

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

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## *Full description of the Individual-based simulation*

We used an individual-based simulation model to test the role of acoustic cues in the settlement success of larval fishes. We describe this model using the short version of the Overview, Design Concepts, and Details (ODD) protocol described by Grimm et al. (2010) and as found in Jovani & Grimm (2008).

*Purpose:* The purpose of this model is to test the hypothesis that transient, intermittent acoustic cues produced at the reef improve settlement success by indicating the position of the reef. 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.

*State variables and scales:* The entities in this model are larval fish navigating the seascape in search of a reef on which to settle. Each fish is characterized by its spatial coordinates on the seascape, which is initially a 2000 meter x 2000 meter grid. Fish can travel beyond this area but cannot cross the y-axis, which represents land. The reef is considered a fringing reef and is at the origin. The model is discrete time and each time step is one minute.

*Process overview and scheduling:* We ran 1000 fish per simulation, and each fish was run independently. In each time step a fish's position is updated. A new direction of travel is chosen using a correlated random walk that is biased towards the reef if the fish is exposed to an acoustic cue in that time step. The fish then travels a defined step length in the new direction of travel. This is repeated until 1) the fish reaches the reef, as defined by coming within one step length of the origin (reef), 2) the end of the simulation is reached, as defined by the pelagic larval duration (PLD), or 3) the distance between the fish and the reef becomes so great it would be impossible for the fish to reach the reef in the time it has left remaining in its PLD.

*Design concepts:* The probability of fish successfully reaching the reef is an emergent property resulting from the swimming behavior of the fish and the pattern of acoustic cues produced at the reef. We assume the fish are adapted to detect and respond to reef-based acoustic cues (Tolimieri et al. 2000; Leis et al. 2002; 2004; Simpson et al. 2005; Huijbers et al. 2012; Parmentier et al. 2015) using the particle motion component of sound or the oscillatory behavior of the swim bladder for pressure detection (Popper & Lu 2000). This latter mechanism is possible because the small size of larval fishes places the swim bladder in very close proximity to the otoliths, at distances similar to that seen achieved by anterior swim bladder extensions seen in adult fishes (Schultz-Mirbach et al. 2012; Atema et al. 2015). This pressure detection mechanism would allow larval fish to detect potential acoustic cues at distance, enabling navigation and increasing the probability of a fish successfully locating reef habitat. Successfully settling on a reef is the objective of the model fish, and is considered achieved if the fish travels to within one step-length of the reef. We tested the impact of acoustic cues on fish settlement under the assumptions that fish can either determine the cue source's direction (Schuijf & Hawkins 1983; Stobutzki & Bellwood 1998; Tolimieri et al. 2004) or the fish can determine the direction of the cue source but with 180° ambiguity (Fay 1984; Myrberg & Fuiman 2002). In other words, the fish is unable to resolve if the source of the cue is in front of itself or behind. Stochasticity is present in the model in the starting position of the fish and the minute of the first day when orientation begins. For each fish we collect the starting location and time it began orientation on the first day, if and when the fish entered the sensory zone, if the fish was successful in reaching the reef, and if so the number of time steps it took.

*Initialization:* Each model run (one fish) is initialized by randomly choosing the x and y coordinates that represent the fish's starting location from within the initial seascape boundaries (2-kilometer square grid). The fish is also randomly assigned an initial direction of travel, and the minute during the first day when it begins to orient the seascape.

