to as the '600 Hz unknown source'). We identified a sound-source signal for these sources to better track their acoustic behavior through time and for comparison between sites. Our goal in defining these signals was to minimize overlap with the frequencies produced by other taxa groups, but still include a significant portion of the energy being produced by each group. Given the significant overlap between the 600 Hz unknown source and the other taxa, we were unable to track this feature. We calculated each group's signal in each power spectrum of all samples after removal of boat and rain interference. The shrimp signal is defined as the average amplitude of the frequencies between 7.5 and 20 kHz in each power spectrum. The toadfish signal is defined as the maximum amplitude of the fundamental frequency, which was found by searching for the highest amplitude between 110 and 140 Hz in each power spectrum (to target the fundamental frequency of the harmonic calls). For the signal for the unnamed fish chorus, we averaged the amplitudes for the frequencies between 1 and 2.2 kHz of each power spectrum. To investigate the temporal variation of these dominant sound sources, we created boxplots representing the amplitudes of each signal for each of the 72 daily recording periods across all recording days. We also plotted the time series of the amplitude of these sound-source signals to inform the patterns of acoustic behavior over the 6 wk of recording.

The dominant source of anthropogenic sound was small-boat-engine noise. We calculated the frequency of boat activity in each of the 72 daily recording periods to examine how the temporal pattern of this noise overlapped with the patterns of biological sounds. We did this by dividing the number of samples in which a boat was observed by the total number of samples for each time period.

## Short-term sampling

### Moon phase survey

The long-term soundscape sampling conducted in 2015 provides high-temporal resolution data to predict the type of acoustic cuescape larval fishes may encounter. We compared these data to recordings collected in July 2013 to examine the temporal consistency of these soundscapes across years for the 4 primary sites. We deployed a hydrophone (nRUDAR, Cetacean Research Technology, range: 1–22 050 Hz, system sensitivity: −159.52 dB re 1V/µPa, sample frequency: 44.1 kHz) at each site to capture the soundscape at dusk and dawn within 1 d of the full, first quarter, new, and second quarter moons. We chose this sampling schedule due to the evidence for dawn and dusk choruses (McCauley & Cato 2000, Lammers et al. 2008, Kaplan et al. 2015), and soundscape variability correlating with moon phase (Staaterman et al. 2014). The hydrophone was placed in a stand to allow it to sit upright on the sediments with the sensor at a height of 0.3 m above the bottom. The unit was connected to a surface float and light and deployed at the reef mid-slope, at a depth of approximately 7 m. We moved the boat away from the recording site and turned off the engine to prevent recording the sounds of wave slap on the hull of the boat. Each recording was approximately 10 min in length, and all 4 sites were sampled between 19:30 and 21:00 h for the dusk recordings and between 05:30 and 07:30 h for the dawn recordings.

We used 4 min of each recording except for 1 file that only had 3 min of clean data available. We processed these data in a way similar to the long-term recordings: we calculated a spectrogram as previously described and took a time average to produce a power spectrum for each recording. To qualitatively compare the distribution of power over biologically relevant frequencies in the short-term data to the long-term data, we next averaged these 16 power spectra (dusk and dawn recordings at 4 moon phases) to create 1 spectrum for each site.

### Fifteen site snap-shot

We conducted ‘snap-shot’ recordings at an additional 11 sites in July 2013 to examine the spatial generality of the soundscapes we recorded at the 4 primary sites. We deployed the same hydrophone unit used for the 2013 moon phase survey for approximately 5 min at a depth of about 6 m at each reef around dusk. We sampled the 15 sites across 3 consecutive nights beginning on 18 July, 4 nights before the full moon. The boat engine was turned off, but we did not move the boat away from the recording sites as in the moon phase survey in an effort to minimize the time spent at each location to prevent the spatial comparison from being confounded with temporal variation.

We extracted 2 min of each recording and calculated power spectra as described above. Using these spectra, we calculated snapping shrimp activity by taking the mean amplitude of the frequencies between 7.5 and 20 kHz (as in the long-term data analysis). The occasional wave slap against the hull of the boat prevented us from calculating the toadfish signal as we had for the long-term dataset. As such, for the extracted 2 min time period, we calculated the percentage of time a toadfish call was present. To test if the acoustic activity of these taxa was related to reef condition, we calculated Pearson's correlation coefficients between the shrimp and toadfish signals and the depth-averaged percent live coral cover, dead coral cover, and sand (A. Altieri unpubl. data).

## Individual-based simulation

We used an individual-based simulation model (sensu Codling et al. 2004) to test the hypothesis that transient, intermittent acoustic cues produced at the reef improve the success of larvae finding the reef. Here we provide a short summary of the model, and refer readers to the Supplement for a more detailed description using an abbreviated version of the Overview, Design concepts, and Details (ODD) protocol described by Grimm et al. (2010) and as found in Jovani & Grimm (2008). We predicted that even if the average sound level at the reef is below detectability at distance, periodic high-amplitude events will enable larval fishes to locate the reef with a higher probability of success than if acoustic cues were not present. In our model, we assumed that fish behaved with positive phonotaxis when a sound was detected, but we emphasize that fishes can show varied behaviors in response to environmental sounds (Radford et al. 2011, Parmentier et al. 2015, Gordon et al. 2018). This assumption was necessary for our fourth objective and is a behavior that has been observed (as cited above). Our model is not species-specific, and we assume that the ranges of sensory and orientation behaviors of species in Almirante Bay are similar to those generally discussed for coral reef fishes (Montgomery et al. 2006, Atema et al. 2015). We simulated fish moving across a seascape in search of a reef settlement site during the latter portion of their pelagic stage. Fish moved as a correlated random walk (Codling et al. 2004, Berenshtein et al. 2018), which became biased in the direction of the reef if an acoustic cue was sensed. We defined cue detection as coming within 100 m of the reef at a time step when a cue was present. We set a static detection distance because, as previously discussed, without knowing the source level of these sounds and the transmission loss specific to this environment, we cannot predict the distance at which the sounds will fall below the hearing threshold. Notably, we did not select any hearing thresholds for the simulated fish, but rather set a static detection distance that we assume is a function of some source level, propagation loss, and hearing sensitivity. Thus, our model results are not specific to either pressure or particle motion hearing thresholds (Nedelec et al. 2016). Our detection distance of 100 m implies that sounds could be detected in the far-field of the source through interaction between the swim bladder and otoliths (Popper & Lu 2000, Atema et al. 2015). As the fish gets closer to the sound source, particle velocity would become an increasingly stronger stimulus. We used a conservative detection distance because we wanted to test the hypothesis that even short-range acoustic cues could improve the success of larvae finding the reef.

Simulated fishes behaved in accordance with the conceptual model of the 3-phase pelagic stage of larval fishes proposed by Huebert & Sponaugle (2009). After the first phase, which includes non-motile eggs and pre-flexion larvae (not included in our simulation model), the fish is capable of active swimming. What differentiates the second and third phases of the pelagic stage is the availability and detection of cues; in Phase 2, the fish is essentially performing a random search that may bring it within sensory range of reef-based cues, but in Phase 3, fish are able to detect cues due to improved cue quality or sensory system development. Larval fishes have been observed to swim at high rates, with speeds increasing through development (Leis & Carson-Ewart 1997, Fisher et al. 2000), and in relatively straight paths (Huebert & Sponaugle 2009). To reflect this behavior, we modeled the fish moving at late-stage swimming speeds and in a direction drawn from a von Mises distribution with a concentration value κ that allowed for significantly directional movement yet with random error (see the Supplement). When a fish encounters a cue indicating the position of a reef, it transitions to Phase 3, and the correlated random walk becomes biased. In our model, we simulated 2 different sensory behaviors that biased movement direction. First, we made the assumption that fish are able to determine the direction from which a sound is approaching (Schuijf & Hawkins 1983, Tolimieri et al. 2004, Fay 2005). Thus, the fish oriented in the appropriate direction towards the reef after cue detection. Second, we also tested the case where fish were able to detect the presence of the sound, but were unable to resolve the direction ('180° ambiguity;' Fay 1984, 2005, Myrberg & Fuiman 2002). Under this assumption, when a fish encountered a cue, there was a 50% probability that the fish would orient in the direction of the sound and an equal probability it would orient in the opposite direction. Under either assumption, the fish reverted back to Phase 2 if the cue became no longer present before it settled or if the fish swam out of the range of the cues. This is the scenario that we tested in the simulation model: the settlement success of fish switching between Phases 2 and 3 based on the position of the fish relative to cues that switched between being present and absent at a rate informed by observations in the recorded soundscapes.

