



FEATURE ARTICLE

Effects of frequency-dependent spatial variation in soundscape settlement cues for reef fish larvae

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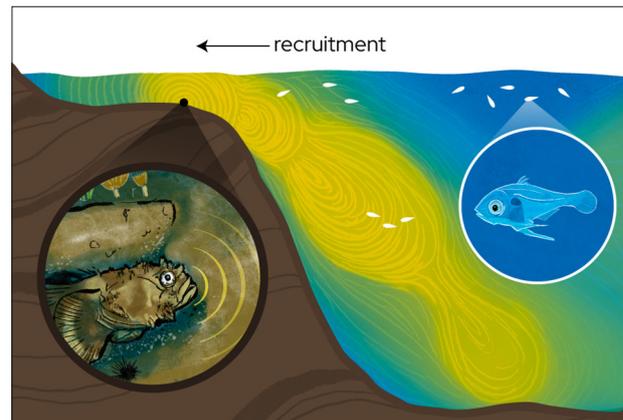
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ABSTRACT: The mechanisms that link reef soundscapes to larval fish settlement behaviors are poorly understood, yet the management of threatened reef communities requires we maintain the recruitment processes that recover and sustain populations. Using a field-calibrated sound propagation model, we predicted the transmission loss in the relevant frequency band as a function of range, depth, and azimuth to estimate the spatial heterogeneity in the acoustic cuescape. The model highlighted the frequency- and depth-dependence of the sound fields fishes may encounter, and we predict these complex spatial patterns influence how sounds function as settlement cues. Both modeling and field measurements supported a non-monotonic decline in amplitude with distance from the reef. We modeled acoustic fields created by sounds at frequencies from 2 common soniferous reef-based animals (snapping shrimps and toadfish) and estimated detection spaces of these sounds for larvae of 2 reef fish species. Results demonstrated that larval depth will influence cue availability and amplitude, and these spatial patterns of detection depend on cue frequency and the larval receiver's auditory sensitivity. Estimated spatial scales of detection coupled with field measurements suggest cue amplitudes might allow some larvae to detect reef-based sounds at a range exposing them to the predicted spatial variation in the acoustic cuescape. In an individual-based model, cues available to even the shortest modeled distances improved settlement success. Our results emphasize the need to consider the frequency- and depth-dependence of the acoustic cues larval fishes encounter to increase understanding of the role of soundscapes in larval settlement.



Spatial variation in the sound field is predicted to influence the reception and use of reef-based acoustic cues by larval fishes undergoing settlement.

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KEY WORDS: Larval fish · Settlement · Acoustic cues · Sound propagation · Soundscapes · Coral reefs · Modeling

1. INTRODUCTION

Larval reef fishes using the reef soundscape during settlement can be considered a 2-part system that functions to improve settlement success and help maintain fish populations. One part of this system is the reef soundscape, which is the combination of both abiotic (e.g. waves against the shore) and biotic

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sounds (Fay 2009, Pijanowski et al. 2011). Coastal habitats have distinct biogenic soundscapes produced by the local soniferous fish and invertebrate communities (Kennedy et al. 2010, Radford et al. 2010, Kaplan et al. 2015). These animals produce sounds under myriad behavioral contexts; some serve as intentional acoustic signals (e.g. mating calls), whereas others occur simply as acoustic by-products of activities like feeding and defending (Versluis et al. 2000, Amorim 2006, Radford et al. 2008, Tricas & Boyle 2014). At any point in time, the biotic soundscape is composed of only the acoustically active individuals, and this subset of the soniferous species pool can vary over relatively short time scales, such as one moment to the next or throughout the day, and over longer time scales influenced by seasonality and lunar phase (Staaterman et al. 2014, Bohnenstiehl et al. 2016, Rice et al. 2017, Salas et al. 2018a). This variation creates a temporally dynamic soundscape composed of sounds with unique amplitude, frequency, and temporal characteristics that can act as a source of sensory information for larvae.

The second part of this system is the receiver of these sounds, the pelagic-stage larval reef fishes that are competent to perceive and respond to acoustic stimuli. The subset of sounds present across both depth and distance from a reef that a given fish is able to perceive at any given time can be defined as the acoustic cuescape (Simpson et al. 2008a,b, Salas et al. 2018a). One possible function of acoustic cues is that they can aid larval reef fishes in their quest to locate and navigate to settlement habitat (Leis et al. 2002, Tolimieri et al. 2004, Simpson et al. 2005, Huijbers et al. 2012, Parmentier et al. 2015). Modeling studies simulating the movement of larvae in response to reef-based cues support an improvement in settlement success when cues can be detected at a greater distance from the source (Armstrong 2000, Codling et al. 2004, Staaterman et al. 2012). Acoustic cues may also improve a larva's ability to assess the appropriateness of potential settlement habitat, which is made possible by different coastal habitats having different soundscapes (Kennedy et al. 2010, Radford et al. 2010, 2014, Bertucci et al. 2015, Butler et al. 2016). For instance, after locating a reef, some species may be attracted to reef acoustic cues and undergo settlement, whereas other species may be repelled (Parmentier et al. 2015) and instead settle at coastal nursery habitats (Nagelkerken 2009). Acoustic cues may allow larvae to make these habitat assessments at distances mitigating the high risk of predation on reefs (Almany & Webster 2006, Simpson et al. 2013). While the specific functions of

acoustic cues remain unclear, it is likely that both the spatial availability (e.g. detection distance) and temporal patterns of cues determine the functions these sounds play in larval settlement behavior. These functions may not be static, as larvae have varied behavioral responses to these cues that may differ by time of day, species, life stage, and acoustic experience (Tolimieri et al. 2004, Simpson et al. 2010, Parmentier et al. 2015). Importantly, acoustic cues operate alongside other sensory sources of information that also function at different spatial scales (e.g. olfactory, visual, magnetic, celestial; Montgomery et al. 2001, 2006, Huijbers et al. 2012), in addition to the influence of oceanographic features (Staaterman et al. 2012, Suca et al. 2020).

Since both sound propagation (Jensen et al. 2011) and hearing sensitivity (Popper & Schilt 2008) are frequency-dependent, we would expect that the sounds created by the soniferous community, which vary in frequency and amplitude, operate at different spatial scales. However, to date, studies predicting the spatial scale of reef-based acoustic cues have not considered this frequency-dependence, since the geometric spreading models typically used provide coarse frequency-independent approximations to transmission loss (TL). Geometric spreading laws estimate propagation loss by assuming that a sound spreads spherically from its source until it reaches the boundaries of the waveguide (i.e. the sea surface and seafloor), after which it spreads cylindrically (Weston 1971). Sound propagating in a shallow-water waveguide will experience repeated interactions with the sea surface and seafloor as it propagates away from a sound source. These boundary interactions create complex interference patterns between upward and downward propagating sound waves, which become increasingly complex with increasing frequency. At each reflection from an interface, the amplitude and phase of the sound wave are perturbed. While the sea surface can be approximated as a pressure release interface for which all sound is reflected without loss, reflection from the seabed is associated with an angle-dependent loss (with the angle defined between the direction of the propagating wave and the seafloor). When the sound speed in the seabed is greater than that of the overlying water (as in the present study), the reflected wave is only strong for low grazing angles, and its amplitude is reduced by the seabed attenuation. Both the limiting angle of reflection (known as the critical angle) and the attenuation depend on substrate type (Jensen et al. 2011). While sediment sound speed is often assumed to be independent of

frequency (at least over small bandwidths), sediment attenuation increases with frequency. These factors create depth-dependent, spatially heterogeneous sound fields, indicating that the spatial availability of these sounds is likely complex and not well characterized by geometric models or considering detection distances alone (e.g. Mann et al. 2007, Wright et al. 2010). This is particularly important for larvae with depth preferences that vary ontogenetically, temporally, and/or with proximity to the reef (Fisher 2004, Leis 2004, Paris & Cowen 2004, Cowen 2006, Irsson et al. 2010, Lecchini et al. 2013), as these behaviors are likely to influence the acoustic cues larvae will encounter.

Modal theory allows for a more rigorous description of underwater sound propagation than geometric spreading laws. Under modal theory (Jensen et al. 2011), the number of propagating modes increases with increasing frequency, water depth, and sediment sound speed. Since each mode represents a wave front propagating through the waveguide at an angle less than the critical angle, the addition of more propagating modes leads to additional wave fronts that constructively and destructively interfere to create increasingly complex spatial patterns. Importantly, these patterns of TL differ significantly from the monotonic decrease in amplitude predicted by geometric spreading. This has important implications for the type of acoustic cuescape larval reef fishes likely experience, as it predicts they encounter a spatially heterogeneous sound field, with regions of high and low amplitude sound, that is dependent on frequency.

In general, we lack a fundamental understanding of which frequencies within the soundscape larval reef fishes actually use as acoustic cues and how this may vary with species and developmental stage. This knowledge gap makes it difficult to predict how degradation, by altering the acoustic cuescape through changing species composition (Piercy et al. 2014, Gordon et al. 2018), disrupts the system that links the soundscape to larval settlement. Degradation will have greater consequences to larvae that use acoustic cues if sounds at the specific frequencies that serve important functions during settlement are reduced in amplitude and/or in the rate of production. To counter these potential impacts, 'acoustic enrichment' has emerged as a means to potentially manage altered soundscapes and recover fish populations; the soundscape of a degraded habitat can be artificially enhanced with speakers broadcasting natural sounds recorded from healthy habitat to attract larvae (Brooker et al. 2016, Gordon et al. 2019). Rec-

ognizing the link between the soundscape and settlement allows us to pursue these management strategies, yet our lack of a mechanistic understanding of how the soundscape is perceived and used by fish larvae makes it difficult to design these artificial systems for maximum effect. This understanding is critical to increase our ability to both predict and mitigate changes in larval settlement caused by anthropogenically driven alterations to the soundscape, an increasingly recognized threat (Duarte et al. 2021, Ferrier-Pagès et al. 2021).

In this study, we predicted the spatial heterogeneity of the acoustic cuescape that larval reef fishes may encounter by using a parabolic equation (PE) acoustic propagation model, taking into account both frequency and depth of source and receiver. To consider if larval fishes might experience the predicted cuescape heterogeneity, we estimated the spatial extent over which larvae may perceive the predicted sound fields created by reef-based sounds. We used species-specific cue source levels and hearing sensitivities for larval fish receivers across a range of potential hearing thresholds (HTs) and specifically for 2 species observed at our reef study site during the study: *Chaetodon ocellatus* (spotfin butterflyfish) and *Abudefduf saxatilis* (sergeant major). These species have contrasting hearing abilities, and the families to which they belong, Pomacentridae and Chaetodontidae, have shown responses to acoustic cues (Tolimieri et al. 2004, Parmentier et al. 2015). *C. ocellatus* juveniles have relatively sensitive hearing that they maintain through ontogeny, whereas *A. saxatilis* has less sensitive hearing (Egner & Mann 2005, Webb et al. 2012). Thus, we predict that these 2 species experience different acoustic cuescapes, with *C. ocellatus* potentially experiencing more of the predicted spatial variation in cue availability and amplitude compared to *A. saxatilis*. The PE modeling approach is widely used in acoustic propagation modeling because it efficiently and accurately handles complexities associated with range-dependent propagation environments. The input parameters for the seabed properties using PE modeling were inferred from measured acoustic data. To consider additional environmental complexities not included in the model, we also conducted ambient noise transects and used these data to estimate the potential detection of the peak recorded amplitudes in the fish-generated frequency range. Lastly, to put our estimations of detection distances into the context of larval settlement, we used an individual-based model to consider how the model-predicted detection distances influenced simulated settlement success.