*Input data:* We defined the acoustic cues the model fish were exposed to by the distance at which the cues are first detected and the rate at which they were produced. The distance from a reef to which a reef-based sound is detectable by a larval fish is dependent on frequency dependent hearing sensitivity, the propagation

environment, and the background ambient sound level that may mask the sound. We assumed some combination of these factors produced cues that are detectable at a distance of 100 meters. We select this conservative estimate of detection distance in order to test the hypothesis that even short distance cues could still aid larval settlement. Support of this hypothesis would indicate that greater distances would further improve settlement success (compared to the null model of no cue use). Cue rate was informed by the long-term recorded soundscapes; we make the assumption that the highest amplitude content in the frequency range fishes detect are most likely to contribute to the cuescape. We assumed all frequencies to be equal in the behavioral response they would elicit from larval fish (but see Simpson et al. 2008). We used frequency to predict which sounds from the recorded soundscapes may be most likely to be detected at distance. The toadfish calls are the highest amplitude sounds produced at three of the four reefs, and the frequencies of these calls match the frequencies to which fishes are most sensitive (Wright et al. 2005; 2010; 2011). At the high coral cover site Finca, the unnamed fish chorus was observed at higher amplitudes than the toadfish. While the higher frequencies of shrimp snaps are least likely to be detectable at distance, we also tested fish responding to a cuescape with a cue available every minute, as snaps from shrimps were observed in every minute of every recording. As such, we used as cues the sounds produced by these three groups, which is a conservative assumption. If multiple taxa contribute to the cuescape, which is most likely the case, then we are underestimating the role of the cuescape in settlement.

We next describe the process of converting the observed temporal pattern of possible cues into model input. We created a cue time series for the 10 days around the full moon period (peak of toadfish activity) and 10 days around the new moon (least amount of toadfish activity) for the two sites that have the most (Seagal) and fewest (Finca) toadfish calls. We also extracted the occurrence of the unknown fish chorus for the period around the new moon for Finca, the site with the highest activity of this group. Each four-minute long wav file recorded during these time periods was detrended and the voltage was converted to pressure using the manufacture 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: 16384 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). We used all recordings as in most cases boat and rain events did not interfere with the visual detection of fish calls. For each recording we noted if there was at least one fish call occurring in each of the four minutes of the recording. If a call was present, we consider there to be a cue in that minute, and if there was no call observed, that minute has no cue. Each recording gives us four minutes of observation, and we repeated the four minute series of cues five times to produce a series of cues for that twenty minute time period. In a case where boat or rain noise did interfere with our ability to detect calls for any given minute, we used the nearest ten values both before and after the 'no data' value to inform the presence or absence of a cue. The probability that the 'no data' value would be replaced with the occurrence of a cue is equal to the percent of minutes with the observed sound in the twenty surrounding time steps. We also created a shrimp-generated cue time series; since there are multiple shrimp snaps available in every minute of every recording, this time series was created by having a cue available in every minute of the simulation. We compared the settlement success of simulated larval fish responding to these six cue time series to fish exposed to the null model of no acoustic cues.

*Submodel:* There is only one submodel, and this submodel determines how a fish moves across the seascape as it searches for reef settlement habitat. This model is inspired by Codling et al. (2004). The initial direction a fish travels is randomly chosen from 0 to  $2\pi$ . The step length is determined by the time step (1 minute) and swimming speed (0.2 meters/second; Leis and Carson-Ewart 1997). Fish move as a correlated random walk, which becomes biased in the direction of the reef if it senses an acoustic cue (i.e. is within 100 meters of the reef at a time step when a cue is present). In each time step, two possible movement vectors are chosen. The first is the step the fish will take if an acoustic cue is not present, and is chosen from a von Mises distribution with  $\mu$  equal to the angle the fish moved in the previous time step, and  $\kappa = 4$ . Biologically,  $\kappa$  represents the orientation and swimming ability of the fish. We chose  $\kappa = 4$  to match field observations of fish swimming along very straight paths and observations of larval fishes capable of swimming at speeds that enable significant horizontal movement (Leis et al. 1996; Leis & Carson-Ewart 1997; Stobutzki & Bellwood 1997; Huebert & Sponaugle 2009). However, our selection of  $\kappa$  was such to introduce error in the fish's orientation. To test this behavior we drew 1000 ten-step paths from the journey of a fish orienting without cues (null model) that failed within the ten day allowed time frame. We chose paths of a length of ten-steps because this represents ten minutes in the model. This allowed us to compare the distribution of turn angles to those observed to be non-random by larval fish swimming in the field over ten minute observations (Huebert & Sponaugle 2009). We tested if the mean direction of each set of ten angles was non-random using a Rayleigh test. Of the 1000 paths, 842 were significantly non-random ( $p < 0.05$ ), with a mean  $r$  statistic of 0.717 (sd = 0.19). Thus, the chosen value of  $\kappa$  allows fish to swim mostly non-randomly, as observed by fishes swimming in the field, but also produces random behavior that represents imperfect orientation and loss in maintaining directionality when fish tend to other survival tasks (e.g. feeding, fleeing predators).