The simulated fish were exposed to 1 of 6 cuescapes informed by the soundscapes we recorded in the 2015 long-term sampling. These cues exhibited spatiotemporal variability and fish switched between Phases 2 and 3 depending on the temporal pattern of the cues and the position of the fish relative to the reef. We tested the settlement success of 1000 fish each on 6 different cuescapes. We created a time series of cues that reflected the 10 d around the full moon period (peak of toadfish activity) and 10 d around the new moon (least toadfish activity) for the 2 sites that have the most (Seagal) and least (Finca) toadfish calls. In this way, we tested both the highest- and lowest-rate cuescapes produced by toadfish in our recordings, and we assume that cue rates observed at other sites and during other time periods produce results intermediate to these extremes. Given the prevalence of the relatively high amplitudes of the unnamed fish chorus at Finca, we also tested settlement success on the cuescape generated by this species during the full moon. We only tested 1 site and moon phase for this cuescape type because of the low temporal variation we observed in the acoustic behavior of this species between sites and across the daily time scale. Lastly, we tested the settlement success of larvae on a cuescape where a cue was available at every time step to simulate fish responding to snapping shrimps, whose snaps were observed multiple times in every minute of every recording at all sites. We compared the settlement success of fish responding to these cuescapes to a null model of fish navigating with no cue use (i.e. they are perpetually in Phase 2).

Our goal was to test how the temporal pattern of cues in these cuescapes influences settlement success. Thus, while we ran 1000 fish on each cuescape, not all larvae entered the sensory zone and therefore they never had an opportunity to be exposed to acoustic cues. As such, we analyzed results in 2 ways. First, we calculated the percent of fish that settled successfully out of all 1000 fish tested in a simulation. Second, we calculated the percent of fish that successfully settled out of the subset that entered the sensory zone, defined as coming within 100 m of the reef (i.e. within detection distance of the cues regardless of whether a cue was present). Using a Pearson's chi-squared test, we tested if the number of successful fish (out of those that entered the sensory zone) in each cuescape tested was significantly different from the number of fish successful in the null model of no cue use. For the null model, we also used the number of fish successful out of those that entered a radius of 100 m from the reef, even though no cues were available at any time. We made this comparison for both when fish could and could not resolve the direction of the cue. For each cuescape tested, we also compared these 2 scenarios using a Pearson's chi-squared test. We are not attempting to predict settlement success probabilities in nature, but rather these results are relevant to only the model environment.

## RESULTS

### Long-term data collection (2015)

Average power spectra (Fig. 2) show that the distribution of acoustic power across frequencies was very similar between sites. During the day and for frequencies less than about 1500 Hz, the spectrum was fairly flat with a slight rise in energy around 600 Hz, which is the contribution by the unknown species assemblage. At night, distinct peaks appeared in the frequency range 100–500 Hz, which are the harmonics of the calls produced by toadfish. Smaller peaks from the fundamental frequency and second harmonic were also present during the day due to isolated daytime calls. There was an elevation at night in the frequency band of the unnamed fish chorus, which was most pronounced at Seagal and Finca. Snaps from shrimp were observed between approximately 2 and 24 kHz; the amplitude of this band

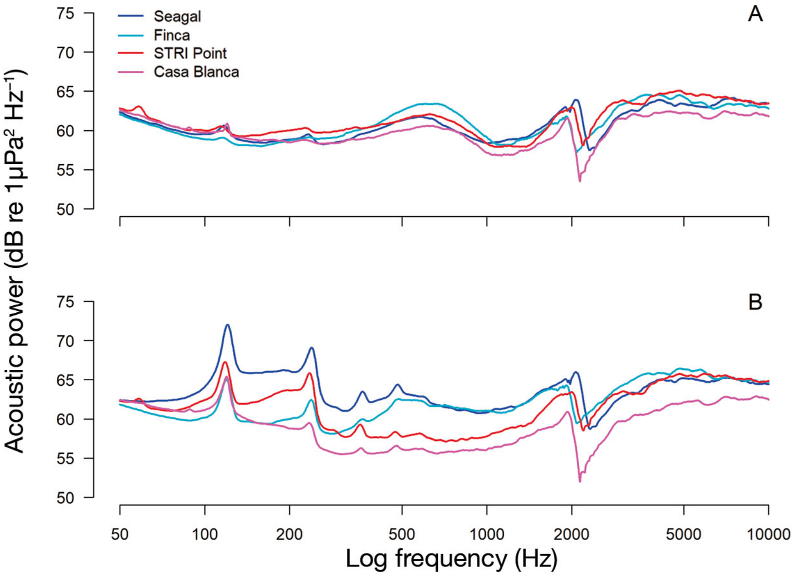

Fig. 2. Average (A) day and (B) night power spectra at the 4 primary reef sites. Power spectra were created for the recordings taken during the long-term sampling period (after the removal of boat and rain noise). To create a day and night mean power spectrum for each site, we averaged all power spectra representing recordings taken during the day (07:00 to 18:00 h), and all spectra for recordings taken during the night (18:20 to 06:40 h), respectively

increased at night compared to day. While there were no site differences in the shape of these spectra, there were differences in amplitude, which were most apparent at night. The feature appearing around 2 kHz was caused by boundary interference and was not biologically produced.

Four frequency groups emerged as the highest-amplitude content in the 4 soundscapes (Fig. 3), relative to the sounds in each 10 s subsample. The lowest frequency group was produced by fish calls, primarily toadfish, as reflected in the dominance of the approximate fundamental frequency (117 Hz) and second harmonic (230 Hz). This species occurred as the highest-amplitude contributor in at least 1 sample in all time bins at all sites. The next grouping going from low to high frequency was the assemblage of unknown species contributing to the noise centered at 600 Hz. The activity of this group was more prevalent at Seagal and Finca, and it occurred most often as the highest-amplitude sound in a subsample during daytime hours, compared to the 2 low-coral-cover sites. The chorus of the unnamed fish species elevated the frequencies greater than approximately 1250 Hz so that they occurred as the highest-amplitude sounds around midnight at all sites. Shrimp snaps were continuously present, and the lower frequencies of these broadband snaps, which occurred as the highest-amplitude content greater than 1500 Hz, were the highest-amplitude sounds in a subsample in nearly all time bins at all sites. The time bins when shrimp snaps never occurred as the highest-amplitude sounds in a subsample (with the exception of Casa Blanca) were in the early night hours (approximately 19:40 to 21:40 h, site dependent) when toadfish were the most active.