2. MATERIALS AND METHODS

2.1. Site description

We conducted sound propagation measurements at a coral reef in Almirante Bay, Bocas del Toro, located on the Caribbean coast of Panama. This reef is fringing and, similar to the reefs across the bay, it slopes from very shallow waters at the mangrove-lined shore down to about 18 m depth. The percent live coral cover, averaged over depth, is approximately 8.6%, with a greater percentage of live coral at shallower depths compared to deeper parts of the reef (Salas et al. 2018a). The condition of this reef reflects several sources of degradation impacting reefs in Almirante Bay (summarized in a fuller site description in Salas et al. 2018a, where the study reef is named STRI Point) and more broadly across the Caribbean, and include eutrophication, overfishing, sedimentation, and bleaching. Following a bleaching event in 2010, this reef recovered poorly, yet its soundscape is representative of those observed at reefs across the bay which share the same soundscape components irrespective of habitat quality. Two dominant soniferous species/taxa groups in the soundscapes across the region include the Bocon toadfish *Amphichthys cryptocentrus* and snapping shrimps (Alpheidae); the acoustic activity of these groups did not correlate with reef condition (Salas et al. 2018a).

2.2. TL measurements using speaker-playback transect

We conducted an acoustic transect using a known sound source: pure tones within the range of early life stage reef fish hearing (generally considered 100–2000 Hz, with higher sensitivity to the lower frequencies in this range; see references in Table S1 in the Supplement at www.int-res.com/articles/suppl/m687p001_supp.pdf, Colley et al. 2016) played from a broadcasting speaker. We played this repeatable sound source at increasing distances from the reef to measure the change in amplitude, then used these data to parameterize the sound propagation model. We conducted this acoustic transect on 24 July 2015 at 13:00 h, targeting a time when the reef soundscape was less active (Salas et al. 2018a) to maximize the detectability of the speaker signal. Employing the principle of reciprocity (Jensen et al. 2011), we deployed a hydrophone at the reef and performed the speaker playback from the boat. A hydro-

phone (nRUDAR, Cetacean Instruments; range: 1–22 050 Hz, sensitivity: -159.52 dB re 1 V μPa^{-1}) was placed in a stand that positioned the sensor 0.3 m above the substrate and deployed off the reef edge at a depth of 19.5 m. We used an underwater loudspeaker (Lubell University Sound UW30) hung facing downward from the boat to a depth of 3.05 m to broadcast the following pure tones at each transect position: 100, 200, 300, 400, 500, 700, 900, 1000, 1200, 1500, 1700, and 2000 Hz. The loudspeaker was connected to a marine amplifier (Pyle 240 W) powered by a marine boat battery, and the sound file was played using an MP3 player (Apple iPod Shuffle). The 12 tones were grouped into 3 sets of 4 frequencies, and the duration of each set was 1 min. This 3 min comb signal was repeated at each transect site a minimum of 3 times, with additional time added depending on the presence of potential noise interference such as passing boats. Transect positions are defined as the distance between the hydrophone at the reef and the locations where we extinguished the boat engine, anchored, and broadcast the comb signal. These positions were at distances of 63, 83, 126, 207, 315, 502, 805, 1508, and 1989 m. Depths at these positions ranged from 21.6–25.3 m, with an increase in depth with distance.

For each frequency set at each transect site, we identified and extracted from the analysis the data containing interference from boat traffic, which was especially high during daytime hours. The combined useable sections across frequency sets and sites ranged from 40–118 s (mean: 89 ± 30 s). At the 2 farthest transect sites, there was not sufficient useable data for all frequencies, especially frequencies <1000 Hz. We produced spectrograms of each section of useable data and extracted the frequency bins of the test frequencies. We calculated the mean and standard deviation across the time bins to obtain the mean acoustic power level for each frequency at each transect site. Since the source level of the speaker source was unknown, we compared the amplitude (received level) of each frequency at each transect site to the received level recorded at the first transect position. We used this relative received level term as our measure of TL (see Fig. 1); as such, it does not reflect total TL between the source and the receiver, but rather the change in sound level between each transect site and 63 m from the source (Site 1). There was variation in the received levels over the duration of the speaker playback (see Fig. 1), and we used the mean relative received level to calibrate the acoustic propagation model.

2.3. Acoustic propagation modeling

We used a parabolic acoustic propagation model (Collins 1993) to predict the frequency-dependent acoustic fields due to a point source as a function of range, depth, and azimuth resulting from sounds produced at the reef. The reef soundscape is the collection of sounds produced by soniferous animals that individually act as point sources. While some fish species produce overlapping calls that can lead to high-amplitude choruses at some times, many biogenic sounds are instead distinct, individual features in the soundscape (McCauley & Cato 2000, Tricas & Boyle 2014, McWilliam et al. 2017a, Bertucci et al. 2020). Further, only a subset of the reef-based sounds at any given time will have the amplitude and frequency characteristics to be detectable by a larval fish within sensory range. Therefore, from the perspective of a larval fish, the reef soundscape may, in many cases, provide intermittent cues versus a constantly present cue source. As such, we modeled sound propagation from an individual point source.

The site-specific bathymetry required by the model was digitized from a regional nautical chart (NOAA). To parameterize water sound speed, we measured the temperature and salinity every 2 m between the water depths of 2–20 m at each transect position using a YSI probe (YSI Pro2030). These data were used to calculate the sound speed profile at each transect position (Fig. S1). Since the maximum depth along the transect exceeded 20 m, we used the sound speed calculated for 20 m for depths >20 m. To infer sediment sound speed and attenuation, we performed a grid search to identify parameter values that produced the smallest error when comparing model-predicted TL to the TL measured in the field in the playback transect. For sediment sound speed, we first searched 20 linearly spaced values between 1500 and 1700 m s⁻¹ and for attenuation between 0 and 1 dB λ⁻¹. We followed this with a finer search of 20 linearly spaced values between 1540 and 1570 m s⁻¹ for sound speed and between 0 and 0.15 dB λ⁻¹ for attenuation. We calculated TL using all combinations of these 2 values for each frequency in the comb signal. The combination of sediment parameters that produced the lowest summed error between the modeled and measured TL across all frequencies and distances was 1557.4 m s⁻¹ and 0 dB λ⁻¹, and these values were used thereafter in the model. See Fig. 1 for best match of the model to the field measurements across the test frequencies. Again, the model-calculated TL does not reflect the total estimated loss over distance from source to receiver, but rather the

change in amplitude at each transect position compared to transect Site 1. We also compared the PE-modeled TL to that predicted by spherical and cylindrical spreading (see Fig. 2) by subtracting the TL predicted for each of these 3 models at each transect site distance from an estimated source level (SL). This SL was estimated by adding the frequency-specific TL predicted using the PE model for each frequency at the first transect site to the received levels measured at the first transect site. The final SL (131.5 dB re 1 μPa² Hz⁻¹) was calculated by taking the mean of the SLs calculated for each of the 12 frequencies. TL was predicted for spherical spreading using $TL = 20 \log_{10}(R)$ and for cylindrical spreading by using $TL = 10 \log_{10}(R)$, where R is the distance (in m) from the source (e.g. the transect positions).

We used the estimated values from the grid search to predict the TL and used that value of TL to predict the associated detection spaces of 2 reef-based sounds for early life stages of *Chaetodon ocellatus* (Webb et al. 2012) and *Abudefduf saxatilis* (Egner & Mann 2005). We defined the detection space as the 3-dimensional model space for a given frequency where the SL minus the TL predicted for that position is greater than the fish's HT at that frequency ($SL - TL > HT$). The angular resolution of this model space was 0.0982 radians, the horizontal resolution was 1 m, and the vertical resolution varied with frequency to allow, at a minimum, 10 samples wavelength⁻¹. It is in this space where we predicted a larval reef fish would be capable of detecting the reef-based sound. We estimated the detection space of a high- and low-frequency (relative to the range of fish-audible frequencies) sound source. For the low-frequency sound source, we used the mating calls of *A. cryptocentrus* because this species produced the dominant fish-generated sound in the soundscapes across this region (Salas et al. 2018a). We parametrized the SL of this sound using the mean amplitude at the fundamental frequency (128.3 dB re 1 μPa² Hz⁻¹ at 116 Hz) and second harmonic (126.5 dB re 1 μPa² Hz⁻¹ at 233 Hz) from calls recorded in the field outside of burrows of their own construction (Salas et al. 2018b). We did not consider the directionality of the calls (Barimo & Fine 1998) but instead assume in the model that the acoustic energy was directed directly off-reef towards the pelagic habitat. We used the sounds of snapping shrimps as an example of a source that produces high frequencies. These animals produce broadband snaps, with peak amplitudes occurring around 2–5 kHz (Au & Banks 1998, Song et al. 2021). For the SL of the 1 kHz component of a snap, we used the mean amplitude of 110.9 dB re 1 μPa² Hz⁻¹ at 1000 Hz as recorded from 2 snapping shrimp species (*Alpheus*

heterochaelis and *A. angulosus*) at 1 m distance in an approximate free field in a tank (Song et al. 2021). Larvae likely use the full audible bandwidth of these snaps, but modeling 1 kHz allowed us to consider the propagation of a high-frequency sound to compare to the low-frequency fish calls. We chose 1 kHz because this frequency is closer to a snap's peak frequency but is still within the range of audible frequencies for many early life-stage reef fishes (Table S1). For both the fish calls and shrimp snaps, we may be overestimating the amplitudes available to larval reef fishes, as these SLs are likely modified by sediments and reef structure before reaching the open water (see Text S1).

We modeled TL for the frequencies of 116 and 233 Hz (representing the toadfish source) and 1000 Hz (representing the shrimp source). Since these animals are distributed across the fringing reef slope, we investigated the effect of source depth by calculating TL with the sound source at a depth of 5, 10, and 20 m in the model. The position of these sound sources in the model was 0.1 m above the substrate. The modeled vertical resolution for these detection spaces was 0.5 m for both 116 and 233 Hz, and 0.15 m for 1000 Hz. We also used the PE model to look more generally at the acoustic fields produced by a source at a depth of 5, 10, and 20 m on the reef slope and at frequencies in the range of predicted hearing by fish larvae. To achieve a minimum of 10 samples wavelength⁻¹, the modeled vertical resolution was 0.375 m for frequencies of 100, 200, 300, and 400 Hz and 0.075 m for 0.8, 1, 1.5, and 2 kHz. For these frequencies, we show the spatial patterns of TL over the same radial used in the modeling of the fish and shrimp frequencies but do not consider detection spaces.