The second possible movement vector represents the orientation of the fish if an acoustic cue is present in the current time step. The angle is also chosen from the von Mises distribution, with  $\mu$  equal to the angle the fish would need to swim to navigate towards the origin (reef) and  $\kappa = 4$ . If an acoustic cue is present, the fish makes the necessary correction in its current heading to swim in the direction defined by this vector. However, if the fish cannot resolve the 180° ambiguity in the direction of the cue source, there is a 50/50 chance this vector is flipped so that the fish will instead orient in the exact opposite direction. The y-axis represents land, and fish are prevented from crossing this axis by reflecting their ending position across the axis if a movement vector would place them in a position where  $x < 0$ . Fish have a pre-determined time span to find the reef, defined by their PLD, which is equal to ten days. PLD here is used not as the entire time the fish is in the pelagic zone (average of about 30 days (Brothers & Thresher 1985)), but rather the portion of its pelagic phase in which the fish has the capability to actively navigate the seascape in search of appropriate habitat (Phase 2 and 3; Huebert & Sponagule 2009).

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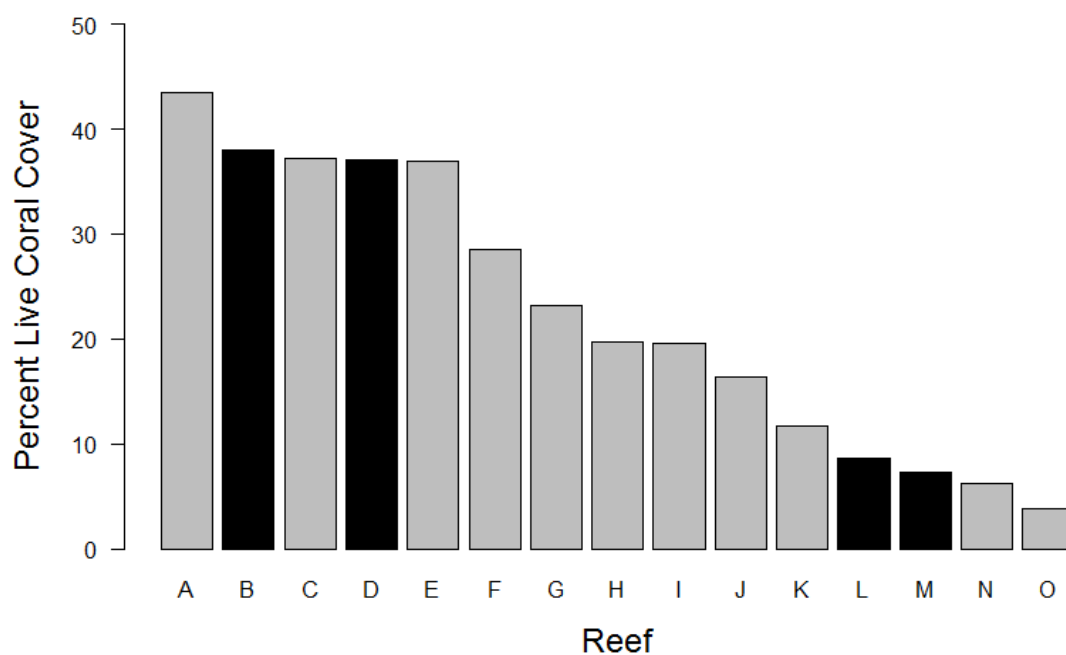