There was a consistent temporal pattern across sites for each of the taxa groups tracked through time using the sound-source signals. Here we show plots for the 2 sites that best display the range of variability in acoustic behaviors observed for each group, and the plots for the other 2 sites can be found in Figs. S2–S4 in the Supplement. While shrimp snaps were observed to occur in every recording, there was a peak of activity at dusk and dawn and higher ampli-

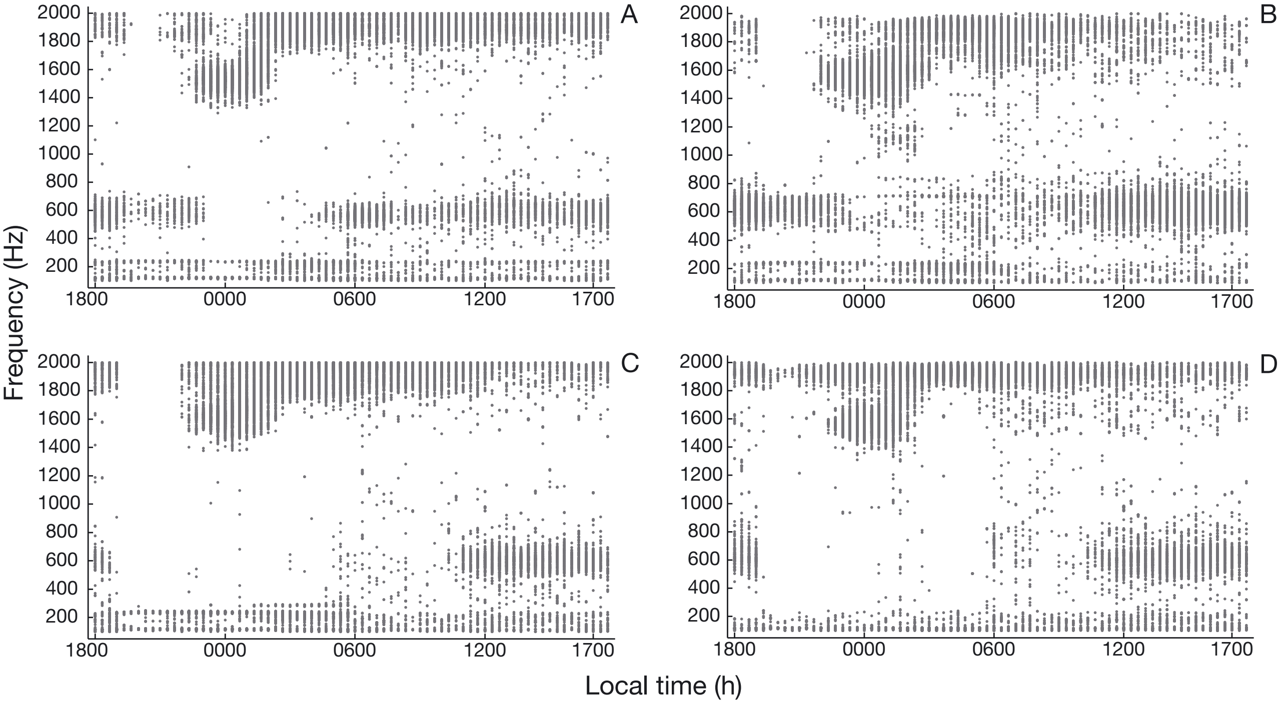

Fig. 3. Highest-amplitude frequencies observed in the 4 reef soundscapes. The recordings taken during the long-term sampling period (minus boat and rain noise) were divided into 10 s subsamples, a power spectrum was calculated for each subsample, and the frequency with the highest amplitude in each power spectrum was collected. The hydrophone at each reef site recorded a 4 min sample 72 times during each 24 h period during the approximately 6 wk long deployment. Each of these 72 recording periods is on the *x*-axis, and the frequencies with the highest amplitude observed in all of the subsamples recorded during each of those periods is plotted on the *y*-axis. Four main taxa groupings emerged. Going from low to high frequency, these are: toadfish *Amphichthys cryptocentrus*, the 600 Hz unknown species assemblage, the unnamed fish chorus around midnight, and snapping shrimps. (A) Seagal and (B) Finca are high live-coral-cover sites and (C) STRI Point and (D) Casa Blanca are low live-coral-cover sites

tudes at night compared to day (Fig. 4, Fig. S2). The magnitude of this diel difference was site dependent and the largest difference was observed at Finca (Fig. 4A), a high-coral-cover site, and the smallest difference was observed at Casa Blanca (Fig. 4B), a low-coral-cover site. This group produced relatively consistent peak levels from day to day with spatial differences in maximum amplitude (Fig. 4C,D, Fig. S2C,D). Vocalizations from the unnamed fish species were absent during the hours outside their nightly chorus, and they were more prevalent (considering relative amplitude) at the higher-coral-cover sites of Seagal and Finca (Fig. 5 and Fig. S3) compared to STRI Point and Casa Blanca (Fig. 5 and Fig. S3), the low-coral-cover sites. Nightly peak amplitude levels varied day to day (Fig. 5C,D, Fig. S3C,D), but this variation did not appear to follow the lunar cycle. This observation is contrary to that observed for the toadfish vocalizations (Fig. 6C,D, Fig. S4C,D), which reached peak levels at all sites around the full moon. The strength of the lunar relationship and chorus amplitude were site-dependent, with the strongest lunar pattern and highest amplitudes occurring at Seagal and the weakest pattern and lowest amplitudes occurring at Finca. Toadfish began calling around 19:00 h at all sites, shortly after which maximum amplitudes were reached (Fig. 6A,B, Fig. S4A,B). Thereafter, calling declined through the remainder of the night, and there was evidence of a weak predawn increase in call production at select sites. Isolated calls were observed during the day. For all taxa groups, the peak of acoustic activity was out of phase with the peak of small boat activity (Figs. 4–6, Figs. S2–S4).

The recorded amplitudes of the maximum amplitude events (Fig. 7) show that even sounds selected as the highest amplitude in a 10 s subsample may not have a high amplitude relative to other sound sour-