The auditory thresholds we used to estimate the detection space for *C. ocellatus* were measured from individuals with a standard length of 21–31 mm, and these fish were not distinguished between the larval and juvenile stages (Webb et al. 2012). Webb et al. (2012) observed similar hearing sensitivity across size, and the authors predicted this is achieved in the smallest fish by the short bladder-to-otolith distance and then later by the development of anterior bladder horns. Similarity of sensitivity across sizes suggests the measurements for the smallest age class in Webb et al. (2012) may reasonably apply to settlement-stage *C. ocellatus*. The auditory thresholds for *A. saxatilis* were measured from newly settled individuals 11–28 mm standard length (Egner & Mann 2005). Except for one case, the specific frequencies we used in this study (116, 233, and 1000 Hz) were not directly tested in these auditory studies. The audiogram for *C. ocellatus* was constructed using 6 frequencies, in-

cluding 100 and 200 Hz (for which thresholds were very similar) and 400, 800, and 1600 Hz (Webb et al. 2012). We interpolated the thresholds for the 3 test frequencies on the audiogram curve. We similarly interpolated the 116 and 233 Hz thresholds for *A. saxatilis* using the audiogram constructed by Egner & Mann (2005) composed of 5 frequencies, including 100, 200, and 400 Hz. The 1000 Hz threshold was tested for this species and we used that value directly. Comparisons between the 2 species were enabled because the audiograms for these 2 species were collected using very similar methodologies. For both species, we adjusted the thresholds by a reduction of $10 \log_{10}(\Delta f)$, where Δf is the critical bandwidth, assumed to be 10% of the center frequency (Yost 2000, Egner & Mann 2005). However, we did not further adjust the thresholds, as in Wright et al. (2010), to account for the observation that HTs obtained via behavioral methods are more sensitive than those obtained using electrophysiological methods by potentially as much as 10–30 dB (Gorga et al. 1988, Kojima et al. 2005, Lavender et al. 2014). As such, our predictions may be conservative if these electrophysiological thresholds underestimate larval hearing sensitivity, which has been studied for very few species; thus these thresholds should not be considered absolute. Due to uncertainties in larval fish hearing, we emphasize that the goal of estimating detection spaces is not to predict absolute detection distances, which could vary by orders of magnitude depending on choice of HT and modifications thereof. Instead, we used these methods to estimate plausible spatial scales of acoustic cues in the modeled environment for larvae with different hearing sensitivities, allowing us to consider how the predicted spatial heterogeneity in acoustic cue amplitude may affect soundscape use by larvae. For a discussion on our use of pressure auditory thresholds, see Text S2.

To take into account this uncertainty in larval reef fish hearing, we also used the PE-modeled TL to provide an estimate of detection distances across an HT range of 55–140 dB re 1 μ Pa. We found the maximum distance (capped at 8 km for this analysis and a minimum potential distance of 1 m) at which SL – TL > HT for the 3 sound sources across the 3 source depths and extracted the depth at which this occurred. To put this wide range of potential HTs into context and to consider additional species, we also plotted the HTs at 100, 200, and 1000 Hz for the smallest age classes of reef or reef-associated species for which audiograms were available (Kenyon 1996, Wright et al. 2005, 2008, 2010, 2011, Table S1). Even if these species do not occur at the study site, we used

these HTs to represent potential hearing sensitivity. As above, if 1000 Hz was not directly tested for a species, we interpolated this threshold if sufficient test frequencies were available. We reduced these thresholds by $10 \log_{10}(\Delta f)$, but again did not employ corrections accounting for behavioral versus electrophysiological methodologies. The range of HTs examined, however, allow one to consider how detection distances may change by a reduction in HT of 10–30 dB.

2.4. Ambient soundscape acoustic transect

We measured the ambient soundscape at increasing distances from the reef to investigate how the amplitude of reef-based sounds changed with distance in the field and in the presence of factors not included in the model (e.g. background noise, source directivity). Without knowing the precise location of any individual sound source (e.g. a fish), we could not estimate TL, but these measurements informed the reef-based sounds a larval reef fish might encounter at the depth and distances we measured. We believe the recorded toadfish and shrimp sounds were from animals on the study reef for reasons discussed in Text S3. We conducted this transect on 25 July 2013 between 19:30 and 21:30 h to target the crepuscular increase in the soundscape known to occur at the reefs across the Bocas region (Salas et al. 2018a) and also more generally across other geographic locations (e.g. Lammers et al. 2008, McWilliam et al. 2017b). Nighttime hours are also a period of larval settlement (Robertson et al. 1988, Stobutzki & Bellwood 1998), so sounds produced at this time may have particular importance. We used 2 hydrophone/recorder packages (nRUDAR, Cetacean Research Technology; range: 1–22 050 Hz, sensitivities: -159.52 and -158.57 dB re $1 \text{ V } \mu\text{Pa}^{-1}$). We placed one unit at the edge of the reef (water depth: 18.5 m) tethered to an anchored rope so that the hydrophone was at a depth of 8 m. This unit, termed the ‘stationary hydrophone’, recorded continuously and allowed us to monitor the temporal changes in the reef soundscape over the duration of the transect recordings. The second hydrophone/recorder unit was positioned at distances of 65, 104, 200, 404, 610, 805, 1006, 1120, and 1500 m from the stationary hydrophone; we started the transect at the closest position and finished at the farthest. At each position, we turned off the boat engine, anchored, and lowered the hydrophone to a depth of 8 m to record the ambient sound. These recordings were continuous with a

duration of approximately 6–10 min. Depth was measured at each transect position and ranged between 22 and 25.5 m, with increasing depth with distance from the reef.

We did not relocate the boat during the recordings, which allowed us to limit the time spent at each position so we could minimize the confounding effect of temporal changes in the reef soundscape with the effect of distance from the reef. However, the proximity of the boat to the hydrophone resulted in recording sounds of small waves lapping against the side of the boat. We extracted segments of the recordings that did not have wave slaps and concatenated these sections to create one sound file for each transect position. The duration of these sound files ranged between 0.3 and 5 min (mean: 1.6 ± 1.5 min). For each of these sound files, we created a spectrogram (window type: Hamming; window size: 2048 samples; overlap: 1024 samples) using MATLAB (v.2018a) and averaged over the time axis to produce a mean power spectrum for each recording site. We used these power spectra to evaluate how the amplitude of the reef-based, biogenic sounds changed relative to background sound levels with distance from the reef. Potential acoustic cues that occur in the reef soundscape can only be detectable by larvae if they are above these ambient levels; otherwise, masking occurs (inability to detect signal of interest because of interference from other sounds; Wysocki & Ladich 2005, Slabbekoorn et al. 2010). We also calculated power spectra (as described above) for the recordings made by the stationary hydrophone during the same time periods that we were at each transect site.

We investigated the potential detectability of the mating calls of *A. cryptocentrus*. The highest-amplitude sounds are more likely to serve as intermittent acoustic cues, yet calculating mean power spectra over units of time considerably longer than the acoustic features of interest underestimates the sound levels of the high-amplitude events. This is particularly true of the low-frequency fish calls that are relatively short (approximately 1 s for the toadfish *A. cryptocentrus*; Salas et al. 2018b) and produced intermittently by each male, but are also high in amplitude relative to background levels and occur at frequencies to which larvae have better auditory sensitivity. We selected 20 of these toadfish calls from the recordings made at the transect positions <1 km and 10 calls from the 1006 m transect position by identifying calls in the spectrogram view of Raven (v.1.5). We exported the start and stop times for each call to use in a custom Matlab program for further analysis. In the recordings made at the closer tran-

sect positions, the calls remained visually distinctive from the ambient noise. With distance, the calls became more difficult to detect visually, yet there remained sufficient energy in the fundamental frequency or second harmonic (as determined in Salas et al. 2018b) to discern some feature in the spectrogram of the characteristic call up to the 1 km transect distance. An increase in surface waves at the 2 farthest transect positions prevented us from having sufficient clean data to include these positions in our analyses. In Matlab, we calculated spectrograms and produced a mean power spectrum of each call. To predict the detectability of these fish calls at each transect distance by potential larval fish receivers, we compared the amplitude of the fundamental frequency and second harmonic to the HTs described above for *C. ocellatus* and *A. saxatilis*.

2.5. Individual-based model

We next used an individual-based model (IBM) to predict how settlement may be influenced by even short-range cues used for orientation, which was an outcome estimated in some cases by the modeling and is a conservative approach in considering the spatial extent over which acoustic cues may operate. We provide a brief description of the IBM here; a full description can be found in Salas et al. (2018a). We simulated larval fish searching for a reef on which to settle, which in the model seascape was considered to be at the origin. The reef was considered fringing by having any position where $x < 0$ to be land, onto which fish could not travel. Movement was modeled as a correlated random walk that transitioned to a biased random walk when the fish encountered a cue (Codling et al. 2004). Acoustic cues were available in a sensory zone surrounding the reef, and the distance between the reef and the perimeter of this sensory zone was the variable tested in the model. We tested distances between 20 and 100 m in increments of 10 m, and between 100 and 500 m in increments of 100 m. We simulated the settlement of 1000 fish for each distance. A larva was considered to have entered the sensory zone if it came within a distance from the reef equal to or less than the detection distance for that simulation. At this point, the larva was capable of being exposed to an acoustic cue that could bias its movement relative to the direction of the reef. Since larvae may be unable to discern the direction of the cue source (either in front or behind the fish, known as the 180° ambiguity; Fay 1984, Myrberg & Fuiman 2006), we conservatively esti-

mated orientating abilities by simulating the fish as having a 50/50 chance of being biased either in the correct direction towards the reef or in the opposite direction of the reef when a cue was encountered.

The model took place in 1 min time steps. Acoustic cues were present in the sensory zone at a rate informed by the rate of toadfish calls recorded at a nearby reef, which had a similar temporal pattern of call rate as the study reef (Salas et al. 2018a; the site called Finca therein during the full moon, the peak of toadfish acoustic activity). Using an intermittent cuescape in the simulation model reflects that larvae may not be perceiving the reef soundscape as a constantly present cue source, but instead more like a 'blinking beacon', where only a subset of the sounds is able to function as cues. In general, cues were available in every time step in the model during the night, but this rate decreased during the day when call rates were low. We also ran a null simulation for each distance where no acoustic cues were available; thus, fish movement was always a correlated random walk because there were no cues present to bias its motion in a direction relative to the reef. For each distance tested, we calculated the difference in the percent of settlement success for fish exposed to acoustic cues compared to the null model of no available cues. Our response variables were the numbers of fish that successfully settled at the reef out of (1) all 1000 fish and (2) the subset of fish that entered the sensory zone for each test distance. By random chance, some fish never entered the sensory zone, and without exposure to cues, these fish cannot be used to compare to the null model, as they essentially were also behaving as the null. For the null simulations, despite no cue availability, we still considered the subset of fish that were within the sensory zone distance for each simulation for comparison to the fish that were exposed to cues.