Fig. S1. Depth averaged percent live coral coverage of all fifteen reef sites. The percent live coral cover observed at the depths 2.4, 4.5, 6.1, 9.1, 12.2, and 15.2 meters were averaged to produce one value for each site. The sites in black represent the four primary reef sites. B = Finca, D = Seagal, L = STRI Point, and M = Casa Blanca

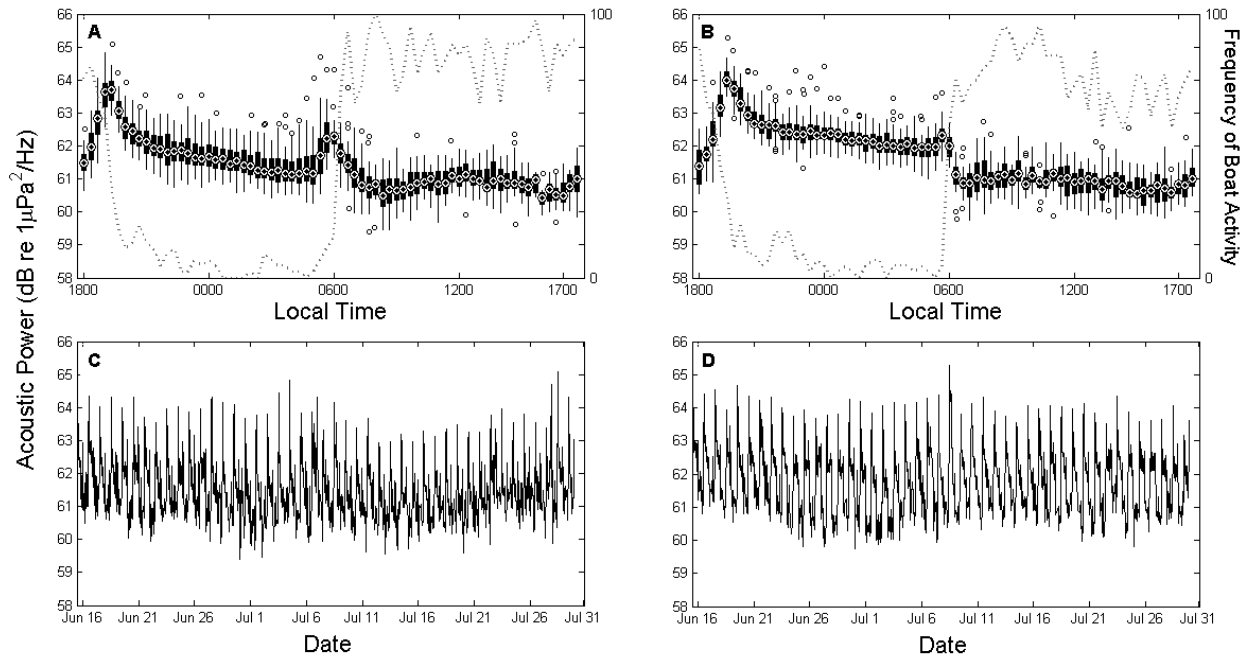


Fig. S2. Temporal variation in the acoustic behavior of snapping shrimps. The shrimp signal, defined as the average amplitude of the frequencies between 7.5 kHz and 20 kHz, was calculated for each power spectrum for all the samples collected in the long-term recordings at the four primary reef sites (after the removal of boat and rain noise). Each boxplot in A (Seagal; high coral cover) and B (STRI Point; low coral cover) describes the amplitude of this signal for all the samples recorded during each of the daily 72 recording periods on the x-axis. Panels C (Seagal) and D (STRI Point) 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 frequency of boat activity is plotted as the dotted gray line in Panels A and B. This represents the percentage the samples recorded at each of the 72 time periods where a boat was observed. Panels A and B: Black dot in white circle = median; box = 25 to 75 percentiles; whiskers = most extreme data points not considered as outliers; circles = outliers