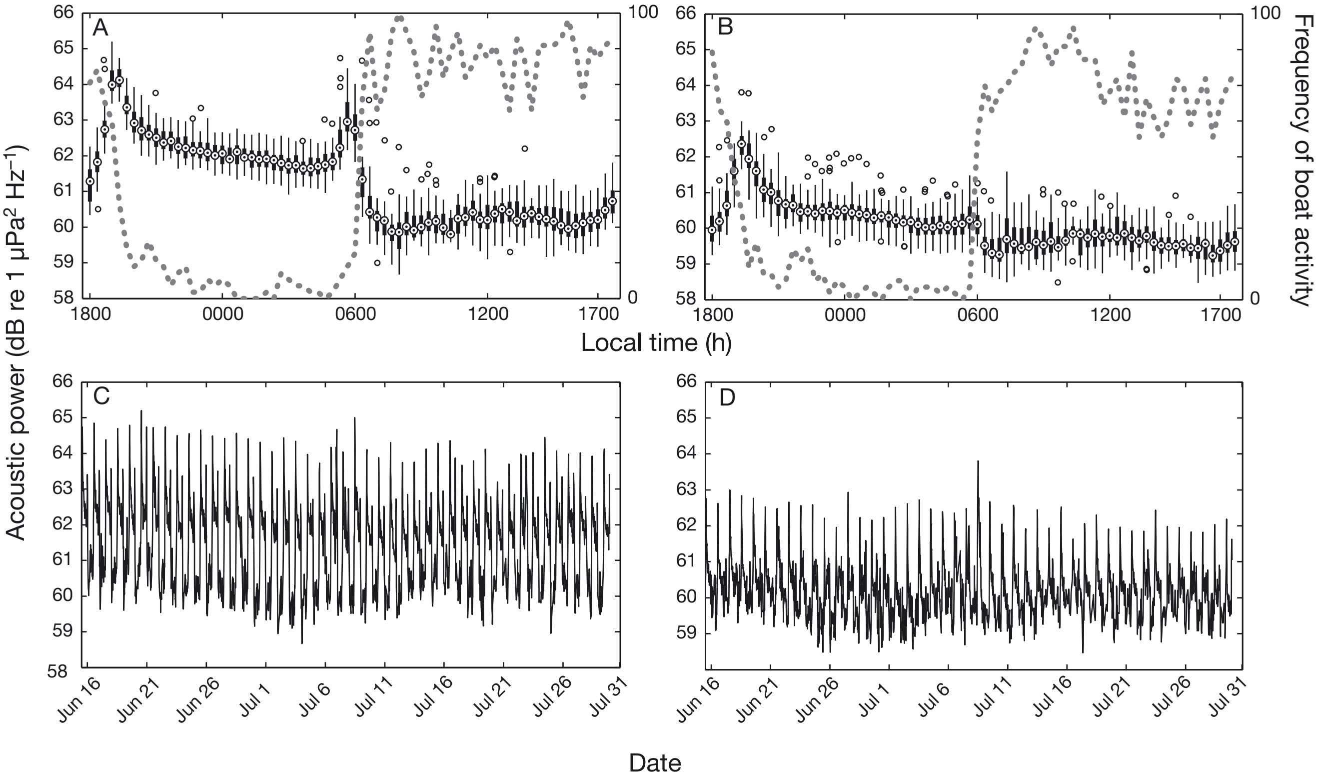

Fig. 4. Temporal variation in the acoustic behavior of snapping shrimps. The shrimp signal, defined as the average amplitude of the frequencies between 7.5 and 20 kHz, was calculated for each power spectrum for all samples collected in the long-term recordings at the 4 primary reef sites (after the removal of boat and rain noise). Each boxplot in (A) Finca (high coral cover) and (B) Casa Blanca (low coral cover) describes the amplitude of this signal for all samples recorded during each of the daily 72 recording periods on the *x*-axis. The frequency of boat activity is plotted as the gray dots; this represents the percentage of samples recorded at each of the 72 time periods where a boat was observed. Black dot in white circle = median; box = 25th to 75th percentiles; whiskers = most extreme data points not considered as outliers; open circles = outliers. (C) Finca and (D) Casa Blanca represent these same data, but not binned by time; plotted is the time series of the shrimp signal from the beginning to the end of the sampling period. The plots for the other 2 sites (Seagal and STRI Point) are given in the Supplement (www.int-res.com/articles/suppl/m605p173_suppl.pdf

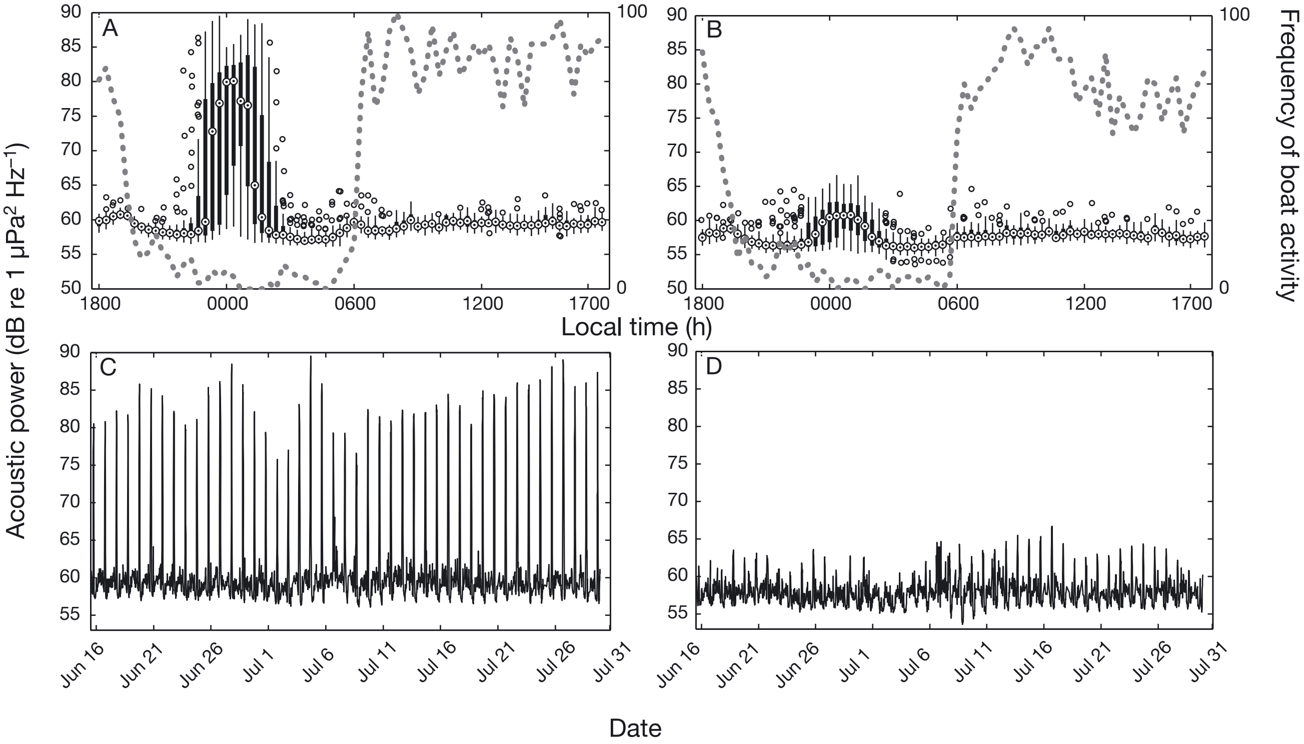

Fig. 5. Temporal variation in the acoustic behavior of the unnamed fish chorus. The signal for the chorus produced by this species was defined as the average amplitude of the frequencies between 1 and 2.2 kHz. The chorus was observed only in the hours around midnight; the boxplots for the other time bins represent ambient sound levels at these frequencies and/or small overlap with the signal for the shrimp-generated frequencies (small crepuscular peaks). See legend of Fig. 4 for a description of these plots. (A,C) Finca, (B,D) Casa Blanca. The plots for the other 2 sites (Seagal and STRI Point) are given in the Supplement

ces when the entire soundscape is considered. The sounds generated by the snapping shrimps and the 600 Hz species assemblage in general are low amplitude relative to the toadfish-generated sounds. The toadfish calls are the highest-amplitude events at all sites except Finca, where the highest-amplitude content is generated by the unnamed fish chorus.

## Short-term data collection (2013)

### Moon-phase survey

The dominant soniferous species observed during July 2013, toadfish and snapping shrimps, were the same species observed during July 2015 for samples taken at the same time of day. The 2013 power spectra revealed similar patterns as seen in the 2015 long-term data (Fig. S5). The site rank of toadfish activity was consistent between years, with Seagal having the highest, followed by STRI Point, Casa Blanca, and lastly Finca. The shrimp activity was highest at the 2 high-coral-cover sites in 2013 and clearly separated from the 2 low-coral-cover sites in the relevant frequencies in the power spectra. This was counter to the observations in 2015, where the 2 coral-cover classes did not group as clearly. In both years, Casa Blanca had the lowest amplitude of the shrimp-generated frequencies.

### Fifteen-reef snapshot

There was spatial consistency in the power spectra of the soundscapes recorded at the 15 reefs (Fig. S6). The same 2 taxa, snapping shrimp and toadfish, contributed to the soundscapes at all sites; the only other biogenic sound observed was produced by an unknown fish at Crawl Caye, a site located in the outlet between Almirante Bay and the Caribbean proper that presumably has a larger species pool than the reefs located in the bay. The mean amplitude of the broadband shrimp snap noise at the 15 sites ranged from 55.5 to 66.0 dB re 1 μPa$^2$ Hz$^{-1}$, and a median of 58.3 dB re 1 μPa$^2$ Hz$^{-1}$. The percent of time during the 2 min samples when a toadfish call was present