3. RESULTS

3.1. Speaker playback transect and sound propagation model

Measured and PE-modeled TLs were not monotonic (Fig. 1). While at most frequencies a general decline in amplitude with distance was found, there were also local increases in amplitude despite moving farther from the sound source. This is counter to the predictions of the spherical and cylindrical spreading models, which assume a monotonic decrease in amplitude with distance (Fig. 2). The TL

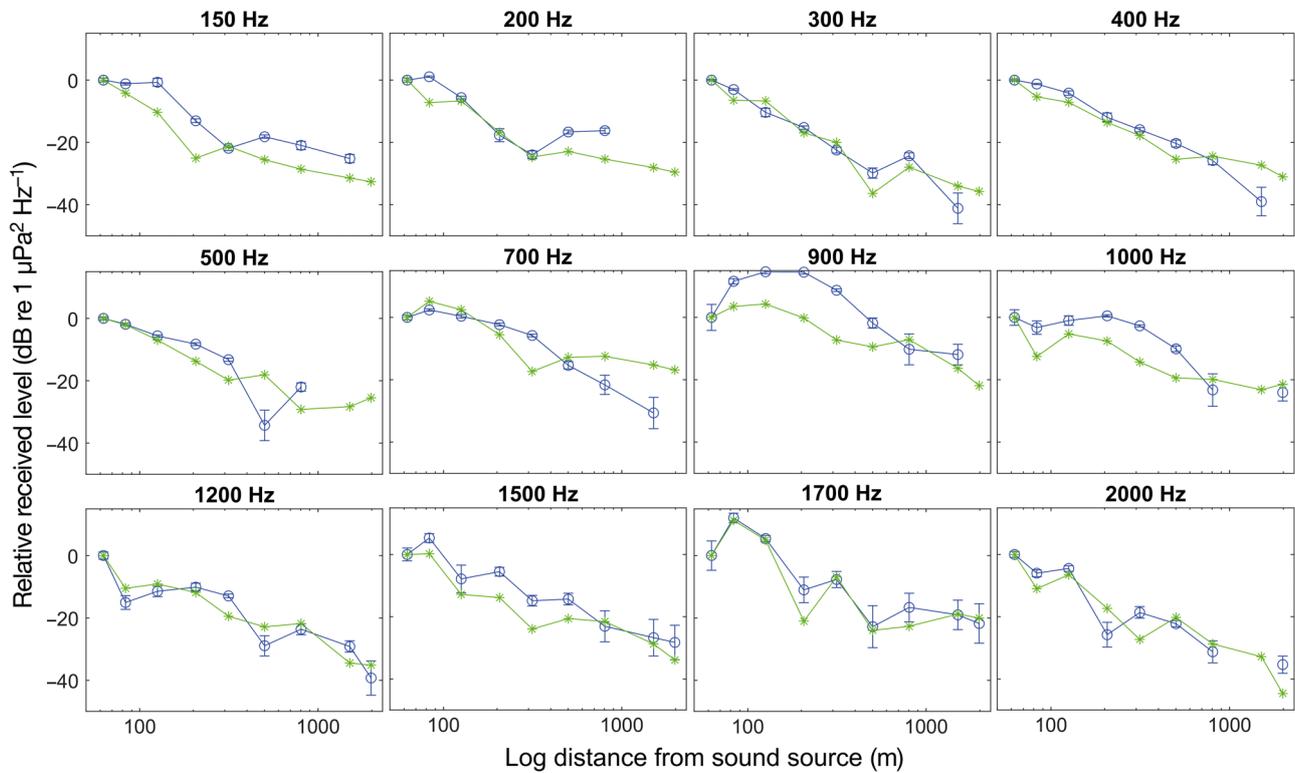


Fig. 1. Measured and modeled frequency-dependent acoustic propagation for 12 test frequencies in the range of larval fish hearing. Received sound levels were measured or modeled at each distance in the playback transect and are shown relative to the level measured or modeled at the first transect site. Blue line: field measurements ± 1 SD in the received sound level over the time of the recording at each site; green line: best-fit results of the field-calibrated propagation model

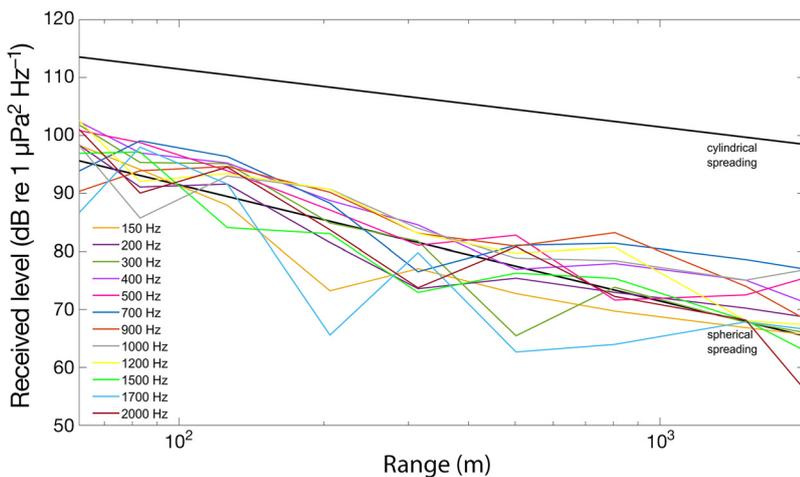


Fig. 2. Comparison of transmission loss (TL) predicted by the parabolic equation (PE) model to geometric spreading models. The PE model-predicted TL is shown for each test frequency and compared to the TL predicted by cylindrical (upper black line) and spherical (lower black line) spreading, which are frequency-independent. Losses were predicted for distances between the source to each site along the playback transect

predicted by the PE model for all 12 frequencies was more similar to the predictions of spherical spreading (Fig. 2). The similarity of the sound speed of the

water column to that in the sediment leads to a small critical angle, thus only sound propagating at angles very close to the horizontal was perfectly reflected at the seafloor. The higher-angle sound was transmitted into the sediments, producing losses more similar to the predictions of spherical spreading than cylindrical.

For all 3 sound source depths, spatial heterogeneity in the predicted acoustic fields increased with increasing frequency (Figs. 3 & 4). Within a frequency, the acoustic field varied with the position of the sound source on the sloping reef; for example, at 100 Hz, TL over distance was greater for a source located at 5 m depth compared to sources deeper on the reef slope (Fig. 3). In general, the complexity of the sound field

increased as the source was placed at greater water depth for any given frequency since the deeper waveguide supports more propagating modes at a

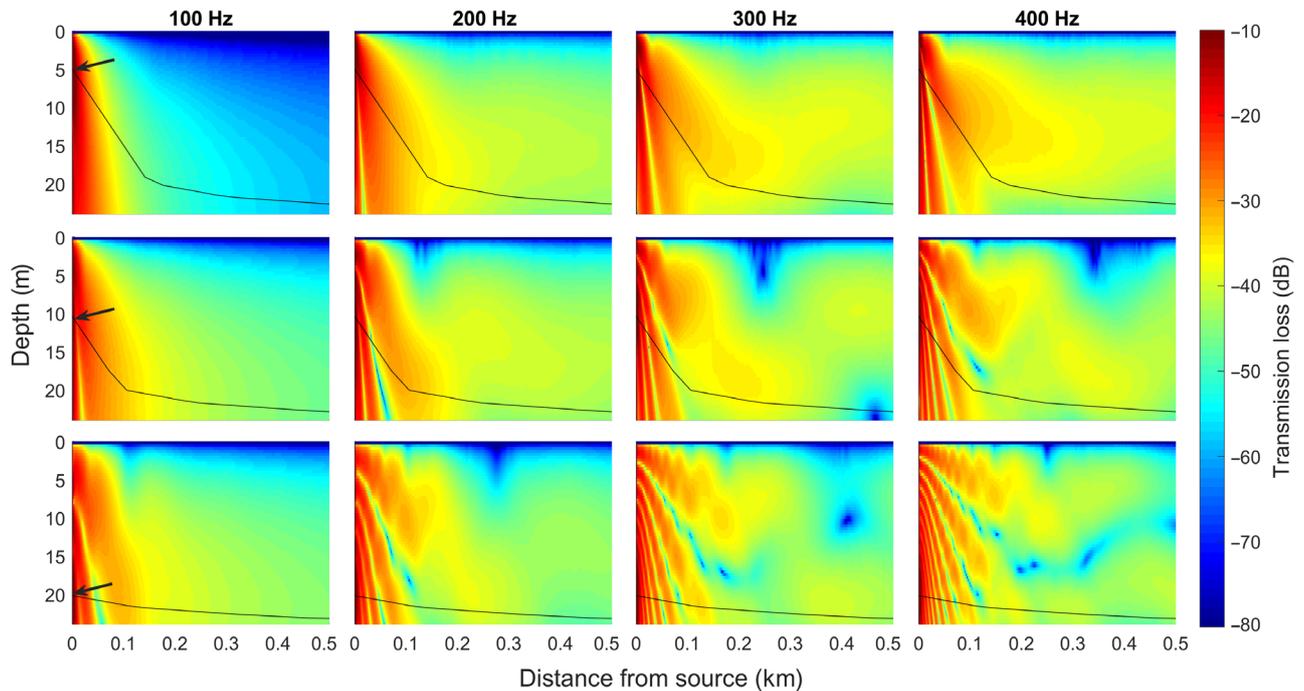


Fig. 3. Predicted frequency- and depth-dependent acoustic fields for low-frequency sounds detectable by reef fish larvae. The field-calibrated acoustic propagation model was used to calculate the transmission loss of sounds produced by a source at a depth of 5 m (top row), 10 m (middle row), and 20 m (bottom row) on the study reef (arrow indicates source depth). Results are shown for a radial extending perpendicular to the fringing reef. Color bar represents transmission loss in dB re 1 m