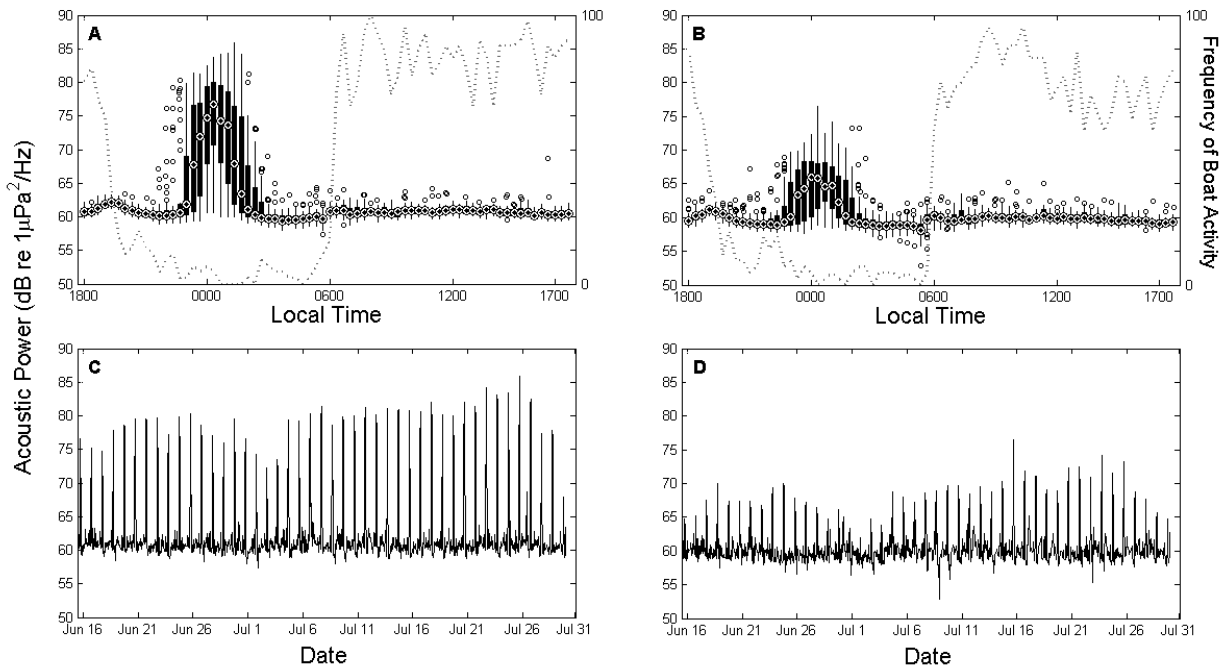


Fig. S3. Temporal variation in the acoustic behavior of the unnamed fish chorus. The signal for the chorus produced by this species was defined as the average amplitude of the frequencies between 1 kHz and 2.2 kHz. The chorus was observed only in the hours around midnight; the boxplots for the other 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 caption for Fig. S2 for a description of these plots. A & C) Seagal, B & D) STRI Point