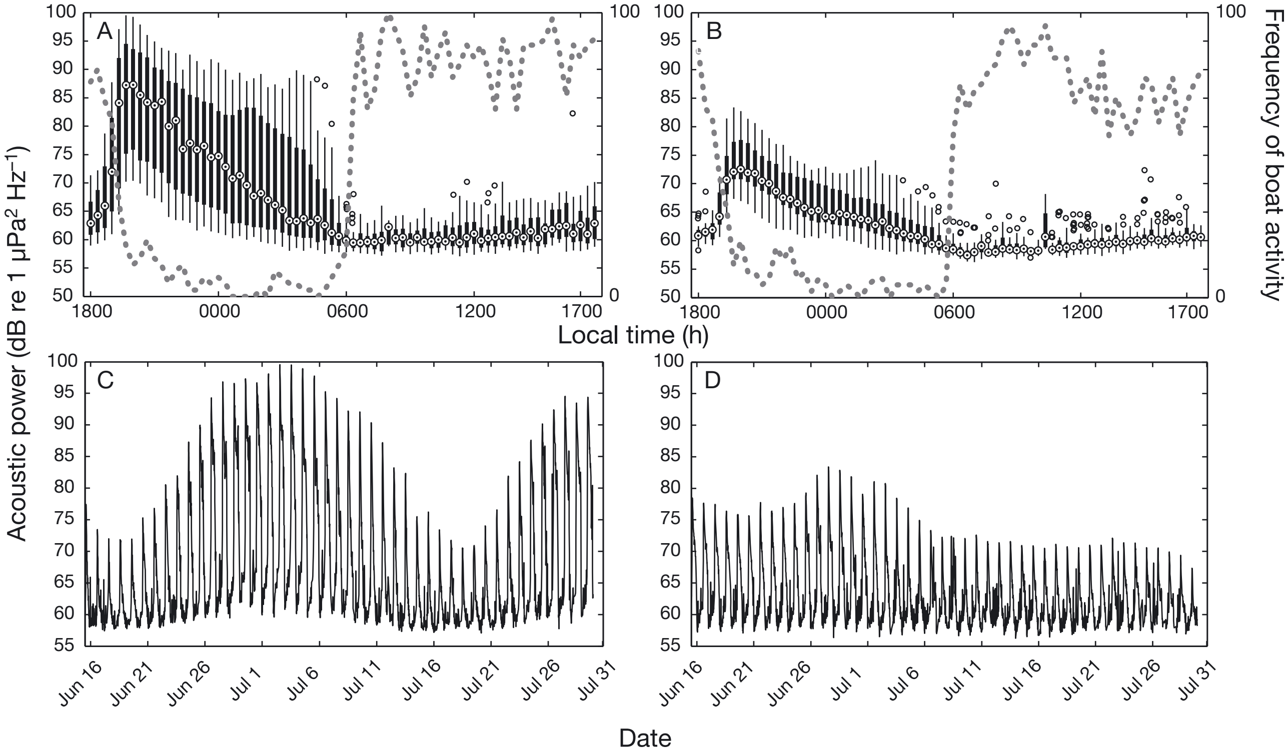

Fig. 6. Temporal variation in the acoustic behavior of the Bocon toadfish *Amphichthys cryptocentrus*. The signal for the toadfish-generated calls was defined as the maximum amplitude of the frequencies between 110 and 140 Hz, in order to target the fundamental frequency of the harmonic calls. See legend of Fig. 4 for a description of these plots. (A,C) Seagal, (B,D) Finca. The plots for the other 2 sites (STRI Point and Casa Blanca) are given in the Supplement

ranged from 0 to 100% with a median of 14.2%. There was no correlation between the shrimp signal and the percent live coral cover ($r = 0.047$, $p = 0.87$), dead coral cover ($r = 0.36$, $p = 0.18$), or sand ($r = -0.20$, $p = 0.48$). Similarly, there was no correlation between the toadfish signal and the percent live coral cover ($r = -0.035$, $p = 0.90$), dead coral cover ($r = -0.15$, $p = 0.60$), or sand ($r = 0.14$, $p = 0.61$).

### Individual-based simulation

The cuescapes tested in the individual-based model are shown in Fig. 8. Toadfish at Seagal during the full moon produced the highest rate of cues (not counting the constantly available cues produced by shrimp), at nearly 100% for the entire simulation (i.e. there was a cue present in almost every minute). This is counter to the other cuescapes, in which generally more cues were available during the night versus the day. While the average amplitude of the toadfish sounds at Finca was low relative to the other sites due to fewer fish calls in total (Fig. 6B), the presence of at least 1 call min$^{-1}$ in many of the samples produced a higher-rate cuescape on average during the full moon than observed at either site during the new moon. The unnamed fish chorus produced the lowest-rate cuescape considering a 24 h time period, with cues available for a few hours around midnight each night and never present during the day hours.

We tested how these cuescapes influenced the settlement success of larval fish using an individual-based model. Out of all 1000 fish and across cuescapes, 15.4–33.8% were successful (settled on the reef) across the simulations where fish could resolve the direction of the cue. For the fish that had 180° ambiguity in direction, 12.1–24.9% were successful. This is compared to a 9.4% success rate of the fish without exposure to cues (null model). Differences observed between cuescapes are significant both when fish had the ability to resolve direction (Pearson's $\chi^2 = 271.94$, df = 6, $p < 0.0001$) and when they did not ($\chi^2 = 166.31$, df = 6, $p < 0.0001$). Across cuescapes, approximately one-third of the fish entered the sensory zone and had the potential to be exposed to an acoustic cue. Of these fish, 51–100% were successful when they could resolve the direction of the cue (Fig. 9). For the fish that had 180° ambiguity in