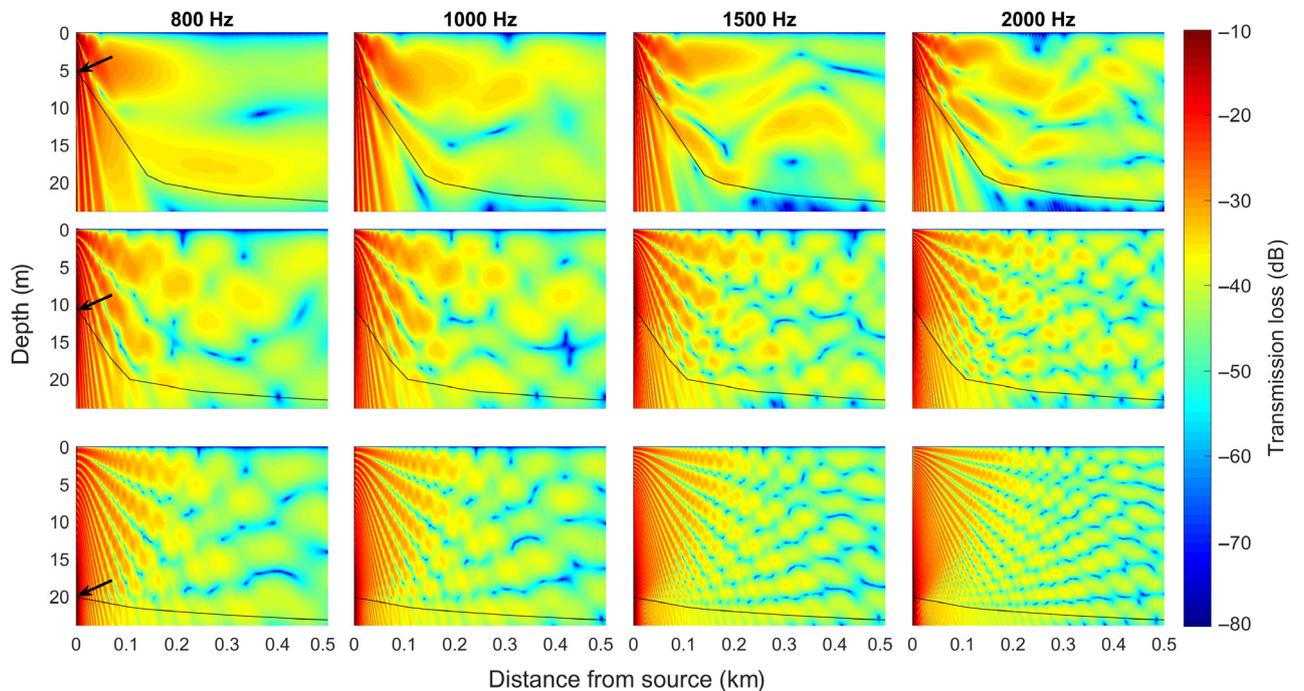


Fig. 4. Frequency- and depth-dependent predicted acoustic fields for high-frequency sounds detectable by reef fish larvae. See Fig. 3 for further details

fixed frequency. Additionally, TL was generally higher closer to the water surface compared to greater depths (Figs. 3 & 4).

The estimated range of potential detection decreased with increasing HT, and cue availability was dependent on source and larval depth (see Figs. 5–8).

This variation was driven partially by water depth, as depth decreased closer to the source and restricted the depth range over which the maximum detection distance could occur (Fig. 5). The estimated detection distance for 116 Hz across the 3 source depths ranged from 0.8 to >8 km for *Chaetodon ocellatus* and between 30–45 m for *Abudefduf saxatilis*. The estimated detection distance for 233 Hz ranged from 4–7.5 km for *C. ocellatus* and 26–27 m for *A. saxatilis* across the 3 source depths. For 1000 Hz, the detection distance across the source depths was 27–38 m for *C. ocellatus*; no detection was predicted for *A. saxatilis* greater than the shortest modeled unit of 1 m.

These estimated detection ranges support that these larvae may encounter some acoustic cues at distances allowing exposure to the predicted spatial heterogeneity in the acoustic cuescape. For both *C. ocellatus* and *A. saxatilis*, the model-predicted detection spaces created by the 2 toadfish-generated frequencies showed spatial heterogeneity that was dependent on frequency and the depth of the modeled call (Figs. 6 & 7). In general, swimming at greater depths would allow a fish to encounter more cues, but there were also nulls in the sound field across the depth

range. The estimated detection spaces for *A. saxatilis*, which has lower auditory sensitivity, were significantly smaller than those for *C. ocellatus*. The estimated detection spaces for *C. ocellatus* for the 1000 Hz component of a shrimp snap (Fig. 8) were significantly smaller than that produced by the toadfish call and showed high spatial heterogeneity that also depended on the depth of the source, and further, that detection would depend on larval depth. Since the 1000 Hz sound was not predicted in the model to be audible to *A. saxatilis* at a distance >1 m, no detection space could be estimated.

The results presented in Figs. 6–8 are for a single radial extending approximately perpendicular to the fringing reef. This radial is representative of the other radials over which TL was modeled, for the patterns of sound propagation showed roughly concentric rings around the position of the sound source (Fig. S2). Fig. S2 highlights that larvae may encounter zones of varying cue amplitude as they approach the reef, at times even experiencing a null where the received level was below the HT. The occurrence of these nulls depended on the frequency and the depth of the larva. For example, a larva swimming at 5 m depth

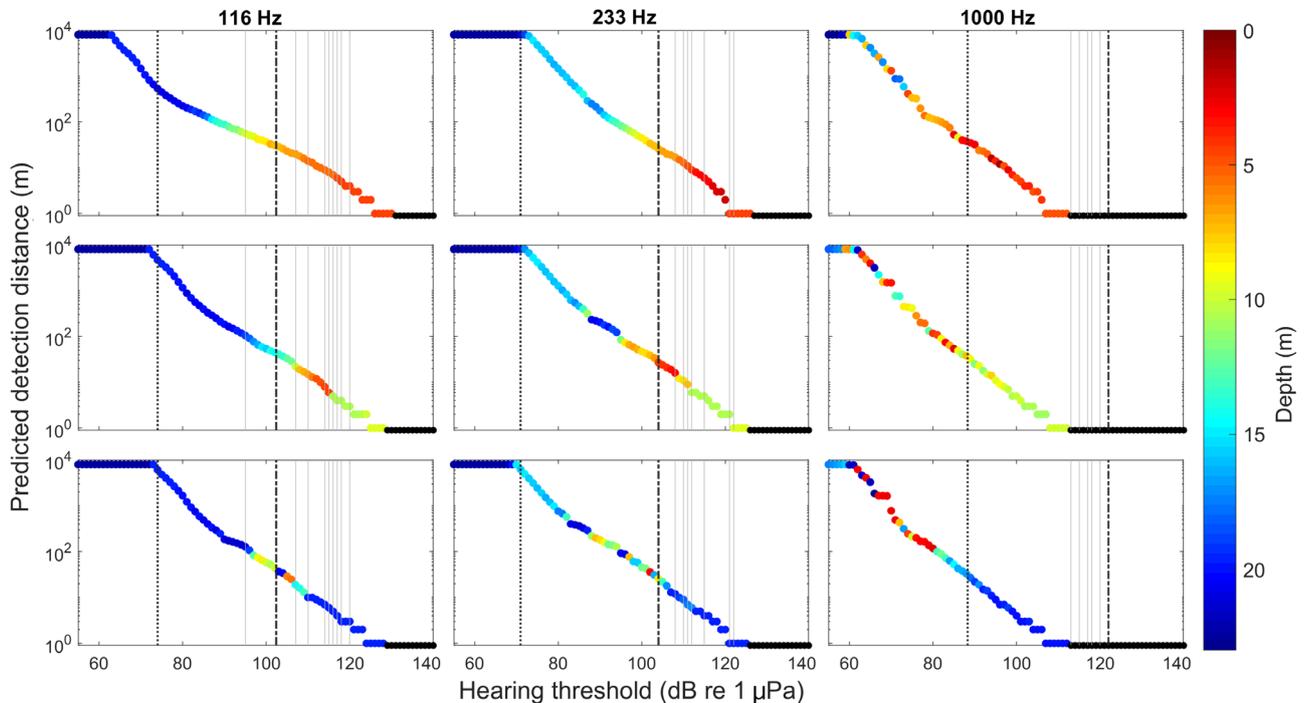


Fig. 5. Depth-dependent detection distances predicted by the parabolic equation model for a range of potential hearing thresholds. The predicted detection distance is the farthest distance where hearing threshold > source level – transmission loss for the toadfish-generated frequencies (116 and 233 Hz) and the 1000 Hz component of a shrimp snap. Color bar represents the depth at which this farthest distance occurred. Source depth was at 5 m (top row), 10 m (middle row), and 20 m (bottom row). Black dots: no predicted detection at any distance >1 m; solid gray vertical lines: thresholds at 100 (first column), 200 (second column), and 1000 Hz (third column) for early life-stage reef fish species (Table S1); black dotted and dash-dot lines: thresholds at the modeled frequencies for *Chaetodon ocellatus* and *Abudefduf saxatilis*, respectively

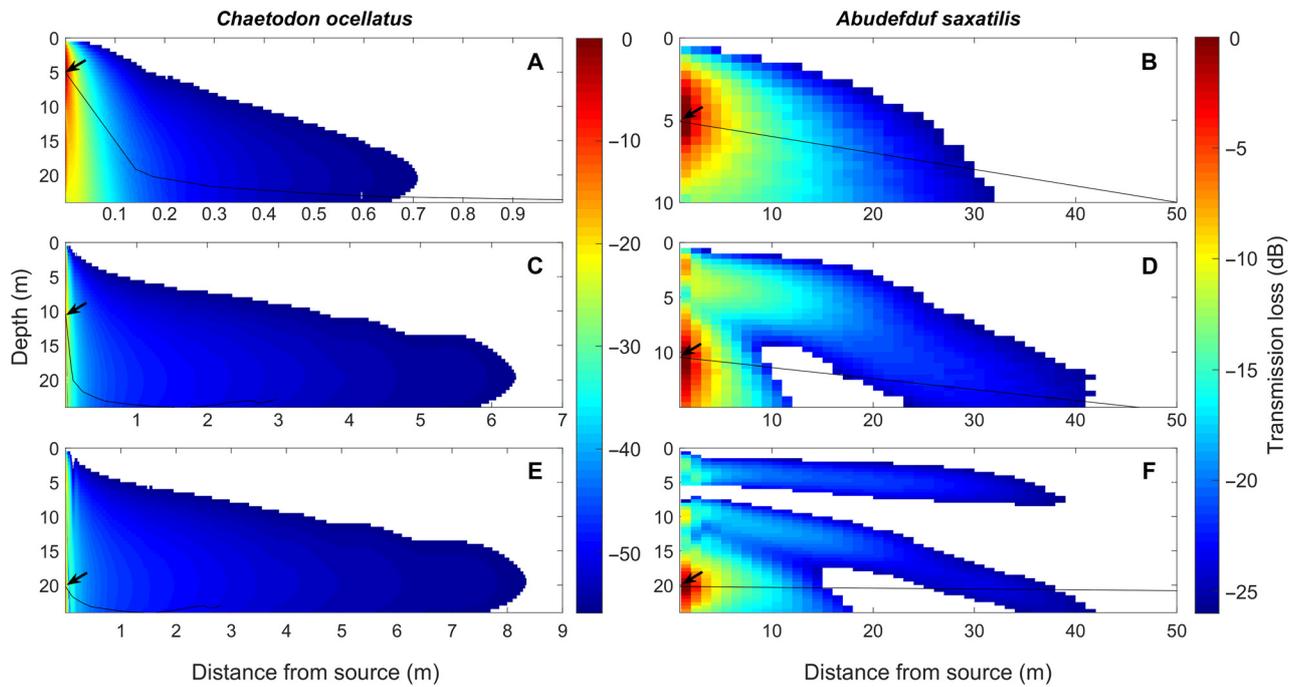


Fig. 6. Estimated detection spaces for the fundamental frequency (116 Hz) of a toadfish call by larvae of *Chaetodon ocellatus* and *Abudedefduf saxatilis*. Modeled transmission loss (TL) was subtracted from the mean source level. Color bar is scaled to indicate where the TL does not exceed the allowable TL for each larval species. The allowable TL is the maximum level that can be subtracted from the source level and still have the received level be greater than the hearing threshold for each species. The fundamental frequency of a call produced by a fish on the reef at a depth of (A,B) 5 m, (C,D) 10 m, and (E,F) 20 m was predicted to be audible at any seascape position where the color is not white. Black arrow: source depth. Color bar represents transmission loss in dB re 1 m over a single radial perpendicular to the fringing reef