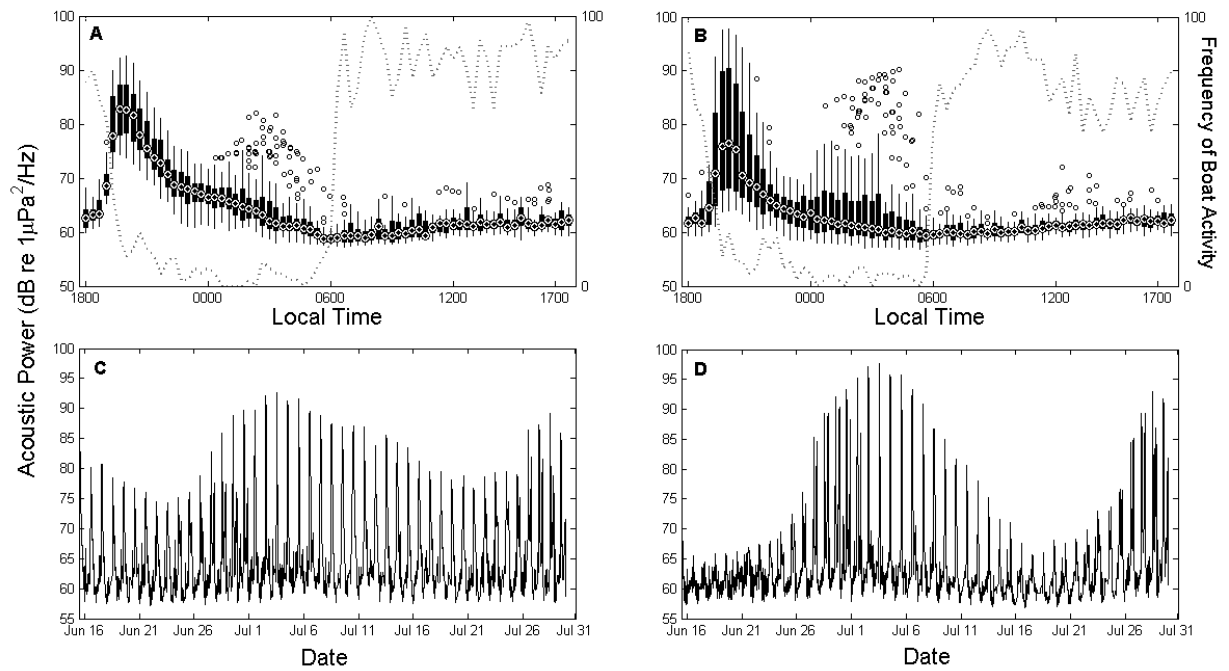


Fig. S4. Temporal variation in the acoustic behavior of the Bocon toadfish, (*Amphichthys cryptocentrus*). The signal for the toadfish-generated calls was defined as the maximum amplitude of the frequencies between 110 Hz and 140 Hz, in order to target the fundamental frequency of the harmonic calls. See caption for Fig. S2 for a description of these plots. A & C) STRI Point, B & D) Casa Blanca.