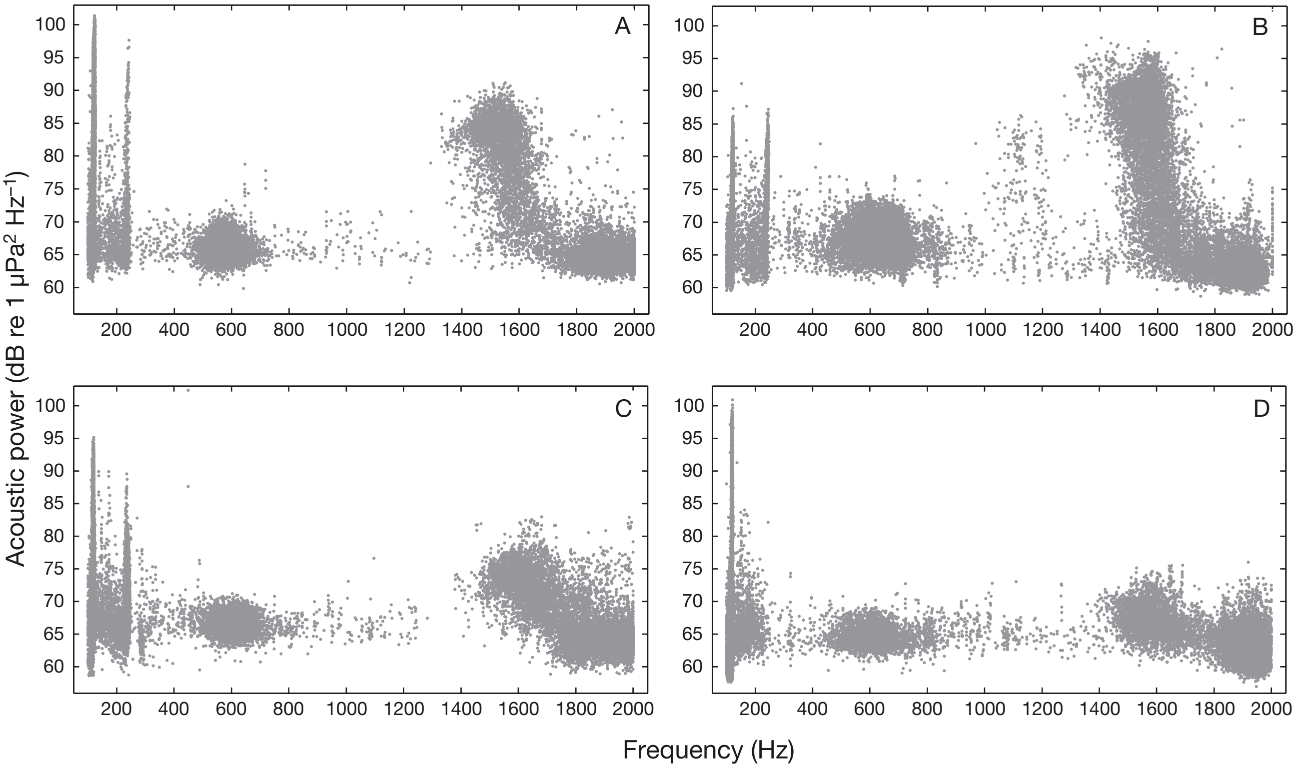

Fig. 7. Relative amplitude of the high-amplitude content. The data in Fig. 3 represent the frequencies of highest amplitude as identified in the 10 s subsamples. Here, these high-amplitude events are plotted again as acoustic power versus frequency to highlight the relative amplitude of these groups. Since we have no knowledge of the distance between the recorded sounds and the animals that produced them, we have no knowledge of the source level of these sounds. However, we can predict likely cues based on the relative amplitude of these groups. The vertical stacks of points in the lower frequencies are the fundamental frequency and second harmonic of the toadfish. The cluster of points occurring between 400 and 800 Hz is the 600 Hz unknown species assemblage. The cluster of points centered around 1600 Hz is the unnamed fish chorus. The points in the highest frequencies are the snapping shrimps. (A) Seagal, (B) Finca, (C) STRI Point, and (D) Casa Blanca

direction, 39.8–83.7% were successful (Fig. 9). The number of successful fish of those entering the sensory zone was significantly different between the cuescapes tested for both fish that could resolve direction ($\chi^2 = 557.02$, df = 5, $p < 0.0001$) and simulations with directional ambiguity ($\chi^2 = 222.54$, df = 5, $p < 0.0001$). All cuescapes enabled more fish to settle successfully compared to the null model in pairwise comparisons (Tables S1 & S2), regardless of the ability to resolve direction (Fig. 9). However, the inability to resolve whether the cue source was in front or behind resulted in a significant decline in success across the cuescapes tested (Table S3).

## DISCUSSION

As has been observed across the Caribbean, the reefs in Almiarante Bay have experienced anthropogenic disturbances that have altered the species composition and health of coral and the diversity and abundance of reef biota. Given that the biological soundscape is produced by fishes and invertebrates, our goal was to consider if, despite this degradation, there still existed sounds that could be possible acoustic cues for larval fishes during settlement. Further, we wanted to know if these potential cues varied across the reefs given the range of coral cover observed in the study area. We were not only interested in the presence/absence of these potential cues, but also how their intermittent nature and temporal pattern could influence successful navigation if they were used for reef localization. We found the same primary contributors to both the soundscapes and the predicted cuescapes despite the range in habitat quality across these sites. These sounds represented both high and low frequencies in the range of frequencies fishes can detect. The temporal pattern of these cues did vary between reefs, but all cuescapes

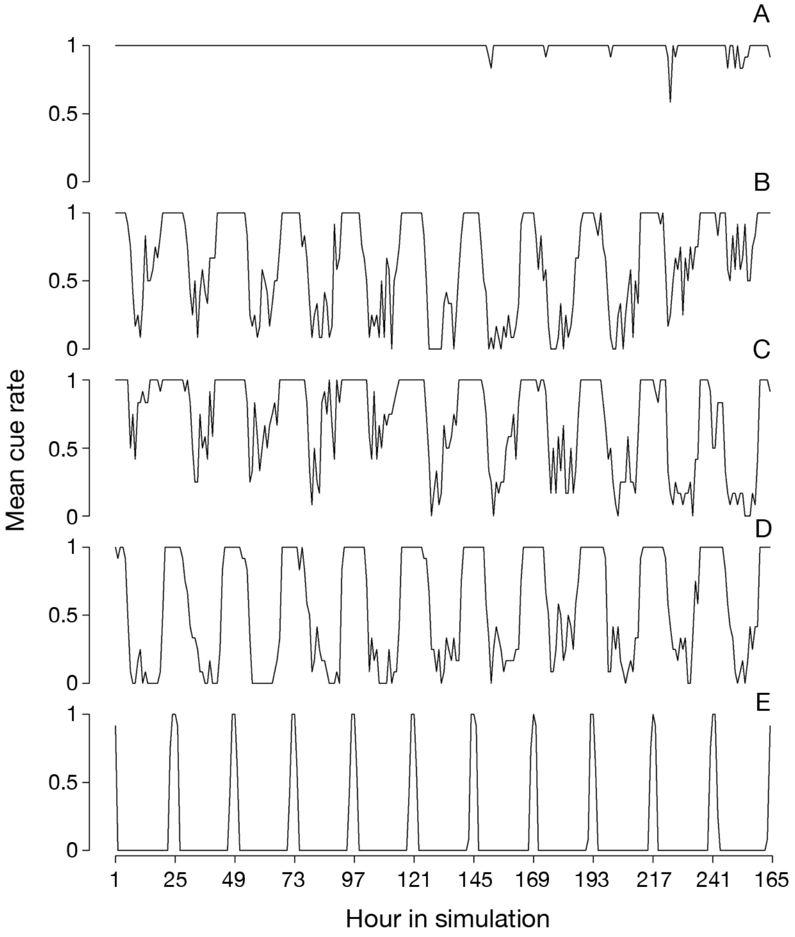

Fig. 8. Cuescapes tested in the individual-based model. The occurrence of the toadfish calls was quantified for the 10 d surrounding the full and new moons in the Seagal and Finca recordings, and the occurrence of the unnamed fish calls was quantified for the 10 d surrounding the new moon in the Finca recording. The hourly average cue rate is plotted here (number of minutes with a cue divided by 60) for simplicity, but note that the cues used in the simulation were informed by data at a higher temporal resolution. Cuescapes were generated by toadfish at Seagal during the (A) full moon and (B) new moon, toadfish at Finca during the (C) full moon and (D) new moon, and (E) the unnamed fish chorus at Finca during the new moon. The sixth cuescape treatment is not shown here and is the shrimp-generated cuescape (a cue available every minute). A null model of no environmental cues present was used as a comparison to these 6 treatments

allowed more settlement than predicted by a null model in the individual-based simulation. This suggests that, in this region, the acoustic cuescape may be resilient to habitat degradation. Here we first discuss the observed soundscapes, followed by our rationale in predicting the relative ability of these sounds to be used as potential cues. We lastly discuss how the observed temporal variation in the production of these potential cues influences reef localization by fish larvae in a model environment.

### Reef soundscapes in Almirante Bay

We observed very similar soundscapes at the 4 primary reef sites, despite the fact that Seagal and Finca represent 2 of the best-quality reefs in the bay and STRI Point and Casa Blanca 2 of the most degraded. Comparisons to recordings taken in 2013 suggest that the 4 primary sites may be representative of the region and the summer soundscape was temporally consistent across years. The lack of a relationship between sound sources and habitat quality, counter to other studies (Kennedy et al. 2010, Piercy et al. 2014), was also reflected in both sample years.

Our soundscape comparisons are largely focused on the contributions of individual species and species groups. Outside of some variation in the composition of sounds present in the 600 Hz species assemblage, we observed the same dominant soniferous taxa at the 4 primary reefs and evidence of this consistency across all 15 sites despite the wide range in coral condition. It is unlikely that these reef communities have not been affected by the sources of degradation the region has suffered given documented effects to the biological community (Cramer et al. 2012, Seemann et al. 2014, Altieri et al. 2017). We suggest that overfishing may have equalized the soundscapes despite the differences in habitat. This hypothesis is supported by Seemann et al. (2014), who predicted overfishing to have led to depauperate fish communities at both high- and low-quality reefs in this region. This prediction was supported by the higher abundance of both herbivorous and carnivorous fishes at a site protected from fishing for tourist diving. Considering the contributions of fishes to soundscapes (McCauley & Cato 2000, Amorim 2006, Tricas & Boyle 2014), overfishing may limit the ability of soundscapes to indicate habitat quality.