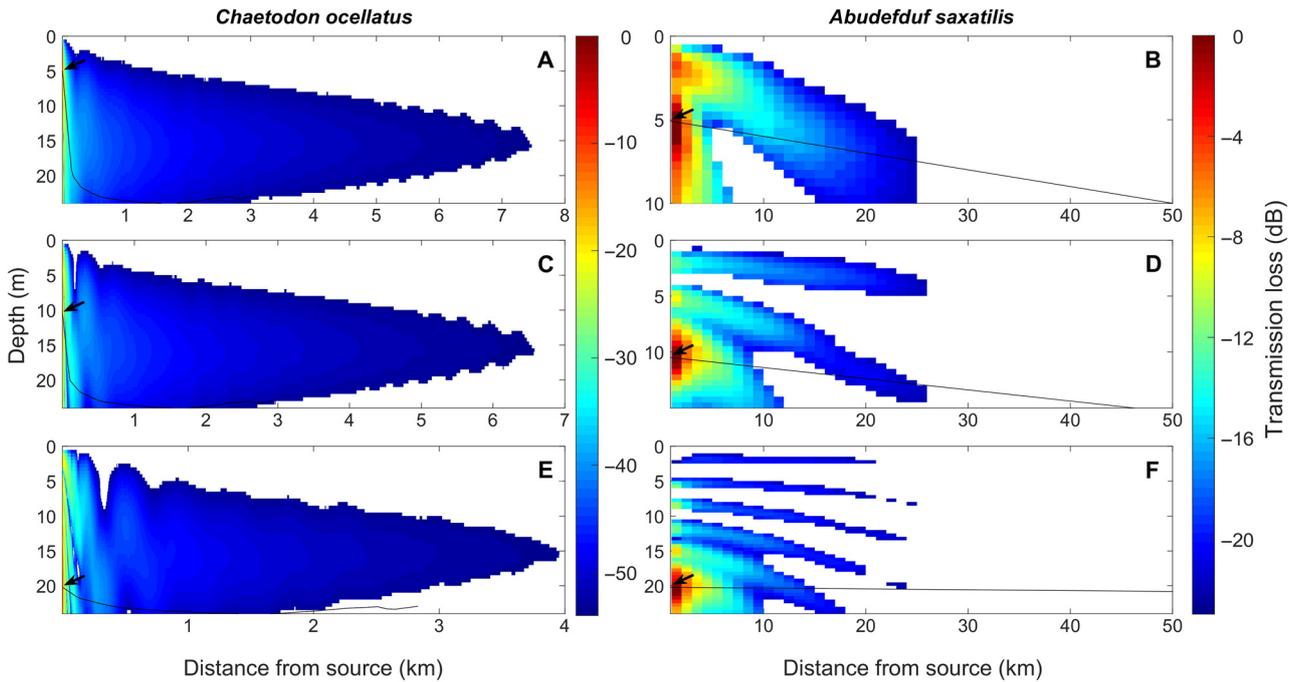


Fig. 7. Estimated detection spaces for the second harmonic (233 Hz) of a toadfish call by larvae of *Chaetodon ocellatus* and *Abudedefduf saxatilis*. See Fig. 6 for further details. Source depth was (A,B) 5 m, (C,D) 10 m, and (E,F) 20 m, indicated by black arrows. This frequency was predicted to be audible at any seascape position where the color is not white

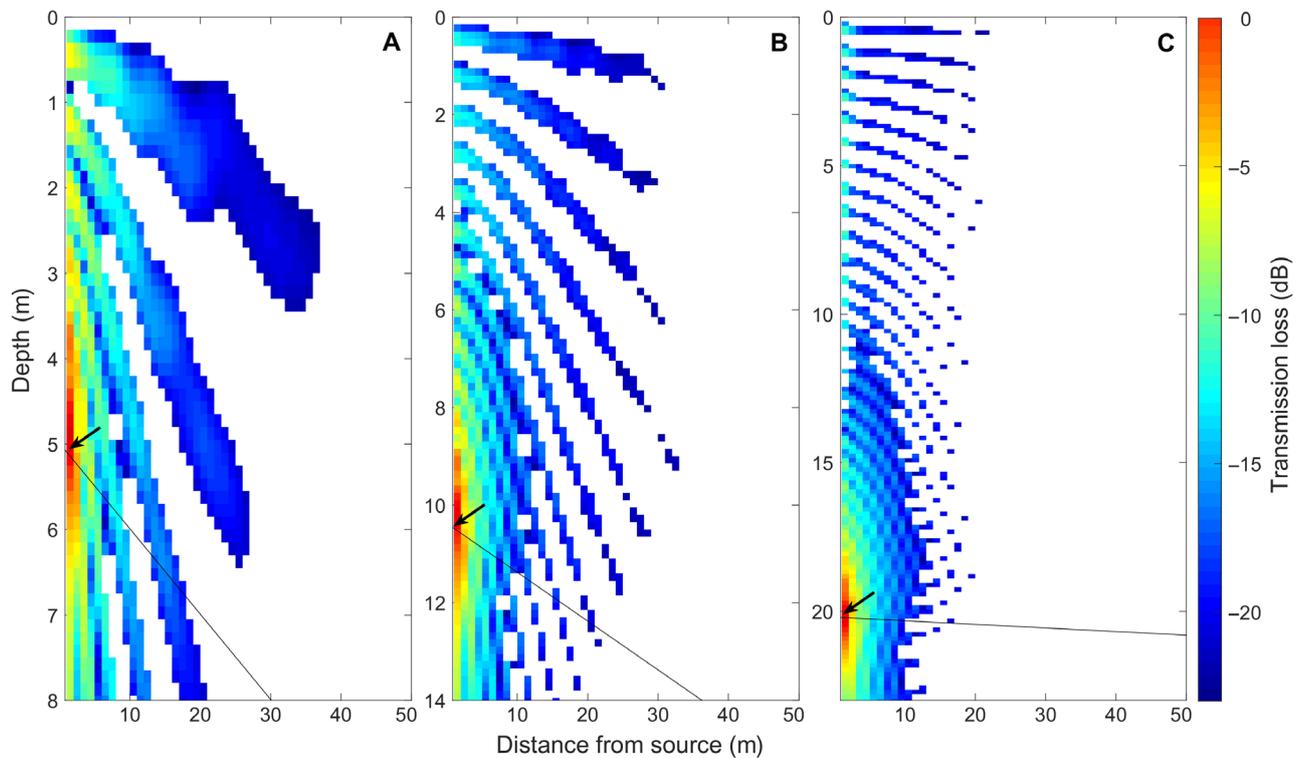


Fig. 8. Estimated detection spaces for the 1000 Hz component of a snapping shrimp snap by larvae of *Chaetodon ocellatus*. See Fig. 6 for further details. Source depth was (A) 5 m, (B) 10 m, and (C) 20 m, indicated by black arrows. This frequency was predicted to be audible at any seascape position where the color is not white

would encounter 2 nulls in the 234 Hz acoustic field (at approximately 0.8 and 0.3 km from the position of the cue source), whereas these nulls were not present in the 116 Hz field (Fig. S2). These nulls were absent for larvae swimming at depths of 10 or 20 m, yet there remained variation in the strength of the cue with distance from the source that did not change monotonically (Fig. S2).

For the other species considered (Table S1, Fig. 5), the maximum detection distances across source depths and species ranged from approximately 3–128 m for 116 Hz and from 1–17 m for 233 Hz. For both frequencies, most species had a detection distance <10 m, and this maximum detection distance depended on larval depth (Fig. 5). Other than *C. ocellatus*, no species was predicted to detect the 1000 Hz sound at the smallest modeled unit of 1 m (Fig. 5). These predictions do not consider adjustments in HTs that take into account discrepancies between behavioral and electrophysiological audiograms. Given the log y-axis, these detection distance predictions would increase significantly with even small reductions of HTs, thereby increasing the spatial extent over which larval reef fishes may encounter the predicted heterogeneity in acoustic cue amplitude.

3.2. Ambient soundscape transect

At all transect positions analyzed, the harmonics of toadfish calls produced at the reef were distinguishable above the ambient background sound level (Fig. S3; see Text S3 for further discussion of these results). The amplitudes of these harmonics decreased with distance, with an exception at 200 m, where the amplitude at the second harmonic was greater than all other recording distances except at the reef, and the amplitude at the fundamental frequency was approximately equal to that recorded at 50 m (Fig. S3). The fundamental frequency and second harmonic of individual toadfish calls extracted from the transect recordings remained above the average HTs for *C. ocellatus* larvae at all transect positions through 805 m (Fig. 9). Thus, it was likely the cue amplitude at these frequencies fell below these HTs at a distance between the 805 and 1007 m transect positions, supporting the potential for detection of reef-based sounds at distances that would expose larvae to the predicted spatial heterogeneity in the sound field. The cue amplitudes at these toadfish-generated frequencies did not equal or exceed the average HTs for these frequencies for *A. saxatilis*.