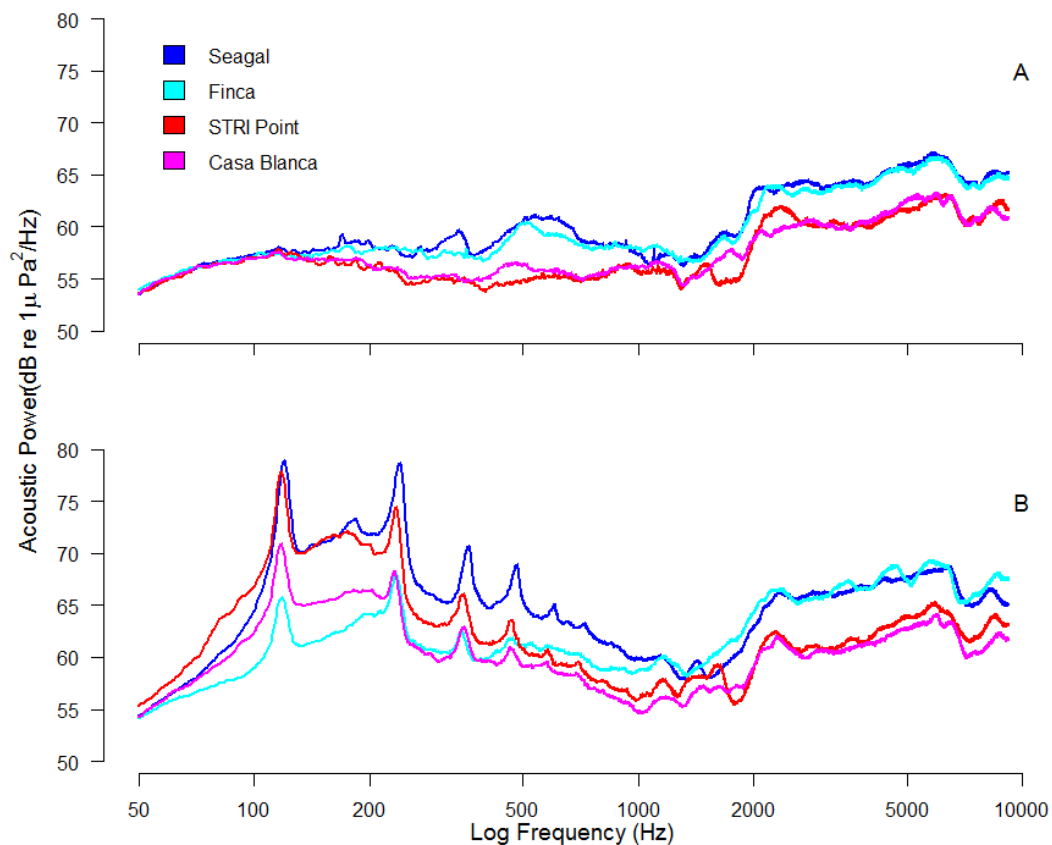


Fig. S5. Average power spectra of the moon phase survey in 2013. Acoustic recordings were taken at dusk and dawn during the new, first quarter, full, and second quarter moons in July 2013 at the four primary reef sites. The spectra for these four time periods taken at dawn (A) and dusk (B) were averaged for each site.