The majority of the sounds we observed at the 4 sites fell into 4 taxa groupings, and we were able to identify the source of just 2 of these. We can consider the life history requirements of these groups, snapping

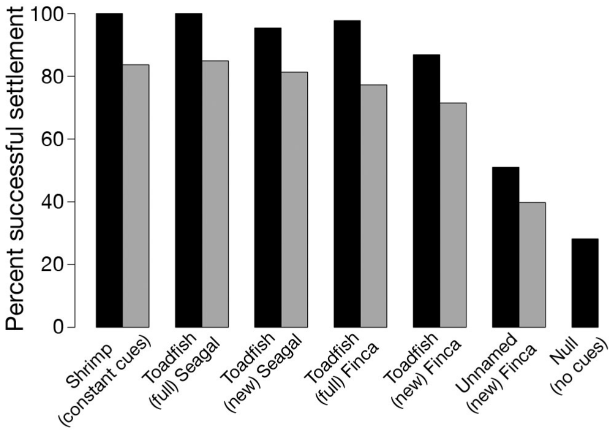

Fig. 9. Settlement success of model fish exposed to cuescapes predicted from the observed soundscapes. Here we considered only those fish that entered the sensory zone (defined as getting within 100 m of the reef). The black bars represent the fish that had the ability to determine the direction of the acoustic cue's source, and the gray bars represent those fish that had 180° ambiguity in determining cue direction (i.e. the fish could not determine if the source was located in front or behind). The treatments match the cuescape time series in Fig. 8 and are defined by the taxa that produced the sound, the site at which the potential cue was recorded, and the moon phase (new or full) at the time of the recording

shrimps and toadfish, to predict if we would expect a relationship with habitat quality. We observed almost continuous snapping activity from shrimps with distinct dawn and dusk peaks and elevated levels at night, which was also observed by Lammers et al. (2008). When we compared the amplitude of the shrimp-generated frequencies across the 15 sites, we did not observe a correlation with percent live coral cover (as in Kaplan et al. 2015, Nedelec et al. 2015). The results of the 15-site snapshot survey are supported in the long-term sampling where STRI Point, a low-coral-cover site, had on average similar amplitudes of the shrimp-generated frequencies as at the 2 higher-coral-cover sites. Live coral cover is not likely a habitat requirement for the shrimps in this region, likely a species assemblage of *Synalpheus*, which are eusocial and form colonies in sponges (Macdonald et al. 2006, Rios & Duffy 2007). Sponge density is high in this region (Seemann et al. 2014), and the overfishing of herbivorous fishes allows the overgrowth of palatable species (Loh et al. 2015), which can include hosts of *Synalpheus* shrimps (Macdonald et al. 2006). It seems unlikely that these shrimps have a reliance on live coral, and their acoustic activity may not necessarily be an indicator of habitat quality.

The second group for which we can consider the relationship between acoustic activity and habitat condition in light of predicted habitat requirements is the toadfish *Amphichthys cryptocentrus*. This species produced the highest-amplitude sounds observed on the reef, and was also observed by Staaterman et al. (2017) to be a dominant contributor to the soundscapes in this region. Similar to the other taxa groups, we observed a strong temporal pattern; peak amplitudes occurred after dusk with elevated levels throughout the night compared to the day, and calling behavior was at its maximum around the full moon. Lunar patterns have been observed in other toadfish species (Maruska & Mensinger 2009, Rice & Bass 2009). We observed spatial variability in the temporal pattern of calling behavior, which differs from the other groups which showed site-specific amplitudes but temporal consistency across sites. Toadfish species typically call in response to neighbors (Fish 1972, Remage-Healey & Bass 2005, Salas et al. 2018), and spatial differences in abundance and distribution may produce site-specific differences in calling behavior. This species likely takes advantage of the reef for its hard structure for burrow construction (Hoffman & Robertson 1983) and the availability of prey. Evidence of prey flexibility (Robertson 1987) suggests that *A. cryptocentrus* may be capable of maintaining population size despite shifts in the reef community. Therefore, for this species we would not predict a relationship between its acoustic signal and reef condition, and this is indeed what we observed when we compared coral condition to both measures of toadfish acoustic activity. Thus, both *A. cryptocentrus* and snapping shrimps are examples of species whose acoustic presence may not indicate the underlying condition of the habitat, despite being dominant components of the reef soundscapes. Both toadfishes (Greenfield et al. 2008) and snapping shrimps (Au & Banks 1998, Freeman et al. 2014 and references within, Bohnenstiehl et al. 2016) are common inhabitants of coastal environments, so these results have implications for both soundscape monitoring and habitat selection by larval fishes if they use these sounds as cues.

The other 2 taxa groups remain unidentified, limiting our ability to place their acoustic presence in an ecological context. The call characteristics and chorusing behavior of the fish that produced the chorus around midnight suggest it may be a Sciaenidae species (Ramcharitar et al. 2006). We observed higher amplitudes at the 2 higher-coral-cover sites compared to the 2 low-coral-cover sites, suggesting this species may be sensitive to reef condition. We cannot compare the 2015 observations to those in 2013 because the timing of the 2013 sampling did not sufficiently overlap with the time window of acoustic activity for this species. However, we did observe the presence of this species in recordings taken during the time of its activity in 2013 for another objective. These 3 species groups (shrimp, toadfish, and unnamed fish chorus) were most active acoustically at night and therefore out of phase with the peak of noise from small boat traffic, the only source of anthropogenic sound we recorded in this region. This suggests that the acoustic communication between these species may not be severely impacted by boating activity. The second taxa group that remains unidentified is the assemblage that contributed to the sounds in the 400–800 Hz frequency range with maximum amplitude around 600 Hz. We observed 3 or 4 distinct sounds across sites that occurred in this group, and these events typically occurred in isolation and not as chorusing behavior. This group may also be sensitive to reef condition because it was observed as the highest-amplitude sound during more time bins during the 24 h period at the 2 higher-coral-cover sites. However, not knowing the identity of these species limits our ability to interpret what their presence might indicate in an ecological context, highlighting the importance of improving our knowledge base of underwater biological sound sources (e.g. Tricas & Boyle 2014).

### Predicting the function of sounds in the acoustic cuescape

We predicted the cuescapes by selecting from the soundscapes the highest-amplitude sounds in the frequency range to which fishes are most sensitive. Our goal was 2-fold: with knowledge of which sounds may be most likely to act as cues, we could (1) ask if these potential cues varied by reef condition, and (2) convert the recorded soundscapes into time series of cues for input into the simulation model to predict how different components of the cuescapes may differentially act as navigational cues, assuming positive phonotaxis. Larval reef fishes are generally most sensitive to frequencies between 100 and 300 Hz using either pressure or particle motion audiograms (Wright et al. 2005, 2010, 2011), and the louder the sound relative to a fish's perception, the higher the chance of detectability. As such, we conservatively predict the sounds most likely to be useful at distances relevant to navigation are the calls of the toadfish and the species that generates the midnight chorus. The lower-frequency harmonics of the toadfish calls are within the optimal sensitivity range for larval fish hearing, and will have less transmission loss compared to higher frequencies, making them more likely to be heard at some distance. Further, they occur mostly at night when larval fishes are most likely to settle (Robertson et al. 1988, Stobutzki & Bellwood 1998) and at high amplitudes relative to the ambient noise; the amplitude of the fundamental frequency can reach over 130 dB re 1 $\mu Pa^2\ Hz^{-1}$ (Salas et al. 2018). The unknown fish chorus is also produced at night, and while the frequencies of these calls are outside of the range to which fishes are most sensitive, the relatively high chorus amplitudes may increase the likelihood of this sound playing a role in the cuescape. Whereas toadfish try to avoid call overlap with neighboring fish (Fish 1972, Thorson & Fine 2002, Salas et al. 2018), we observed no such behavior for this chorusing species. Calls produced at the same time are more likely to increase the amplitude of these frequencies at distance, versus calls produced independently, allowing sounds that may be lower in amplitude in isolation to serve as a stronger cue when overlapping in chorus. Thus, the acoustic communication behavior of soniferous species is also important when considering the role they may play in the cuescape.