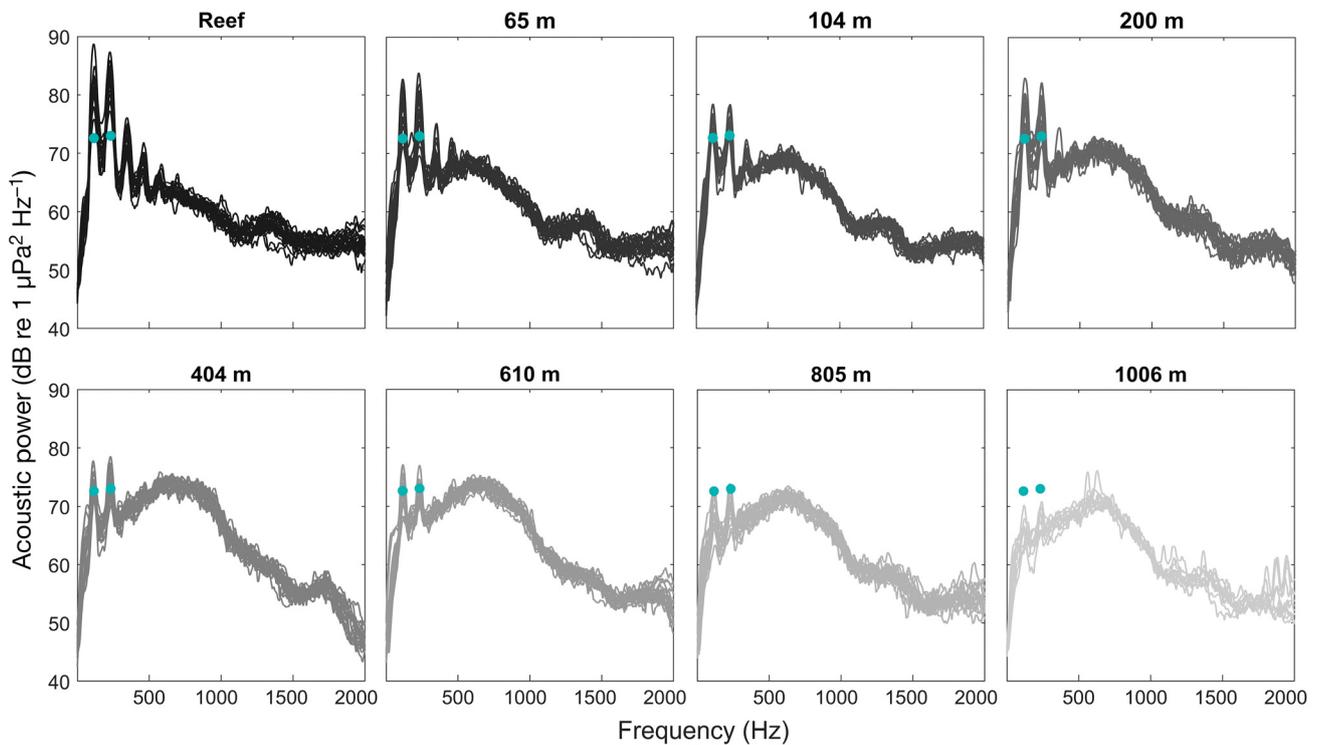


Fig. 9. Power spectra of individual toadfish calls recorded at increasing distance from the study reef during the ambient noise transect. Low-frequency peaks represent the toadfish harmonics; teal dots: hearing thresholds for *Chaetodon ocellatus* at 116 and 233 Hz. The toadfish call was predicted to be audible if the amplitude of at least one of the harmonics exceeded hearing threshold

3.3. IBM

In the simulations with acoustic cues available, the percent of successful settlement across all fish ranged from 12.9–45.4%. Success increased with detection distance, except for small decreases of about 2% for detection distances of 60 and 70 m compared to 50 m, due to stochasticity in the model. For the null simulations and across all fish, percent successful settlement ranged from 7.9–12.9%, with no pattern with distance. Considering only the fish that entered the sensory zone, percent successful settlement in the presence of cues ranged from 88.3–75%, with a general decrease with increasing distance. For null simulations, success decreased from 76.1–15.4% as detection distance increased. For all detection distances tested, the percent of larvae that settled successfully was greater in the presence of cues compared to the null simulation (Fig. 10). This was observed when considering all 1000 fish in each simulation and the subset of fish that entered the sensory zone. For all 1000 fish, the difference in the percent of successful fish ranged from 2.4–35.9% in the presence of cues

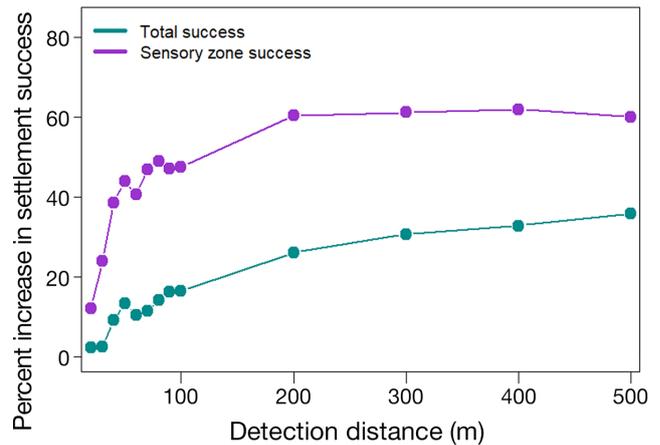


Fig. 10. Predicted effect of acoustic cue detection distance on larval settlement success. An individual-based model was used to simulate the settlement of 1000 fish exposed to acoustic cues with variable detection distances. The percent of successful fish out of all 1000 (total success) and the subset of fish that got within the sensory zone of the reef (sensory zone success) was calculated and compared to the same metrics for null simulations that had no cues available. The difference between the simulations with and without cues is shown here. All values are greater than zero, indicating that acoustic cues available at all tested detection distances improved settlement compared to no cue use

compared to the null model (Fig. 10). For the subset of fish that entered the sensory zone, the difference in the percent of successful fish ranged from 12.2–61.9%, again compared to the null. The percent of successful settlers increased with detection distance, except for small decreases at 60 and 500 m due to model stochasticity.

4. DISCUSSION

Coastal soundscapes are increasingly recognized as an important component of the settlement process of some fishes and invertebrates (Tolimieri et al. 2000, Simpson et al. 2005, Radford et al. 2007, Stanley et al. 2010, Vermeij et al. 2010, Lillis et al. 2013, 2018). Indeed, management of the soundscape is seen as a necessary component of ocean stewardship (NOAA 2016), and approaches such as acoustic enrichment and anthropogenic noise reduction may be viable strategies to improve larval recruitment and encourage ecosystem recovery (Holles et al. 2013, Lillis et al. 2015, 2018, Gordon et al. 2019, Ferrier-Pagès et al. 2021). Uncertainty in the mechanisms that link the soundscape to larval settlement behaviors makes it difficult to predict how larvae are affected by anthropogenically driven changes in the soundscape and how management strategies can best be employed. Our field measurements and propagation modeling highlight that the acoustic fields experienced by larvae may be more complex than previously considered by examining only horizontal detection distances. Our results support that larvae may experience 3-dimensional variation in the acoustic cuescape; thus, the acoustic cues a fish experiences may be dependent on its position in the water column. Further, this depth variation is frequency-dependent. Since the potential acoustic cues produced by soniferous species occur across a broad range of frequencies, the acoustic cuescape produced by a low-frequency fish will be different from the higher frequency content of an invertebrate, with potential concomitant differences in cue function. The position of the sound source on the sloping reef also influenced the predicted cuescape, suggesting potential consequences of the depth variation in coral health observed at the reefs in Alimirante Bay. Fishes live in a 3-dimensional environment, and our frequency- and depth-dependent modeling and field results support that the acoustic cuescapes larvae experience need to also be understood at the same scale.

4.1. Frequency- and depth-dependent sound propagation creates complex acoustic fields

A sound's frequency and SL and the hearing sensitivity of a given fish will largely determine the 3-dimensional spatial extent of the acoustic fields (e.g. Figs. 6 & 7) that a larval reef fish experiences. Since there are nearly unlimited possible combinations of these variables, we considered these sound fields both more generally and using specific examples of potential sources and receivers. The results of both the speaker playback transect and the propagation model showed complex propagation patterns dependent on the frequency of the potential acoustic cue. Counter to predictions made by geometric spreading models, the received levels we measured for the transect did not decrease monotonically with increasing distance from the sound source. For all but one test frequency (400 Hz), we measured amplitudes that exceeded received levels measured closer to the source (Fig. 1). These local increases in sound level show a spatial patchiness in amplitude that may have important implications for how larvae perceive the soundscape. There are also implications for how field measurements are conducted, as these results suggest spot measurements are likely to misrepresent the sound fields larvae are actually experiencing. For example, there was an approximate 10 dB increase in the received sound level of the 500 Hz tone at the 800 m transect position compared to the amplitude measured at the 504 m position (Fig. 1). Thus, a larva may be more likely to detect the 500 Hz component of a fish call at a distance of 800 m compared to some distances closer to the sound source. Whereas geometric spreading models predict that higher amplitudes indicate proximity to the reef, our results suggest that local amplitude alone may not be an indicator of reef proximity for some frequencies. However, we did observe a general overall trend of decreasing amplitude with distance at all frequencies (but see 900 Hz), which suggests larvae may be able to gain information about their position relative to the reef if they are able to sample and integrate average amplitudes over time and space, similar to olfactory cue use (DeBose & Nevitt 2008).

In the playback transect, the observed variation in amplitude over distance was greater at the higher test frequencies (Fig. 1), supported by normal mode theory. A sound propagates away from its source along multiple paths, interacting with the sea surface and ocean bottom as it travels through the wave-

guide. A sound at a given frequency will propagate if it excites at least one normal mode by satisfying the boundary conditions imposed by the air and sediment interfaces. At higher frequencies, the waveguide will support more propagating modes than at lower frequencies. Each propagating mode represents a plane wave propagating down the waveguide at an oblique angle with respect to the horizontal boundaries. The interaction of the different waves creates patterns of interference. This interference can be constructive or destructive depending on if the sound waves are in or out of phase because the amplitude of combined sound waves is additive. Since there are more modes at higher frequencies, the interference pattern is more complex. These interference patterns are highlighted by the spatial heterogeneity in the sound fields predicted for different frequencies (Figs. 3 & 4) and may influence how these sounds function as cues. In the predicted sound fields for all modeled frequencies, there is greater TL in the surface waters due to the high impedance contrast between water and air. Larvae shallower in the water column would be predicted to experience a lower amplitude low-frequency cuescape since the greater TL makes it less likely that the received level of low-frequency sounds will exceed HTs (Sprague et al. 2019). Thus, vertical migration behaviors will have consequences for the type of acoustic cuescape larvae encounter; diel shifts may place larvae in the upper water column during the night when low-frequency fishes typically chorus, or larvae undergoing ontogenetic shifts may encounter higher amplitude sounds in deeper waters. However, generally less spatial variation in the TL of low frequencies may allow these sounds to provide more information about proximity to a reef.

The spatial scales of amplitude variation became finer with increasing frequency because of the increase in the number of propagating modes and resulting interference. The predicted fields in Figs. 3 & 4 are not static conditions through which a fish could navigate, but instead are available only instantaneously. Thus, even small differences in the horizontal and vertical position of a larva could have consequences for the type of acoustic cuescape it experiences, especially for higher frequency sounds. Even at distances very close to the source (i.e. <50 m), there are nulls in the sound field that are dependent on depth (Fig. 3 & 4). Yet while there may be a null in the field created by the independent propagation of a single source, that same seascape position may be ensonified by a sound produced elsewhere on the reef. For example, the null at a distance of

approximately 0.4 km in the 300 Hz sound field created by a source at 20 m depth may be ensonified by another source (e.g. at 5 or 10 m; Fig. 3). Thus, while there is increasing patchiness in the predicted acoustic fields with increasing frequency, the interaction of multiple soniferous animals distributed across the reef may prevent persistent nulls in the cuescape of any one frequency, depending on the rate at which sounds that can serve as cues are produced. In this way, despite having more spatial patchiness in amplitude, encountering a higher frequency cue may, over a temporal average, be less dependent on larval depth compared to the lower frequency sounds. For more discussion on modeling decisions that influenced our predictions of the acoustic cuescape, refer to Text S1.