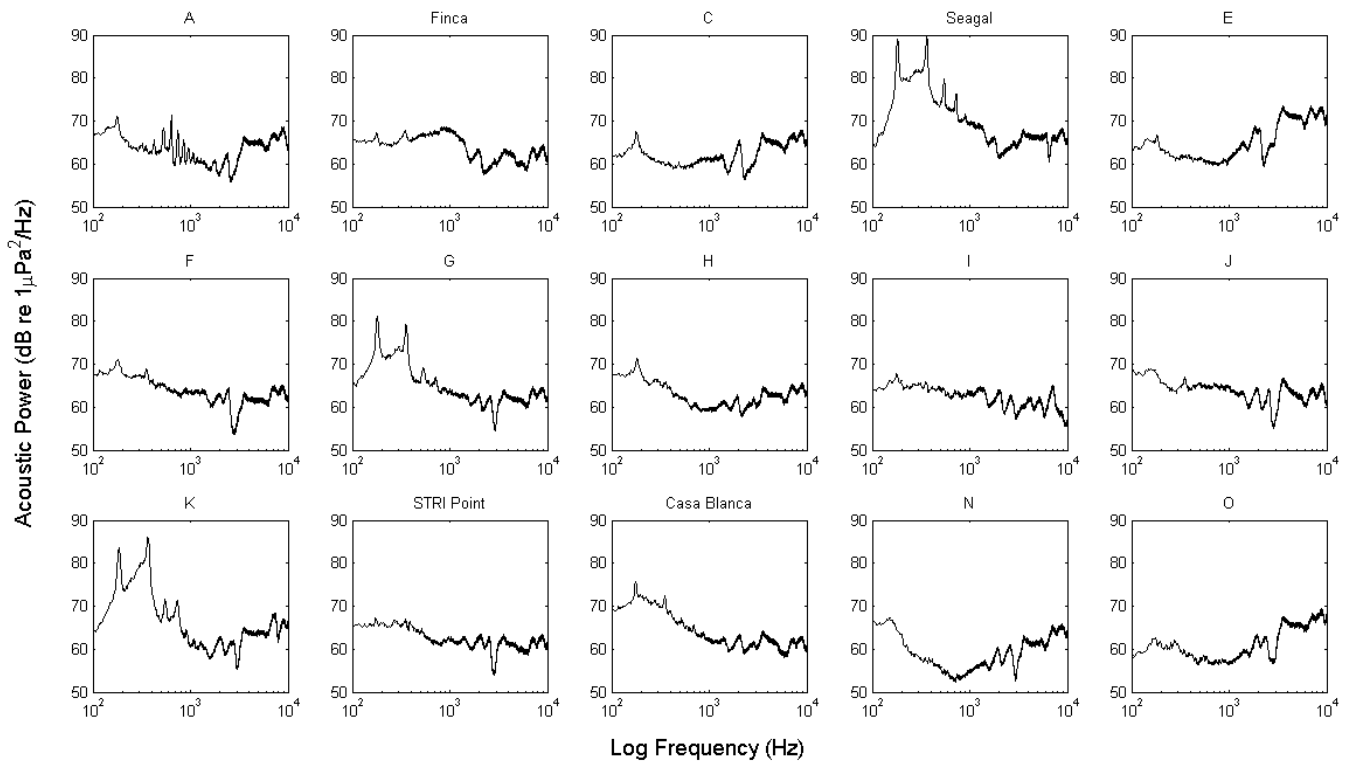


Fig. S6. Snap-shot acoustic sampling at fifteen reef sites in Almirante Bay. The fifteen reef sites were acoustically surveyed at dusk in July 2013, and an average power spectrum was calculated for the data collected at each site. The sites are organized by their depth-averaged percent live coral cover; the site with the highest coral cover (labelled A) is in the upper left panel and reading right to left and down the rows takes one to the site with the lowest coral cover (labelled O). These letters match those used in Fig. S1, and the four primary site names are explicitly labelled. The low-frequency peaks (e.g. at Seagal, sites G and K) are produced by the toadfish species *Ampichthyses cryptocentrus*. The higher amplitude of high frequencies is contributed to snapping shrimp activity. The feature at site A at approximately 700 Hz to 1000 Hz is produced by a fish species observed only at that site, which is located at the mouth of the bay and likely exposed to a greater species pool.

Table S1. Settlement success of the fish that had the ability to resolve the direction of the cue. 1000 fish total were run in each simulation, but only the fish that entered the sensory zone are considered here. A pairwise Pearson's Chi-Square test was used to test for significant differences between the number of fish that settled successfully in each cuescape treatment compared to the null model.

Cuescape	# Entered Sensory Zone	# Successfully Settled	Chi-square	P-value
Shrimp	295	247	191.94	<0.0001
Toadfish Seagal Full	293	249	200.39	<0.0001
Toadfish Seagal New	300	244	176.73	<0.0001
Toadfish Finca Full	322	249	156.26	<0.0001
Toadfish Finca New	319	228	120.17	<0.0001
Unnamed Fish Finca New	304	121	9.01	<0.01
Null (no cues available)	333	94		

Table S2. Settlement success of the fish that did not have the ability to resolve the direction of the cue. 1000 fish total were run in each simulation, but only the fish that entered the sensory zone are considered here. A pairwise Pearson's Chi-Square test was used to test for significant differences between the number of fish that settled successfully in each cuescape treatment compared to the null

Cuescape	# Entered Sensory Zone	# Successfully Settled	Chi-square	P-value
Shrimp	338	338	373.67	<0.0001
Toadfish Seagal Full	313	313	353.49	<0.0001
Toadfish Seagal New	303	289	295.83	<0.0001
Toadfish Finca Full	321	314	334.36	<0.0001
Toadfish Finca New	323	279	223.66	<0.0001
Unnamed Fish Finca New	302	154	33.53	<0.0001
Null (no cues available)	333	94		

Table S3. Results of pairwise Pearson's Chi-Square test comparing the number of successful settlers in simulations where the fish could resolve the direction of the cue and simulations where the fish had 180° directional ambiguity. The analysis included only the fish that entered the sensory zone.

Cuescape	Chi-square	P-value
Shrimp	57.21	<0.0001
Toadfish Seagal Full	48.47	<0.0001
Toadfish Seagal New	27.6	<0.0001
Toadfish Finca Full	60.08	<0.0001
Toadfish Finca New	20.58	<0.0001
Unnamed Fish Finca New	7.21	<0.01