We predict that the relatively lower-amplitude sounds produced by the snapping shrimps and the unidentified 600 Hz assemblage are less likely to act as navigational cues for larval fishes, although they may still be detectable (Brumm & Slabbekoorn 2005, Lugli 2010) and used for other functions such as habitat selection (Simpson et al. 2008b). Snapping shrimps produce broadband snaps and occurred above approximately 1750 Hz within the frequency range we used to identify the high-amplitude content. These are frequencies to which larval fishes have low sensitivity, so high amplitude is required for these sounds to be detectable, especially at distance from the reef. While an individual shrimp snap has a high source level, the peak occurs at 2 kHz (Au & Banks 1998), well above the frequencies to which larval fishes are most sensitive. The low amplitudes at which we observed these sounds supports that these shrimp snaps would be unlikely to act as long-distance cues. This is also supported by their behavior; snaps occur in isolation, and *Synalpheus* shrimps typically occupy sponges and other crevices so their sounds will be reduced due to absorption or reflection by these materials. Lastly, we hypothesize that the 600 Hz species assemblage is unlikely to be a source of navigational cues due to this group's relatively low amplitudes at frequencies higher than those to which fishes are most sensitive.

In summary, we hypothesize that the high-amplitude, low-frequency fish-generated sounds are most likely to serve as navigational cues in the acoustic cuescape produced by the soniferous organisms on these reefs. These same cue sources were present at all 4 reef sites despite the variation in habitat quality, and these predicted cues improved settlement success in the simulation model. Thus, while arguably a greater diversity of acoustic cues was available before anthropogenic disturbance, we predict that even in present-day conditions, there remain sounds from which larval fishes may benefit. The availability of sounds spanning the range of frequencies that fishes can detect at both high- and low-condition reefs suggests that some components of the acoustic cuescape may be resilient to degradation in this region. Behavioral tests using larvae from this region would be required to assess if the sounds available in these soundscapes aid in either habitat location and/or selection. We will next consider how the spatiotemporal variation we observed in the potential cue sources may impact successful settlement under the assumption that they are used for orientation to reef habitat.

## Modeled settlement in response to the acoustic cuescape

We used a simplified movement model to investigate how acoustic cues may influence settlement success. However, we acknowledge that several factors influence settlement and that fishes most likely use a combination of different cue types (Atema et al. 2015). Of the 1000 fish we tested in each simulation, about one-third were successful for most treatments and we attribute this success rate to the specific parameters of the model, namely detection distance relative to 'dispersal' (distance started from the reef). However, our treatments are related to the cuescape, so it is most informative to calculate percent success out of those fish that actually entered the sensory zone. Here we focus on results from the simulations where the fish had the ability to determine cue direction. Out of those fish that entered the sensory zone and had a cue available at all times (e.g. the shrimp cuescape), 100% experienced successful settlement. When we consider the cuescape to be made of intermittent cues composed of the high-amplitude events, we predicted a decrease in settlement because a fish could either (1) enter and leave the sensory zone during a period with no cue production, or (2) lose orientation towards the reef in the interval between cues. We saw evidence of this occurring since the percent settlement fell below 100% for all cuescapes tested that provided less than constantly available cues. However, the magnitude of this decline depended on the species generating the cues, the reef, and the moon phase. For both Seagal and Finca, fish exposed to the toadfish-generated cue had greater settlement during the full moon because of a higher cue rate. Similarly, fish navigating in the cuescape produced by Seagal had greater settlement than those at Finca because the Seagal soundscape produced a higher rate of cues. A more significant decline in settlement success was seen for fish using the cuescape generated by the unnamed fish chorus, where only 51% of fish that entered the sensory zone were successful. When all cuescape treatments were compared to the null model of no cues, however, it is clear that having some cue enabled higher settlement, even if intermittent or present for only a few hours during a 24 h period. This remained true even if fish were unable to tell the direction of the cue. Regardless of the cuescape tested or the ability to orient, most fish failed because they did not encounter the sensory zone. This finding highlights the importance of understanding the distance at which cues (of any type) may operate and how this distance may change with reef degradation. It also suggests that even with ambiguity in determining cue direction, acoustic cues still could improve settlement success.

The different taxa groups created cuescapes that varied in their ability to orient larvae to the reef. If we assume that larvae respond with equal positive phonotaxis to all of the observed cue sources tested in the model, the snapping shrimp cue enables the greatest settlement success, followed by the toadfish, and lastly the unnamed fish chorus. The shrimp cue was constantly available at all sites, and the lack of a relationship between cue rate and habitat condition suggests that if fishes used this cue they would be equally likely to settle on low- or high-quality habitat. The acoustic behavior of the unnamed fish species did not vary temporally across the 4 sites, although higher amplitudes were observed at the 2 higher coral cover sites. Given the chorusing behavior of this species, it is possible that the detection distance of this cue may be greater at these sites, potentially increasing settlement at the higher-quality sites compared to the lower-quality sites. The potential acoustic cue created by toadfish did show temporal variation across the sites, and when we tested the 2 most dissimilar sites, we observed a small, but significant, difference in settlement success. The pattern of toadfish activity we observed showed that this potential cue was at its weakest around the new moon, which is the preferred settlement period for larval fishes (Robertson et al. 1988, Robertson 1992). However, the cue available during the new moon still enabled significantly more settlement compared to the null model. We observed the identity of the cue producers to be identical across sites, and all temporal patterns of these cues allowed more fish to settle successfully compared to the null model, regardless of the ability of fish to determine cue direction. These results suggests that the acoustic cuescape in this region has maintained biological sources of sound that could serve the function of guiding larval fishes to reef sites, despite a loss of coral cover and widespread overfishing. It is important not to discount the potential impact of the anthropogenic soundscape, namely here the presence of small boat noise. This interference was primarily present during the day, and reef fishes generally settle at night (Robertson et al. 1988, Stobutzki & Bellwood 1998). However, they are constantly navigating their environment, and the engine noise could interfere with the use of daytime cues and their overall ability to orient (Holles et al. 2013, but see Jung & Swearer 2011).

## CONCLUSION

Our results suggest that even short-distance reef-based cues, acoustic or otherwise, could serve a valuable function of attracting fishes to settlement habitat once they get within distance by chance or through the use of another cue type that may operate over larger spatial scales. When we consider acoustic cues as intermittent — as we observed in the recorded soundscapes — we introduce cue rate as an important cue characteristic to consider. Our results suggest that these acoustic cues need not be constantly present in order to be beneficial to settling larvae. All temporal patterns of these cues enabled improved settlement rates in the movement model. However, the predicted cuescapes are composed of sounds differing in frequency and amplitude, suggesting detectability at different spatial scales and different functions (e.g. navigation to the reef or selection of a settlement site after arriving). Further, different cue sources will likely be differently affected by human impacts. If larval fishes use as cues sounds from organisms that are sensitive to changes in habitat (e.g. potentially the unnamed fish chorus), then soundscapes from poor-quality habitat may limit recruitment of fishes and prevent larvae from falling into a habitat trap (Battin 2004). The habitat trap concept will apply only to species whose fitness is dependent directly or indirectly on live coral cover. On the other hand, such a mechanism could limit post-disturbance recovery (Gordon et al. 2018) of populations for species with more flexible habitat requirements. If the primary acoustic cue sources are not sensitive to changes in habitat (e.g. shrimps or toadfish), reefs representing a broader range of habitat conditions may be equally advertised by their acoustic cuescapes. In this study, we support that acoustic cues can be valuable components of the total cuescape fishes experience, even if detection distances are short and the cues are available only intermittently. This broadens the conditions under which acoustic cues may be relevant and important components of a fish's sensory world.

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