This approach of considering the reef soundscape as a collection of independent point sources is different from that taken by others that considered the reef a continuous source of sound and used time-averaged acoustic data to model propagation (e.g. Radford et al. 2011). Considering the reef soundscape as continuous from the perspective of larvae requires the assumption that every sound in the reef soundscape is detectable and/or the sounds they do use as cues are produced at a consistently high rate that approaches continuous. Here, we approached the question more conservatively given the uncertainties in larval reef fish hearing and in which components of the soundscape they actually use as cues. Reef acoustic cues may occur along a continuum from no detection to intermittent to nearly continuous depending on myriad factors including larval HT, larval depth and distance from the reef, and spatiotemporal variation in and degradation to reef soundscapes. Presumably, a fish with low hearing sensitivity will detect a smaller subset of the sounds in the reef soundscape and thus perceive cues as intermittent. Snapping shrimp sounds are produced at a rate that verges on continuous, but a given larva at a given seascape position may not detect enough snaps to perceive them as such. Until we better understand acoustic cue-mediated larval behaviors, we suggest not assuming all sounds can be used as cues, as this may underestimate the effect of degradation on a reef's ability to recruit larvae through its soundscape.

Comparing the modeled TL to geometric models (Fig. 2), we observed that the TL calculated by the PE model produces levels that are on average consistent with spherical spreading. This is a result of the seabed parameters—specifically, the sediment sound speed (1557 m s^{-1}), which was close to the sound speed of water at the seafloor (1543 m s^{-1}).

Indeed, the critical angle (the limiting angle of complete reflection from the bottom) for this waveguide is 7.7° . Typical values of sound speed in unconsolidated sediments can range up to 1800 m s^{-1} . Seabeds with higher sound speeds have larger critical angles and can produce TL that more closely approximates cylindrical spreading. Veritably, sedimentation is a contributing factor to our study site's poor condition, and we observed fine, silty sediments on and off the reef which are consistent with the relatively low sound speeds inferred from the acoustic data. Other reefs in Almirante Bay have experienced less sedimentation, and harder, sandy substrates may produce larger detection spaces of the same reef-based sounds for the same larval species, potentially creating differences in how these sites recruit larvae. Although geometric models can be useful in bounding the average TL larval fishes might experience, these models lack the spatial structure predicted by full-wave models. Additionally, geometric models do not account for the frequency dependence of the TL, which can be significant.

4.2. Estimated spatial extent over which larvae may experience spatially heterogeneous sound fields

The spatial extent over which a larva experiences a spatially complex acoustic cuescape will depend on where in the seascape it can detect reef-based sounds (i.e. $HT > SL - TL$). To consider examples of the spatial scales over which the predictions in Figs. 3 & 4 may apply, we estimated detection distances of several species of reef fish larvae and detection spaces for 2 potential acoustic cue sources and 2 larval reef fish species. We relied on absolute pressure thresholds, which we acknowledge is limited, as these values do not include particle motion detection (see Text S2) and are affected by testing conditions (Ladich & Fay 2013). However, these are the best available pressure data to inform larval hearing capabilities, and we acknowledged this uncertainty and the potential that HTs may be 10–30 dB lower than predicted by exploring a broad range of thresholds (Fig. 5). None of the predicted distances should be interpreted as absolute, but rather as estimated ranges used only to consider if the predicted sound fields, and thus spatial heterogeneity, may be experienced by larvae in the modeled scenario.

In general, early life stage reef fishes have higher sensitivity to lower frequencies (see references in Table S1, Colley et al. 2016), and we see this in the

predicted detection distances in Fig. 5 and comparing the estimated frequency-dependent cuescapes for *Chaetodon ocellatus* (Figs. 6–8). This supports that the spatial patterns created by lower frequency sounds may be of higher relevance to larval reef fishes. Considering both the fundamental frequency and second harmonic together, since they are produced simultaneously in a toadfish call, the estimated detection distances ranged from 3–128 m across source depths for species other than *C. ocellatus* and *Abudefduf saxatilis*. There was significant 3-dimensional amplitude variation within 128 m from the source in the 100 Hz sound field (Fig. 3), which would translate to a spatially variable acoustic cuescape for these larvae. Yet much less of this depth variation would be experienced within 3 m from the source for species with lower sensitivity. However, even a relatively small reduction in HTs (i.e. 10 dB) would substantially increase the spatial scale of detection and thereby exposure to more of the predicted heterogeneity in the sound field.

The results supported that the high-frequency components of the reef soundscape may be more limited in their role to act as acoustic cues, especially since the hearing of some pre-settlement larvae may be restricted to $<1 \text{ kHz}$ (Wright et al. 2011). No species with an available or interpolated 1 kHz threshold except *C. ocellatus* could detect the 1 kHz component of a shrimp snap at any modeled distance (Fig. 5). Again, however, these results would change with a further reduction in HT, and in the case of broadband shrimp snaps, fishes are likely using all frequencies within the audible bandwidth. Critically, for all of these results, the detection distance depended on the depth of the larva in the water column (Fig. 5). These maximum detection distances assumed the larva is at the optimal depth to detect the first potentially available cue upon its approach to the reef. In general, there was a pattern for the maximum detection distance to occur deeper in the water column for the 2 toadfish frequencies, and this pattern was considerably more variable for the 1 kHz component of a snap, as reflected in comparing similar frequencies in Figs. 3 & 4.

We next predicted the 3-dimensional acoustic cuescapes (in the absence of *in situ* factors like masking) created by the low- and high-frequency sources by using estimates of HTs for *C. ocellatus* and *A. saxatilis*. *A. saxatilis* has HTs more representative of the other species examined, while *C. ocellatus* is a species with particularly high hearing sensitivity (Table S1, Fig. 5). The key result is that species with different hearing sensitivities may

experience vastly different acoustic cuescapes that show variation across depth. As predicted, the detection space for *C. ocellatus* for the toadfish call is orders of magnitude larger than predicted for *A. saxatilis*. Yet both species would experience the predicted spatial variation in the cuescape, as the depth-dependent TL led to strong depth-dependence in the predicted audible fields for both sources and larval species (Figs. 5–8 & S2), mirroring the predictions made using the general sound fields. The consequences of a larva's depth position may be highest at night, since the peak toadfish call rate occurs after dusk (Thorson & Fine 2002, Salas et al. 2018a). Since more of the water column is ensonified at closer ranges, a fish close to the source when the sound is produced is more likely to detect the cue regardless of depth. A larva of either species would have a greater chance of detecting a cue at frequencies of the toadfish call over a much larger volume of the seascape compared to the detection spaces predicted for the shrimp-generated frequency. The estimated detection space for *C. ocellatus* for a shrimp snap is also depth-dependent with more fine-scale spatial heterogeneity (Fig. 8) than predicted for the toadfish call. These results support that frequency-dependent depth variation in acoustic cue amplitude may strongly influence how larvae are able to use these cues, and further these perceived acoustic fields may vary widely across individuals depending on hearing sensitivity.

The amplitude of toadfish calls remained above the HT for *C. ocellatus* in the ambient soundscape transect up to a distance between 0.8 and 1 km (at a depth of 8 m), providing *in situ* support that reef-based cues occur at amplitudes and distances that could expose larvae to a spatially heterogeneous cuescape. Further, these field measurements supported the model predictions for low frequencies, as in general there was a decline in amplitude with distance, yet spatial heterogeneity was observed (e.g. at the 200 m transect position; Figs. 9 & S3). There was a decrease in call rate, but not individual call amplitude (Salas et al. 2018b), during the transect. Therefore, the time series of average power spectra in Fig. S3 reflects both this decrease and the effect of distance. Background sound levels increasingly masked the diminishing received level (Figs. 9 & S3) until the calls were no longer discernable. This comparison of time-averaged power spectra (Fig. S3) and the power spectra calculated over only individual toadfish calls (Fig. 9) highlights how the former may underestimate, in some cases, the amplitudes of reef-based sounds encountered by larvae.

4.3. Influence of short distance cue detection on settlement success

For even the low-frequency cue of the toadfish call, the model predicted detection distances typically <100 m for the larval reef species we considered. The benefits of long- versus short-distance detection should not obscure that cues detectable at even relatively short ranges may still benefit larvae, especially compared to if those cues were not available. The addition of acoustic cues substantially increased the percentage of successful larvae. For example, if a fish moved to within 30 m of the reef, the presence of cues increased successful settlement by almost 25%, even when cues were intermittently available. In comparison to the correlated, unbiased random walk, settlement was always more successful with cues detectable at all distances tested. In the model, as in nature, fish were subject to losing their orientation relative to the reef, yet the availability of even intermittent cues allowed them to re-orient to the reef's location to improve navigation across any distance. These cues can be a variety of cue types that operate at different spatial scales (Montgomery et al. 2001, Myrberg & Fuiman 2006), and our results support that acoustic cues operating at short distances (e.g. <100 m) may contribute to improving success during the critical settlement transition for even species with relatively low hearing sensitivity.

In general, settlement success was improved when cues were detectable at a greater distance from the source, similar to other studies (Armsworth 2000, Codling et al. 2004, Staaterman et al. 2012). In the null simulations, the success of fish that moved within the sensory zone distance of the reef highlights that, in the absence of cues, greater success with decreasing 'detection distance' simply indicates that the closer to the reef a fish gets by chance, the higher the likelihood it will, by chance, encounter the reef. Larvae that moved to within 100 m of the reef had a greater success rate than those that got within 500 m, even if fewer fish in total got within range of the closer distances. While larvae can encounter a settlement site by a random walk, the chance of successfully locating the reef can be improved by using cues at even short distances. We tested depth-independent detection distances, and future iterations of this model should include vertical movements of larvae with depth-varying, frequency-dependent cues.

5. CONCLUSIONS

Understanding the mechanisms that link the soundscape to larval fish behaviors is important to best predict and manage changing soundscapes. A research challenge is the complexity of the system. In each stage of the system—sound production, acoustic propagation, and cue reception by larvae—variation will substantially affect the spatial scales over which cues operate, and likely also their functions for larval reef fishes. Using a well-established underwater propagation model coupled with field measurements, we have shown that the presence and amplitude of the acoustic cues that reef fish larvae may experience likely depend on their vertical position in the water column. Additionally, we have shown that fishes may encounter a non-monotonic decrease in cue amplitude with distance from the reef. These spatial patterns suggest larval behaviors like vertical migrations may influence acoustic cue use, and, to the extent that these patterns occur in nature, larvae may have evolved behaviors to adapt to this spatial complexity like integrating cue strength over distance or positioning at optimal depths. The frequency of potential acoustic cues is a key driver of these sound fields; thus, the frequency characteristics of the active local soniferous species community will strongly influence the spatial pattern of the available acoustic cuescape. Reducing the diversity of soniferous species through habitat loss and degradation may have unknown consequences on larval settlement behaviors until we understand which frequencies they use as cues and whether the species that produce these frequencies are resilient to anthropogenic change. Recognizing that different components of the soundscape will contribute differently to the acoustic cuescape requires acknowledging frequency-dependent propagation and the resulting depth-dependence of cues. It is only through incorporating this natural variation and complexity into our modeling and empirical approaches that we will be able to sufficiently understand how acoustic cues function in larval settlement and how to best conserve these ecological functions of the soundscape.

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